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# Micronekton spatial ecology: distribution, diversity and importance for the structure of the southwest Pacific pelagic ecosystem.

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## THÈSE

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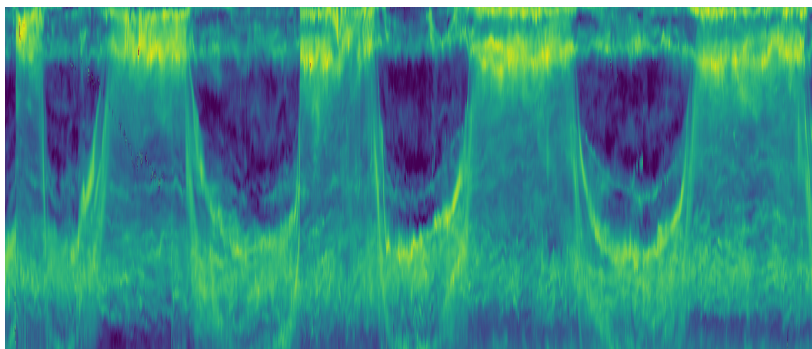
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**Aurore RECEVEUR**



### **Écologie spatiale du micronecton : distribution, diversité et importance dans la structuration de l'écosystème pélagique du Pacifique sud-ouest**

#### **Jury**

|                                   |   |                       |
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**Thèse préparée au sein de la CPS et du centre IRD de Nouméa, Nouvelle-Calédonie**

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## Résumé

L'écosystème pélagique Néo Calédonien est le théâtre d'une forte diversité de prédateurs, comme les oiseaux marins ou les cétacés. Cette diversité est rendue possible par la grande diversité d'habitats physiques. La récente création du Parc marin Naturel de la Mer de Corail a ouvert un besoin d'informations précises sur le fonctionnement de cet écosystème remarquable, notamment sur la dynamique du micronecton et de son rôle central dans les réseaux trophiques, d'autant plus que ce maillon est le plus méconnu. Dans ce contexte, cette thèse a pour objectif d'étudier la dynamique et la diversité du micronecton; et dans un deuxième temps d'analyser son influence sur la répartition des prédateurs. Dans le **2<sup>ème</sup> chapitre**, nous avons utilisé des intensités acoustiques d'ADCP (Acoustic Doppler Current Profiler) acquises à travers 54 campagnes réparties sur 19 ans pour évaluer les variabilités saisonnières et inter-annuelles de micronecton et sa distribution spatiale dans la couche 20-120m. Nous avons montré une diminution de son abondance relative de 1999 à 2007 suivie d'une augmentation jusqu'en 2017. Nous avons également mis en évidence l'influence d'ENSO avec une augmentation de l'abondance durant les phases El Niño. Enfin, nous avons montré une faible corrélation spatiale entre les prédictions de SEAPODYM, un modèle écosystémique, et nos prévisions d'intensités acoustiques. Dans le **3<sup>ème</sup> chapitre**, nous avons regardé la variabilité de la distribution verticale du micronecton et tenté d'en comprendre les forçages physiques à travers l'analyse de données d'EK60 acquises pendant six campagnes entre 2011 et 2017. Le développement d'un cadre statistique a permis de lier les distributions verticales de micronecton aux conditions environnementales et de faire de la biorégionalisation. Nous avons identifié trois régions acoustiquement homogènes : (1) au nord de 21°S avec une faible DSL (Deep Scattering Layer) et une faible SSL (Shallow Scattering layer), (2) le coin sud-ouest (SSL intense à 80m et SSL très intense à 30m) et (3) le coin sud-est (SSL intense et DSL très intense à 550m). Au cours du **4<sup>ème</sup> chapitre**, nous nous sommes concentrés sur la diversité du micronecton et les facteurs physiques la régissant. Pour cela, nous avons analysé les 22 espèces les plus nombreuses, présentes dans 141 chaluts, à l'aide d'une méthode multi-variée. Sept grands assemblages ont été décrits, principalement influencés par le moment de la journée et la profondeur du chalut, puis par la température, l'oxygène et la bathymétrie. L'assemblage prédominant au nord était dominé par les crustacés et au sud par les céphalopodes et poissons. Les deux chapitres suivant ont utilisé les prédictions verticales de distribution du **2<sup>ème</sup> chapitre**. Nous avons prédit l'évolution du micronecton en changement climatique dans le **5<sup>ème</sup> chapitre**. Une simulation océanographique régionale innovante, réalisée à partir d'un modèle biogéochimique dynamique couplé (NEMO-PISCES), a été utilisé pour forcer la modélisation acoustique et le modèle SEAPODYM. Les deux ont prédit une diminution moyenne de l'abondance de micronecton d'ici 2100, mais l'acoustique prédisait une forte augmentation pour la couche bathypélagique (environ 400-600m) alors que SEAPODYM prédisait la plus forte diminution pour cette même couche. Les changements d'abondance étaient majoritairement dus à la modification de la structure de la colonne d'eau, avec un approfondissement de la thermocline. Enfin dans le **6<sup>ème</sup> chapitre**, nous avons lié l'abondance relative des proies à la distribution de neuf prédateurs : le thon jaune, le thon germon, la dorade coryphène (CPUE), le puffin, le pétrel, le fou à pieds rouge (données de marquage), les dauphins, les globicéphales et les baleines à bec (comptages par survol aérien). L'abondance des proies influençait la distribution de six des neuf prédateurs. Cette approche nous a permis de montrer que les données d'abondance des proies mesurées par acoustique pouvaient améliorer les modèles de distribution des prédateurs dans une certaine mesure.

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## Abstract

New Caledonian pelagic ecosystem has been showed to contain strong diversity of top predators, as seabirds and cetaceans. This diversity is supported by variability in physical environment (*e.g.* ridges and seamounts), offering a large diversity of habitats. The recent creation of the Natural Park of the Coral Sea created needs of robust information on the productivity and functioning of this remarkable ecosystem, including micronekton dynamics and their pivotal role in food webs. This food web link has been highlighted as the largest gap of knowledge. In this context, the PhD firstly aimed to study the biodiversity and the functioning of micronektonic compartment through acoustics and trawl around New Caledonia. In a second part, it aimed to analyze influence of prey on top predators' distribution. In the **second chapter** we used backscatter echo-intensity data of Shipboard Acoustic Doppler Current Profiler, recorded during 54 cruises across 19 years to assess micronekton seasonal and inter-annual variabilities and spatial distribution in the 20-120m layer. We showed a decrease of micronekton relative abundance until 2007 and then an increase, as well as an enhancement during El Niño events. Sea surface temperature was the main factor driving the backscatter variability. Finally, we showed poor spatial cohesion between SEAPODYM predictions, an ecosystem model, and our backscatter predictions. During the **third chapter**, we focused on micronekton vertical distribution variability and the understanding of forcing oceanographic parameters through analyze of EK60 from six cruises happening between 2011 and 2017. We developed a statistical framework to link typical vertical distributions to environmental conditions and used it to predict acoustic vertical profile over a larger area to do bio-regionalization. We found three acoustically homogenous regions : north of 21°S with weak DSL (Deep Scattering Layer) and weak SSL (Shallow Scattering layer), the southwest corner (intense SSL at 80m and very intense SSL at 30m) and the southeast corner (intense SSLs and very intense DSL at 550m). During the **fourth chapter**, we looked at the species diversity distribution and its physical drivers. For that purpose, we analyzed the 22 most numerous species present in 141 trawls with a multi-variates method. Seven major assemblages were identified, mainly driven by moment of the day and trawl depth, and then by temperature, oxygen and bathymetry. Globally, predominant northern assemblages were dominated by crustaceans and southern assemblages by less crustacean and more cephalopods and fish. The last two chapters used the methodology of the 3<sup>th</sup>. We predicted micronekton evolution in climate change in the **5<sup>th</sup> chapter**. We used an innovative oceanographic regional simulation from a coupled dynamical-biogeochemical model (NEMO-PISCES) to force acoustics modeling and SEAPODYM. Both methods predicted a micronekton abundance decreasing by 2100 in the Coral Sea, but acoustics predictions showed a large increase for the bathypelagic layer (about 400-600m) whereas SEAPODYM showed the largest decrease for this same layer. Micronekton abundance changes were mainly driven by water column structure change, through mainly a deepening of the thermocline. Finally, in the **last chapter** we linked prey relative abundance to nine predators taxa distribution : yellowfin and albacore tuna, dolphinfish (analyzed through CPUE), shearwater, petrel and red-footed booby (tagging data) and Delphinae, Globicephalinae and Ziphiidae (aerial survey count). Preyscape shaped six out of nine predators distributions and we described the nine spatial distributions. Our approach allowed us to show that prey abundance data collected using acoustic methods can slightly improve distribution models for predators.

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## Scientific contributions

### First author publications

Receveur, A., E. Kestenare, V. Allain, F. Menard, S. Cravatte, A. Lebourges-Dhaussy, P. Lehodey, M. Mangeas, N. Smith, M.H. Radenac, C. Menkes. 2020. "Micronekton distribution in the southwest Pacific (New Caledonia) inferred from Shipboard-ADCP Backscatter data". *Deep Sea Research Part I*. (**Chapitre 2**)

Receveur, A., C. Menkes, V. Allain, A. Lebourges-Dhaussy, D. Nerini, M. Mangeas, and F. Menard. 2019. "Seasonal and spatial variability in the vertical distribution of pelagic forage fauna in the southwest Pacific". *Deep Sea Research Part II*. (**Chapitre 3**)

**Submitted, in revision** Receveur, A., E. Vourey, A. Lebourges-Dhaussy, C.E. Menkes, F. Menard, and V. Allain. "Micronekton Richness and Assemblages in the Natural Park of the Coral Sea". *In Frontiers in Marine Sciences*. (**Chapitre 4**)

**Submitted soon** Receveur, A., T. Gorgues, C. Menkes, C. Dutheil, O. Aumont, P. Lehodey, V. Allain, F. Menard, S. Nicol, and A. Lebourges-Dhaussy. "Exploring the Potential Future of the Coral Sea Micronekton". *In prep. for Global Change Biology*. (**Chapitre 5**)

**Submitted soon** Receveur A., Allain V., Lebourges-Dhaussy A., Menkes C., Ménard F., Laran S., Vidal E., Ravache A., Hare S. , Weimerskirch H., Borsa P. Habitat predictive modelling of nine top predators with respect to the abundance of pelagic prey in the southwest Pacific. (**Chapitre 6**)

### Other publications

Lorrain, A., H. Pethybridge, N. Cassar, **A. Receveur**, V. Allain, N. Bodin, L. C.A. Bopp, Choy, L. Duffy, B. Fry, N. Goni, D.S. Graham, A.J. Hobday, J.M. Logan, F. Menard, C. Menkes, R.J. Olson, D. Point, A.T. Revill, C.J. Somes, J.W. Young. 2019. "Trends in Tuna Carbon Isotopes Reflect Global Changes in Pelagic Phytoplankton Communities." *Global Change Biology*.

Houssard, P., A. Lorrain, L. Tremblay-Boyer, V. Allain, B. S. Graham, C. E. Menkes, H. Pethybridge, L. Couturier, D. Point, B. Leroy, **A. Receveur**, B.P. Hunt, E. Vourey, S. Bonnet, M. Rodier, P. Raimbault, E. Feunteun, P.M. Kuhnert, J.M. Munaron, B. Lebreton, T. Otake, Y. Letourneur. 2017. "'Trophic Position Increases with Thermocline Depth in Yellowfin and Bigeye Tuna across the Western and Central Pacific Ocean." *Progress in Oceanography* 154 : 49–63. <https://doi.org/10.1016/j.pocean.2017.04.008>.

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## International conferences and workshops

**WGFASST, Galway, 2019** - Forecasting vertical distribution variability of pelagic forage fauna in the south Pacific.

**CLIOTOP, Taiwan, 2018** - Acoustic characterization of micronekton vertical distribution related to the environment around New Caledonia (south-west Pacific).

**WGFASST, Seattle, 2018** - Acoustic characterization of micronekton distribution in the surface layer related to the environment across the New Caledonian economic zone (south-west Pacific).

**AGU 2016, San Francisco** - El Niño revisited : the influence of El Niño Southern Oscillation on the world's largest tuna fisheries.

## Scientific reports and other presentations

Valérie Allain, Aurore Receveur, Élodie Vourey, Annie Portal, Jeff Dubosc, Laurent Millet, Damien LAGRANGE, Philippe Borsa, Chloé Yven, Dianne Gleeson, Elise Furlan, Jonas Bylemans, Christophe Menkes, Gildas Roudaut et Anne Lebourges-Dhaussy, 2019. "A la découverte du micronekton de l'océan de Nouvelle-Calédonie : les proies des thons et autres grands prédateurs marins". Note d'informations.

Valérie Allain, Christophe Menkes, Aurore Receveur, Elodie Vourey, Martine Rodier, Céline Bachelier, Gildas Roudaut, Antoine Nowaczyk, Annie Portal et Laurent Millet, 2019. "L'exploration de l'océan de Wallis-et-Futuna : une diversité à découvrir, des monts sous-marins à explorer". Note d'informations.

Christophe Menkes, Patrick Lehodey, Inna Senina, Thomas Gorgues, Valerie Allain et Aurore Receveur, 2019. "L'impact du changement climatique sur l'écosystème de l'océan de Nouvelle-Calédonie". Note d'informations.

Christophe Menkes, Patrick Lehodey, Inna Senina, Thomas Gorgues, Valerie Allain et Aurore Receveur, 2019. "L'impact du changement climatique sur l'écosystème de l'océan de Wallis-et-Futuna". Note d'informations.

Receveur A., V. Allain. 2017. "A young scientist studies marine biodiversity in the open ocean". SPC Fisheries Newsletter 152, 10-15.

Receveur A., S. Nicol, L. Tremblay-Boyer, C. Menkes, I. Senina and Lehodey P. 2016. "Using SEAPODYM to better understand the influence of El Niño Southern Oscillation on Pacific tuna fisheries". SPC Fisheries Newsletter 149, 31-36.

Les six newsletters du projet BIOEPALGOS - <https://fame1.spc.int/fr/projets/biopelagos>

**C'Nature 2019, Nouméa** - Restitution publique du projet BIOPELAGOS.



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## Le projet BIOPELAGOS



Les pays et territoires du Pacifique se caractérisent par de petites surfaces terrestres (2%) et de vastes zones océaniques (98%) et l'océan Pacifique représente à lui seul 48% de l'océan mondial. L'océan et les organismes vivants constituent un lien important entre tous les pays et territoires du Pacifique. Ils se partagent l'océan qui est une source majeure de revenus, par exemple à travers les droits d'accès à la pêche au thon (ces droits fournissent entre 11 et 63% des revenus annuels de pays tels que Kiribati, Tuvalu ou les Etats fédérés de Micronésie [Bell *et al.*, 2015]). C'est également une source essentielle de protéines pour la sécurité alimentaire : la consommation moyenne de poisson varie de 30 à 148 kg/hab/an dans les îles du Pacifique [Bell *et al.*, 2011] contre une moyenne de 19 kg/hab/an pour le monde [FAO, 2016]. Enfin l'océan a une valeur culturelle et patrimoniale importante dans la région (route navigable, mythologie ou encore espèces emblématiques).

L'importance de l'écosystème océanique et de sa biodiversité pour les communautés du Pacifique ne doit donc pas être sous-estimée. Contribuant à tous les aspects de la vie, l'océan offre de nombreux services aux populations du Pacifique, aux gouvernements (par l'accès à la pêche) et à l'emploi (à bord des navires de pêche et dans les usines de transformation). Il contribue également aux services culturels par la présence de mammifères marins, d'oiseaux marins, de requins et de tortues qui ont une valeur patrimoniale et récréative (*e.g.* l'observation des baleines). Enfin, l'écosystème océanique lui-même contribue de manière significative à la régulation du climat par sa contribution au puits de carbone océanique. Avec une population humaine qui demeure extrêmement vulnérable aux impacts des changements climatiques, ce service écosystémique traduit à lui seul le rôle crucial que jouent des écosystèmes océaniques pour la vitalité de la région du Pacifique et de ses habitants. Dans ce contexte, la conservation et la gestion durable des océans est essentielle à la subsistance et au développement des pays et territoires du Pacifique.

Le paysage océanique du Pacifique (*Pacific Oceanscape* en anglais) a été conçu par son excellence Anote Tong, Président de Kiribati, au début de 2009 et le concept a été approuvé par les dirigeants du Forum des îles du Pacifique à leur 40<sup>ème</sup> réunion en août 2009. L'objectif du cadre est d'assurer la santé et le bien-être de l'océan et des populations par la gestion intégrée des océans, l'adaptation aux changements environnementaux et climatiques. L'une des actions identifiées est l'utilisation de la planification spatiale de l'espace marin pour améliorer la gestion des ZEE (Zone Économique Exclusive) afin de soutenir le développement économique tout en maintenant les fonctions des écosystèmes et l'intégrité de la biodiversité des zones côtières et marines. La planification spatiale de l'espace marin est un outil per-

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mettant d'associer un développement socio-économique durable et dans le même temps une conservation de l'environnement et de la biodiversité pour perpétuer les services que les écosystèmes fournissent aux populations, particulièrement dans le contexte du changement climatique et du besoin critique de stratégie de résilience. Cette planification spatiale nécessite des informations sur l'utilisation de l'océan, l'état des écosystèmes et l'impact des perturbations de l'environnement sur ces écosystèmes. Cependant dans la plupart des pays et territoires du Pacifique, les décideurs sont confrontés à un manque important d'informations qui empêche, entrave ou retarde leurs décisions. C'est particulièrement vrai en ce qui concerne les zones océaniques offshore qui sont difficilement accessibles à la recherche en comparaison des zones côtières.

C'est dans ce contexte de besoins locaux de conservation et de gestion durable qu'a été pensé le projet **BIOPELAGOS**, appliqué à deux territoires français du Pacifique : la Nouvelle-Calédonie et Wallis-et-Futuna. En Nouvelle-Calédonie, après la mise en œuvre en 2014 du parc marin de la mer de corail (catégorie VI des aires protégées de l'UICN) qui couvre l'ensemble des eaux océaniques de la ZEE, les autorités sont en train d'élaborer un plan de gestion qui exige des informations spatiales (par exemple répartition spatiale des usages ou des espèces). Wallis-et-Futuna a entamé des négociations avec des entreprises de pêche étrangères en vue d'attribuer l'accès à la pêche au thon. Toutefois, aucune pêche industrielle de thonidés industrielle hauturière n'a été pratiquée dans cette ZEE à ce jour et il n'existe aucune information sur ses ressources pélagiques océaniques. En outre, la ZEE de Wallis-et-Futuna se caractérise par la présence de nombreux monts sous-marins qui sont susceptibles d'avoir des niveaux élevés de biodiversité et d'être particulièrement vulnérables à la pêche industrielle et aux autres impacts humains.

Le projet **BIOPELAGOS**, co-géré par la CPS (Communauté du Pacifique) et l'IRD (Institut de Recherche pour le développement) vise à apporter un soutien scientifique aux territoires français du Pacifique pour contribuer à des prises de décision éclairées sur la gestion durable et la conservation de la biodiversité de leurs écosystèmes océaniques. Le projet **BIOPELAGOS** a duré 3 ans (du 30 juin 2016 au 29 juin 2019) et a été financé par un programme BEST 2.0 de l'Union Européenne. Trois thématiques étaient envisagées :

- **L'acquisition de nouvelles connaissances** à travers la collecte de données dans chaque territoire pour combler les lacunes en matière de connaissances et améliorer la compréhension de la biodiversité et du fonctionnement de l'écosystème océanique. Pour cela, des campagnes à la mer, des campagnes de marquage des oiseaux marins (pétrels et puffins) et du barcoding et metabarcoding génétique ont été réalisés.
- **Le renforcement des capacités humaines** pour former des personnes et partager et diffuser l'information recueillie. Pour cela, une étudiante en thèse et des étudiants de niveau Master ont été encadrés, des journées d'information auprès du grand public ont été organisées et des échanges réguliers ont été menés avec les institutions des territoires partenaires.
- **La synthèse des connaissances**, pour fournir des recommandations scientifiques à l'appui de décisions éclairées sur la conservation, la gestion durable et la résilience des écosystèmes océaniques. Pour cela, une base de données a été constituée rassemblant les jeux de données historiques et nouvellement acquis sur le domaine océanique; les données ont été analysées pour comprendre les interactions trophiques et pour identifier des zones de forte biodiversité. Une modélisation sur le changement climatique a été mise en place pour explorer les évolutions spa-

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tiales d'abondance du micronecton et des thons. Six notes ont été rédigées pour synthétiser les informations les plus pertinentes pour la conservation et la gestion durable des ressources pélagiques et ont été diffusées au niveau régional. Elle sont disponibles à l'adresse suivante : <https://fame1.spc.int/fr/projets/biopelagos>.

C'est dans le cadre de ce projet que ma thèse a été financée avec pour objectif de rassembler et analyser l'ensemble des données récoltées sur l'écosystème pélagique pour en comprendre son fonctionnement et sa diversité. Les objectifs ont été affinés au cours des premiers mois, et sont donnés à la fin de l'introduction générale. L'inclusion de la thèse dans un projet européen m'a permis de participer aux réunions avec les différents gestionnaires et ainsi d'appréhender les relations entre scientifiques et décideurs. J'ai également participé à une campagne en mer de 15 jours réalisées en 2018 autour de Wallis et Futuna, j'ai participé à l'encadrement d'une étudiante de Master 2, et enfin j'ai participé et mené différentes actions de sensibilisation sur le milieu marin. Dans ce cadre, des outils pédagogiques ont été développés et sont présentés en annexe 8 de cette thèse.



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# Chapitre 1

## Introduction

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## **Écologie spatiale du micronecton : distribution, diversité et importance dans la structuration de l'écosystème pélagique du Pacifique sud-ouest**

Ce chapitre introductif vise à situer le contexte écologique et scientifique dans lequel s'inscrit ce travail de thèse. Dans un premier temps, nous donnerons des éléments de compréhension sur la structure et le fonctionnement d'un écosystème pélagique, puis sur les menaces qui pèsent dessus. Dans un second temps, nous décrirons les différents maillons de l'écosystème pélagique du Pacifique sud-ouest, puis nous détaillerons sa gestion. Ensuite nous aborderons les questions scientifiques de cette thèse. Finalement, nous résumerons les outils utilisés pour répondre à ces questions, en détaillant les moyens d'observation, les outils d'analyse(s) et nous finirons par la présentation du plan du manuscrit.

### **1.1 Contexte général : qu'est-ce qu'un écosystème pélagique ?**

#### **1.1.1 La diversité de ses habitants**

Le terme « écosystème » naît en 1935, défini par Arthur George Tansley. Il propose ce terme pour remplacer « communauté biotique » ou « biome » qui n'incluent que les êtres vivants dans leurs définitions [Tansley, 1935]. Il argumente notamment que, même si ce sont les animaux qui sont au centre de l'intérêt humain, ils forment un tout avec leur environnement physique qui les contrôle et qu'on ne peut donc pas les en dissocier. Ce sont ces écosystèmes ainsi formés qui, du point de vue de l'écologiste, sont les unités de base de la nature à la surface de la terre. Ces systèmes peuvent être de toutes sortes et de toutes tailles. L'humain isole ces systèmes pour pouvoir les définir, les décrire et les comprendre. Cependant il est important de garder à l'esprit que ces systèmes ne sont pas seulement inclus dans d'autres systèmes plus grands, mais se chevauchent, s'imbriquent et interagissent les uns avec les autres. L'isolement est en partie artificiel, mais c'est la seule façon possible de procéder. Tansley [1935] inclut également pour la première fois la notion d'interaction entre les composants qui organisent les écosystèmes. Ces interactions permettent à l'écosystème d'atteindre un état relativement stable : les biomasses des différents compartiments sont régulées grâce aux interactions avec les compartiments qui l'entourent. Ces interactions sont pour la plupart trophiques et environnementales. La définition actuelle proposée par l'Organisation des Nations Unies (ONU) en 2000 d'un écosystème se rapproche fortement de la définition de Tansley de 1935 : « complexe dynamique composé de plantes, d'animaux, de micro-organismes et de la nature morte environnante agissant en interaction en tant qu'unité fonctionnelle » [Millennium Ecosystem Assessment, 2005]. Les écosystèmes sont définis la plupart du temps par leur position géographique, on sépare souvent dans un premier temps les écosystèmes marins des écosystèmes terrestres. Cette thèse s'est concentrée sur un écosystème marin en particulier : l'écosystème pélagique, océanique ou encore appelé de haute mer.

Le domaine océanique est le plus vaste de la planète, environ 14 milliards de km<sup>3</sup>, il inclue toute la colonne d'eau de tous les océans et mers du globe. Il commence là où le domaine néritique se termine, c'est-à-dire au-delà du plateau continental et ne comprend pas le domaine benthique, c'est-à-dire les organismes et milieu à proximité du fond (Figure 1.1). Comme expliqué dans le paragraphe précédent, ces limites sont très arbitraires mais servent à mieux définir les milieux d'études.

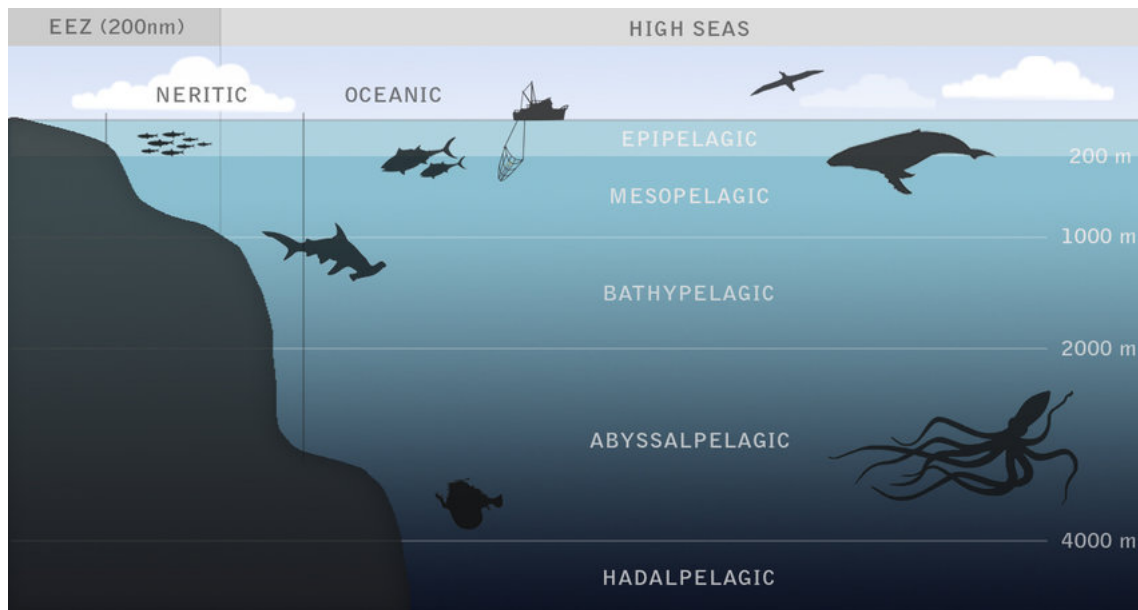


FIGURE 1.1 – Délimitation des couches verticales de l'écosystème pélagique. Figure extraite de [Davis et al. \[2012\]](#).

Le milieu pélagique est structuré verticalement par des gradients de densité, de lumière et de nutriments principalement. On appelle communément zone épipélagique la couche de surface où 99% de la lumière est absorbée et sa limite inférieure est généralement comprise entre 100 et 250 mètres (Figure 1.1). Viennent ensuite les zones mésopélagique, bathypélagique, abyssale et hadale. Cette thèse se limite à l'étude des couches épipélagique et mésopélagique. La lumière pénètre dans la couche épipélagique, rendant ainsi la production primaire possible grâce à la photosynthèse. Les processus physiques qui régissent ce milieu seront décrits par la suite.

Ce vaste domaine pélagique est également le milieu de vie de nombreuses espèces dont l'homme fait partie (Figure 1.2). La diversité des espèces et des interactions entre espèces est un facteur clé de l'écosystème. En effet, cette diversité apporte de nombreux biens et services utiles à l'homme mais également à l'écosystème lui-même [[Worm et al., 2006](#)]. La diversité assure aux écosystèmes une certaine stabilité et une résilience potentielle de leur productivité [[Cardinale et al., 2012](#)]. Les services de la diversité rendus à l'homme ont été classés en quatre grands groupes par [Beaumont et al. \[2007\]](#) :

- Les services de production qui regroupent les ressources alimentaires et autres, animales et minérales, exploitées par l'homme ;
- Les services de régulation qui maintiennent un équilibre chimique et permettent de se protéger contre les aléas naturels ou encore l'absorption du CO<sub>2</sub> par l'océan ;
- Les services culturels auxquels on peut associer une valeur économique par exemple pour le tourisme ;
- Et enfin les potentiels futurs usages qu'on en fera (Table 1.1).

Pour mesurer la diversité d'un écosystème, il est nécessaire d'en connaître les espèces présentes. [Davis et al. \[2012\]](#) proposent une classification des espèces marines basée sur le milieu principal de vie, la capacité natatoire et la taille des espèces (Table 1.2). On y retrouve des grandes espèces migratrices telles que la baleine à bosse qui partage son milieu de vie entre les eaux froides des pôles et les eaux tropicales plus chaudes. Y sont également présentes, les petites espèces pélagiques comme les anchois ou les sardines, et les espèces passant une partie de leur vie en milieu côtier comme le grand dauphin ou même en



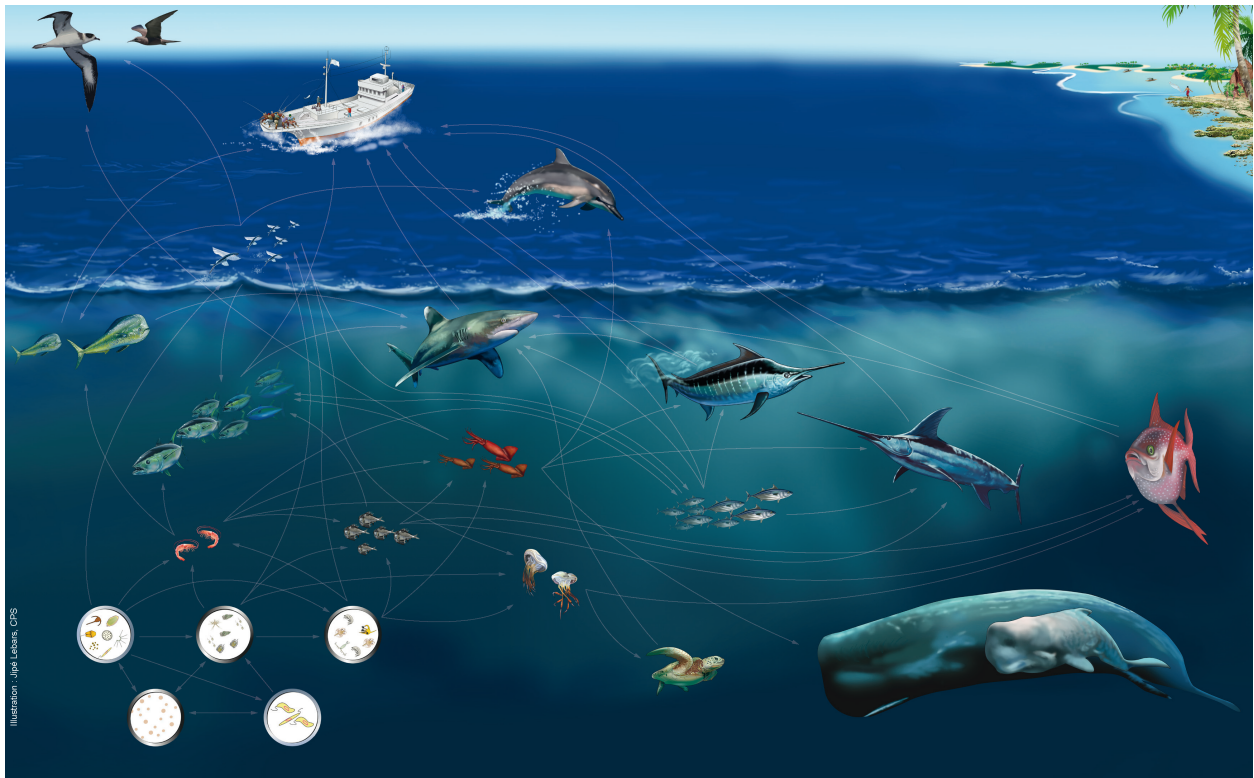


FIGURE 1.2 – Schéma de l'écosystème pélagique adapté au Pacifique sud (Source CPS).

TABLEAU 1.1 – Biens et services fournis par la biodiversité marine. Tableau adapté d'après [Beaumont et al. \[2007\]](#) .

| Catégorie                  | Biens ou services  |
|----------------------------|--|
| Service de production      | Approvisionnement alimentaire<br>Matières premières  |
| Service de régulation      | Régulation des gaz et du climat<br>Prévention des perturbations (protection contre les inondations et tempêtes)<br>Stockage et recyclage des déchets   |
| Service immatériels        | Patrimoine culturel et identité<br>Loisirs<br>Sensation de bien-être (avantages de non-utilisation)<br>Bénéfices cognitifs (e.g. éducation, recherche) |
| Valeur d'usage de l'option | Avantages futurs inconnus et spéculatif  |

eau douce comme l'anguille. Cette classification ne prend pas en compte les relations trophiques entre espèces qui sont matérialisées par les flèches blanches sur la Figure 1.2, et qui sont donc nombreuses et complexes. L'image de la chaîne trophique du petit poisson qui est mangé par le moyen poisson qui est lui-même mangé par le gros poisson a depuis plusieurs années laissé la place à cette représentation de réseau trophique où toutes les espèces sont inter-connectées. Une autre classification fréquente des espèces est basée sur leur niveau trophique, on retrouve communément les producteurs primaires en bas de la pyramide (phytoplancton), puis les consommateurs primaires (zooplancton), les prédateurs intermédiaires (micronecton) et les prédateurs supérieurs (ou « top predators », *e.g.* thon). Si on considère l'énergie totale disponible d'un niveau trophique (*i.e.* 100%), en moyenne 10% est effectivement converti en biomasse dans le niveau suivant, avec une variation comprise entre 1 et 20% [Pomeroy, 1979], il s'agit de la loi de Lindeman. Ce taux de transfert d'énergie s'explique par deux raisons principales : (1) il y a une perte d'énergie à chaque niveau par la respiration et l'excrétion et (2) les consommateurs du niveau suivant n'assimilent pas toute la matière organique disponible. Dans les écosystèmes marins, la taille d'un organisme peut être un meilleur prédicteur de sa position trophique que sa taxonomie [Jennings *et al.*, 2001]. Ce constat a donné naissance à la théorie des spectres de taille qui dit que le nombre d'individus par niveau trophique est de plus en plus petit au fur et à mesure que l'on s'élève dans la pyramide trophique et que cette réduction de nombre est compensée par une augmentation de la taille [Boudreau *et al.*, 1991]. La théorie du spectre de taille est de plus en plus utilisée pour paramétrer les modèles de réseau trophique [Blanchard *et al.*, 2011; Maury *et al.*, 2007]. Bien que cette approche ne donne pas nécessairement un aperçu des interactions au niveau des espèces, elle présente l'avantage de reposer sur des relations écologiques et physiologiques qui sont largement applicables à l'ensemble des taxons et des régions.

En dénombrant les interactions trophiques correspondant à chaque espèce (Figure 1.2), les poissons volants, les calamars et les crevettes sont les espèces qui arrivent en tête avec pas moins de 9 interactions pour chaque espèce. Ce constat met en avant le rôle clé du micronecton dans le réseau alimentaire : ce sont ces espèces qui font le lien entre les organismes de niveaux trophiques inférieurs influencés fortement par l'environnement et tous les prédateurs supérieurs. Nous nous sommes particulièrement intéressés à cet échelon trophique au cours de la thèse. Le micronecton est composé de tous les organismes mesurant entre 1 et 20cm et constitue la nourriture des prédateurs supérieurs. On y retrouve une grande diversité d'espèces : des poissons, des crustacés, des mollusques ou encore des organismes gélatineux. Le micronecton inclut également un grand nombre d'organismes de façon transitoire lors de leur développement larvaire et juvénile, et pas uniquement d'espèces pélagiques. On retrouve par exemple de nombreuses larves de poissons récifaux dans le micronecton [Allain *et al.*, 2012]. Malgré le rôle primordial de ce groupe, il est encore le maillon le moins étudié de l'écosystème marin [Conchon, 2016]. Comme le montre le nombre d'études disponibles en fonction de certains mots clés, le micronecton arrive en dernière position (Figure 1.3) [St. John *et al.*, 2016]. L'intérêt pour ce compartiment encore très peu étudié est cependant en train de grandir, notamment car il représente potentiellement une nouvelle ressource alimentaire importante (Figure 1.4) [Hidalgo & Browman, 2019].

TABLEAU 1.2 – Typologie des espèces marines de plus de 1cm. Les espèces sont regroupées selon leur écologie et leur capacité à se déplacer. Tableau adapté d’après [Davis et al. \[2012\]](#).

| Groupe d’espèces                | Description   | Exemple d’espèces                  |
|---------------------------------|---|------------------------------------|
| Espèces pélagiques très mobiles | Espèces qui voyagent sur de très grandes distances de façon saisonnière ou au cours de leur vie. Ce groupe se compose principalement d’oiseaux et de grands cétacés         | Albatros<br>Baleine à bosse        |
| Grand pélagique océanique       | Espèces de taille raisonnable qui habitent principalement des eaux océaniques et sont capables d’effectuer des mouvements importants sur des périodes relativement courtes. | Thon<br>Requin océanique           |
| Petits pélagiques océaniques    | Espèces relativement petites qui ne se déplacent que sur de petites distances dans des eaux à prédominance océanique.   | Dorade coryphène<br>Raie pélagique |
| Grands pélagiques littoraux     | Espèces pélagiques de grande taille limitées aux zones littorales pendant la plus grande partie ou la totalité de leur vie et capables de se déplacer modestement.          | Grand dauphin                      |
| Petits pélagiques littoraux     | Petites espèces pélagiques limitées aux zones littorales pendant toute leur durée de vie et capables de se déplacer modestement.  | Sardine<br>Maquereau               |
| Espèces pélagiques diadromes    | Espèces anadromes qui migrent entre des distances importantes entre les rivières d’eau douce et l’océan pélagique.  | Saumon<br>Anguille                 |

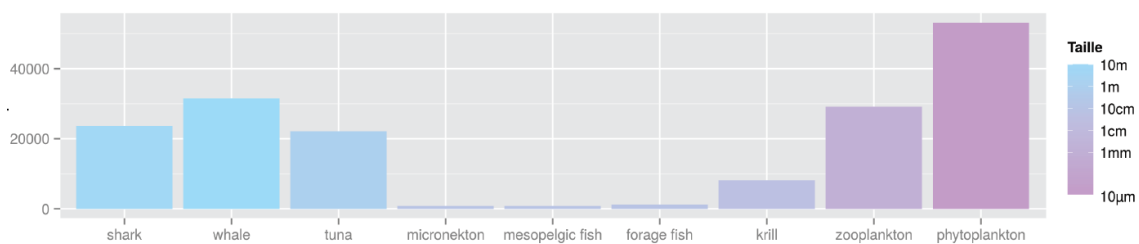


FIGURE 1.3 – Nombre d’études disponibles sur [sciencedirect.com](http://sciencedirect.com), en fonction du mot clé choisi. Les groupes d’organismes sont classés par niveau trophique du plus élevé au plus faible, la couleur des barres représente la taille moyenne du groupe considéré. Figure extraite de la thèse de Anna [Conchon \[2016\]](#).

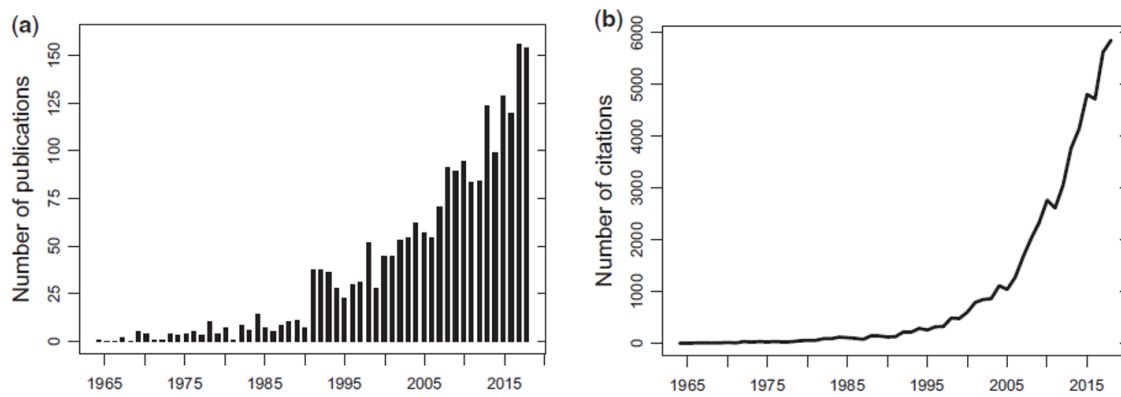


FIGURE 1.4 – Le nombre de publications (a) et de citations (b) par an qui ressortent d'une recherche dans la collection de base du Web of Science pour le terme "mésopélagique" sur la période 1945-2018, effectuée le 25 février 2019. Figure extraite de [Hidalgo & Browman \[2019\]](#).

### 1.1.2 Les contrôles trophiques qui régissent l'écosystème

Nous avons vu dans la section précédente que les biomasses des espèces d'un écosystème étaient régulées en partie par les interactions alimentaires. Ces interactions sont également appelées contrôles trophiques et on en distingue généralement trois modèles (Figure 1.5) [[Cury et al., 2002](#)]. Le contrôle par le haut (ou *top down control*) est un écosystème où c'est la biomasse de l'échelon  $n$  qui contrôle la biomasse de l'échelon  $n-1$  : si les prédateurs diminuent, les proies augmentent car elles sont moins mangées, le zooplancton diminue car il est plus mangé et le phytoplancton lui augmente. On peut voir que dans ce cas de figure, les réponses sont inversées pour chaque échelon trophique. Le contrôle par le bas (ou *bottom-up control*) est comme son nom l'indique, un système où c'est la production primaire qui régite tous les échelons : si cette dernière diminue, la biomasse de zooplancton diminue elle aussi, et par cascade, celle des proies et des prédateurs. Dans ce cas, c'est l'environnement qui est le régulateur principal de l'écosystème. Ce type de contrôle existe notamment dans l'*upwelling* du Pérou où l'on observe une alternance entre anchois et sardines. Ces deux espèces n'ayant pas le même habitat optimal, l'abondance de leur population respective s'alterne au cours du temps dues à des variations de conditions environnementales. Même si l'effet exact des facteurs environnementaux contrôlant cette alternance n'est pas encore parfaitement compris, l'impact du phénomène ENSO (*El Niño Southern Oscillation*) a été largement montré [e.g. [Bertrand et al. 2004](#), [Chavez et al. 1999](#), [Chavez et al. 2003](#)]. La pression de pêche très forte dans cette région se rajoute aux facteurs environnementaux. Les fortes variations de biomasses pouvant passer de centaines de milliers de tonnes à pratiquement zéro dans les cas extrêmes [[Lluch-Belda et al., 1989](#)] peuvent avoir un effet dramatique sur les populations humaines exploitants ces ressources [[Allison et al., 2009](#); [Barange et al., 2014](#); [Bell et al., 2011](#)]. Dans les zones moins productives et plus diversifiées en terme de proies, le lien à l'environnement des proies est encore plus complexe à comprendre et les connaissances sur ces contrôles sont encore assez limitées [[St. John et al., 2016](#)].

### 1.1.3 L'hétérogénéité spatio-temporelle des processus marins

La complexité de ces systèmes est accrue par la forte variabilité spatio-temporelle des processus physiques, de l'influence de ces processus sur les échelons trophiques, et des interactions entre espèces. De plus, la tridimensionnalité du milieu marin, et particulièrement sa composante verticale, complique en-

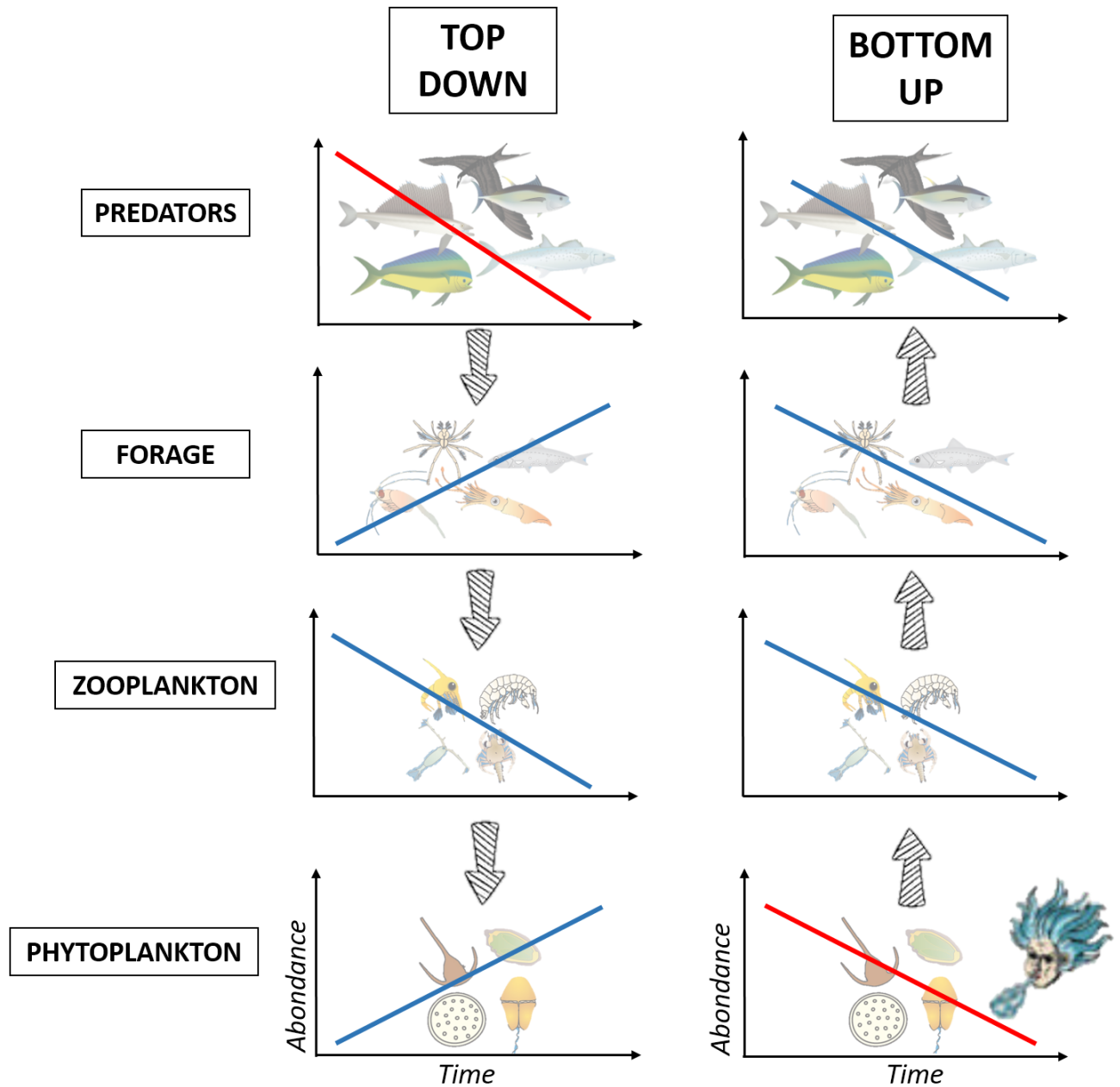


FIGURE 1.5 – Les trois types de contrôles trophiques, l'effet de l'environnement est représenté par le visage soufflant du vent, Figure adapté d'après [Cury et al. \[2002\]](#). Les tendances rouges représentent l'élément déclencheur des cascades dans chaque cas de figure.

core la compréhension des processus. La majeure partie de l'écosystème marin est plongée dans le noir et subit des fortes pressions, rendant cet espace inaccessible aux moyens d'échantillonnage traditionnels. Finalement, la complexité de ce tableau est encore accrue par les interactions entre les espèces et l'environnement qui sont changeantes au cours du cycle de vie d'une espèce. Une espèce va être mangée par différentes espèces au cours de son cycle de vie par exemple. On peut citer le cas étonnant de la morue de mer du nord qui peut se nourrir de ses propres juvéniles (cannibalisme) [Folkvord, 1991]. Enfin, les conditions océanographiques favorables au stade larvaire sont souvent différentes des conditions favorables au stade adulte.

Hunt & Schneider [1987] proposèrent un découpage des échelles temporelles et spatiales des processus adapté au milieu marin : on y retrouve l'échelle fine (inférieure à 1km), l'échelle grossière (de 1 à 10km), la méso échelle (de 10km à 1000km), la macro échelle (de 1000km à 10000km) et enfin la méga échelle (supérieure à 10000km) (Figure 1.6). Ces échelles spatiales sont associées à leurs gammes temporelles respectives. Comme on peut voir avec les quelques exemples de phénomènes physiques superposés, les échelles physiques prédéfinies chevauchent les phénomènes physiques mais comme pour le découpage vertical du milieu (Figure 1.1), elles permettent de mieux définir et classer les différents processus. Plus les échelles sont petites, plus les phénomènes sont instables et donc compliqués à prédire.

Avec son temps de croissance rapide (1-2 jours), la dynamique du phytoplancton est étroitement liée à la dynamique des nutriments dont la distribution tridimensionnelle est influencée par les processus physiques. Ainsi, on retrouve par exemple une forte production primaire dans les *upwellings*, où la remontée de nutriments, calquée sur celle des températures plus fraîches des couches profondes, enrichit la surface. L'influence de la physique sur le zooplancton est plus complexe et on observe dès ce niveau trophique, une décorrélation spatio-temporelle des processus [Smeti *et al.*, 2015]. Cette décorrélation s'amplifie avec le niveau trophique, et il est souvent complexe de comprendre ce qui conditionne la dynamique spatio-temporelle des prédateurs supérieurs [Bellier *et al.*, 2012; Godo *et al.*, 2014; McHuron, 2018; Scales *et al.*, 2017], d'autant qu'à cette dynamique océanique s'ajoutent les comportements biologiques des animaux tels que migrations entre habitats de ponte et d'alimentation par exemple.

Le micronecton a-t-il aussi une dynamique spatio-temporelle complexe? La Figure 1.7 regroupe les processus dynamiques majeurs du micronecton à toutes les échelles spatiotemporelles identifiées par les polygones noirs et les moyens d'échantillonnage identifiés par les rectangles bleus et gris, et le noir en trait gras. A échelle journalière, les migrations nyctémérales sont majoritaires (*Diel Vertical Migration* ou DVM). Chaque jour, la majorité des espèces de micronecton parcourent verticalement des centaines de mètres, migrant du domaine mésopélagique où elles résident durant le jour à la zone épipélagique où elles passent la nuit. Ce mouvement est aujourd'hui reconnu comme la plus grande migration animale au monde [Hays, 2003] et a été observé dans tous les océans de la planète [Bianchi & Mislán, 2016; Klevjer *et al.*, 2016]. Cette migration verticale est généralement expliquée comme une échappatoire à la prédation visuelle pendant la journée. La nuit, les organismes remontent en surface pour s'alimenter [Pearre, 2003]. Le micronecton a également une dynamique saisonnière [e.g. Harding *et al.* 2011] et est sensible aux variations océanographiques interannuelles [Chavez *et al.*, 2003; Staby *et al.*, 2011]. Cependant, l'intérêt récent (Figure 1.4) que nous portons au micronecton restreint la couverture temporelle des données disponibles pour étudier des tendances sur le long terme. La difficulté d'observation et d'échantillonnage sur lesquelles nous reviendrons dans cette introduction complexifie également l'étude de cet

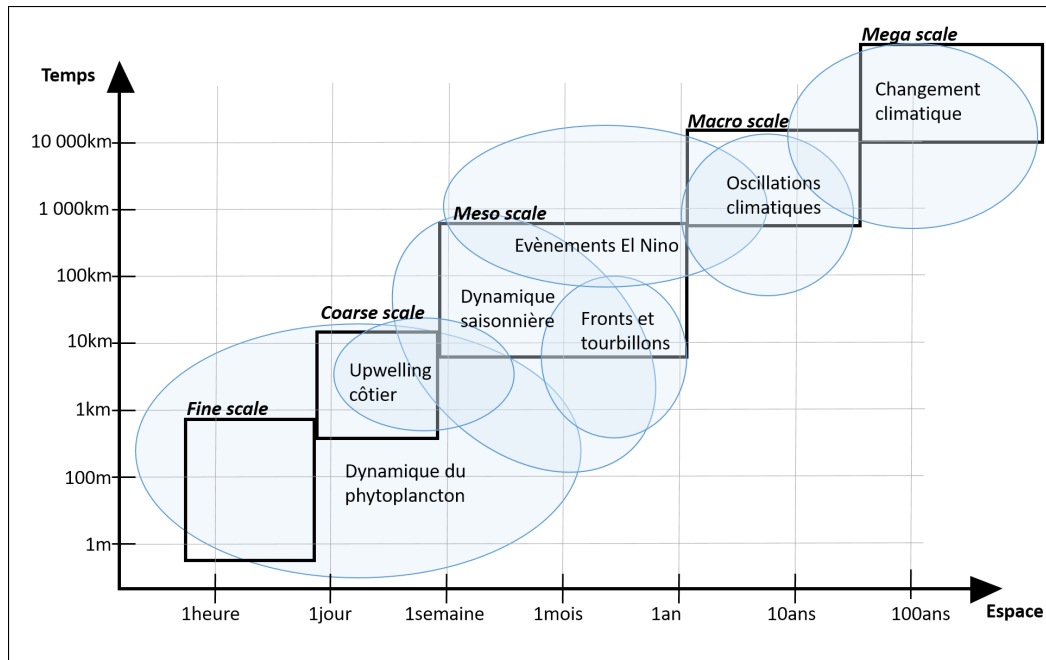


FIGURE 1.6 – Diagramme spatio-temporel représentant la structure hiérarchique du milieu marin. La représentation des processus physiques a été adaptée de [Racault et al. \[2014\]](#) et les 5 échelles ont été extraites de [Hunt & Schneider \[1987\]](#).

échelon trophique (par exemple les phénomènes I, H et G ne sont recoupés par aucun moyen d'étude sur la Figure 1.7). Au niveau mondial, la biomasse estimée d'organismes mésopélagiques varie grandement. En 1980, [Gjøsaeter & Kawaguchi \[1980\]](#) estimaient la biomasse totale de micronecton à environ 1Gt, estimation basée sur des données de chalutage. Depuis cette estimation a été revue à la hausse : en 2014 [Irigoiien et al. \[2014\]](#) proposèrent une estimation entre 14.3 et 19.5Gt d'après des mesures acoustiques. Cependant une étude récente de modélisation a remis en question ces estimations, avec une biomasse modélisée de 2.4Gt [[Anderson et al., 2019](#)]. Enfin, [Proud et al. \[2018b\]](#) ont développé un modèle pour calculer la biomasse de micronecton à partir de données d'acoustique active (38kHz) acquises dans les couches profondes. Leurs estimations varient globalement entre 1.8Gt et 16Gt. D'après leurs conclusions, la présence/absence et le volume de la vessie natatoire, la distribution des tailles et le ratio de la forme des organismes sont des facteurs clés à déterminer pour améliorer l'estimation de biomasse.

#### 1.1.4 Les écosystèmes marins sous pression au cœur des préoccupations environnementales

##### De nombreuses menaces affectent ces écosystèmes

Ayant présenté les contraintes naturelles imposées aux écosystèmes marins, nous présentons maintenant les pressions anthropiques. En effet, depuis plusieurs années les sonnettes d'alarme sont tirées quant à l'état de santé général des écosystèmes marins. Deux faits majeurs, étroitement liés, reviennent régulièrement : l'effondrement des stocks de poissons exploités et la baisse globale de biodiversité, cataloguée comme la sixième extinction majeure que connaîtra notre planète [[Barnosky et al., 2011](#); [Davis et al., 2018](#)]. Alors que la population humaine augmente rapidement, avec près de 9.7 milliards d'habitants prévus pour 2050 [[Barnosky et al., 2012](#)], les pressions induites sur les écosystèmes augmentent

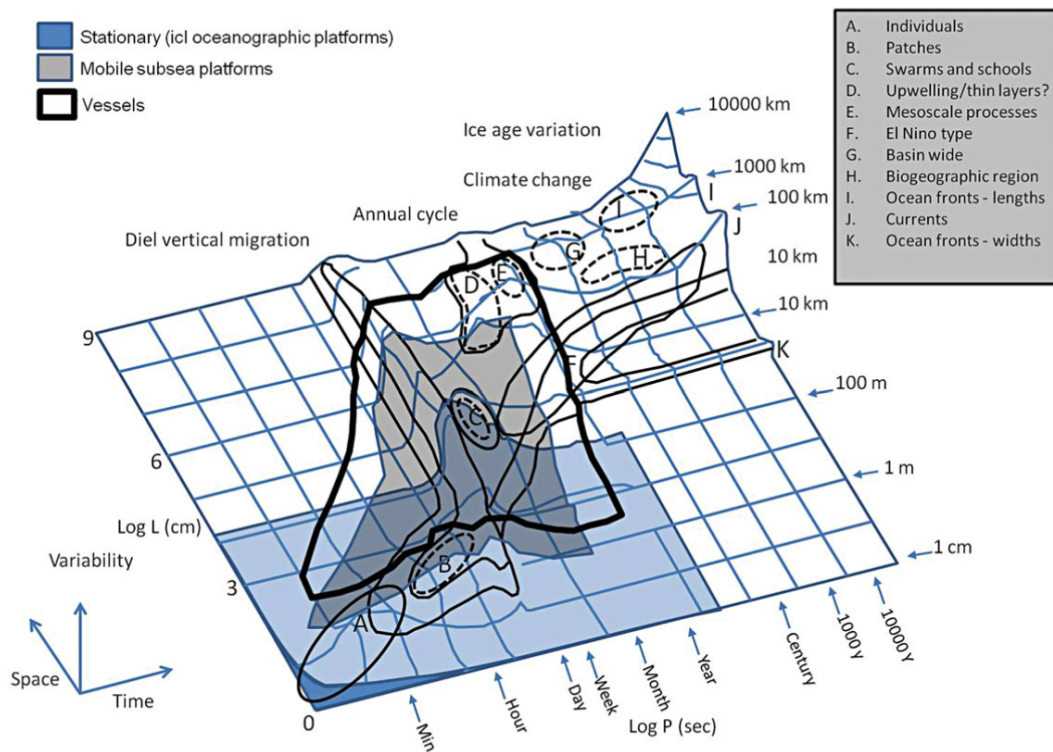


FIGURE 1.7 – Dynamiques spatio-temporelles du micronecton. La surface illustre la variation spatio-temporelle du micronecton. Les phénomènes importants pour la compréhension et l'évaluation des écosystèmes, ainsi que leur extension dans le temps et dans l'espace, sont indiqués sur le dessus de la surface de variabilité et sont identifiés par des lettres majuscules. Le diagramme est étendu pour illustrer l'utilisation de diverses plates-formes, leur potentiel de couverture, leur chevauchement et leur caractère unique dans le temps et l'espace. Schéma extrait de [Godo et al. \[2014\]](#).



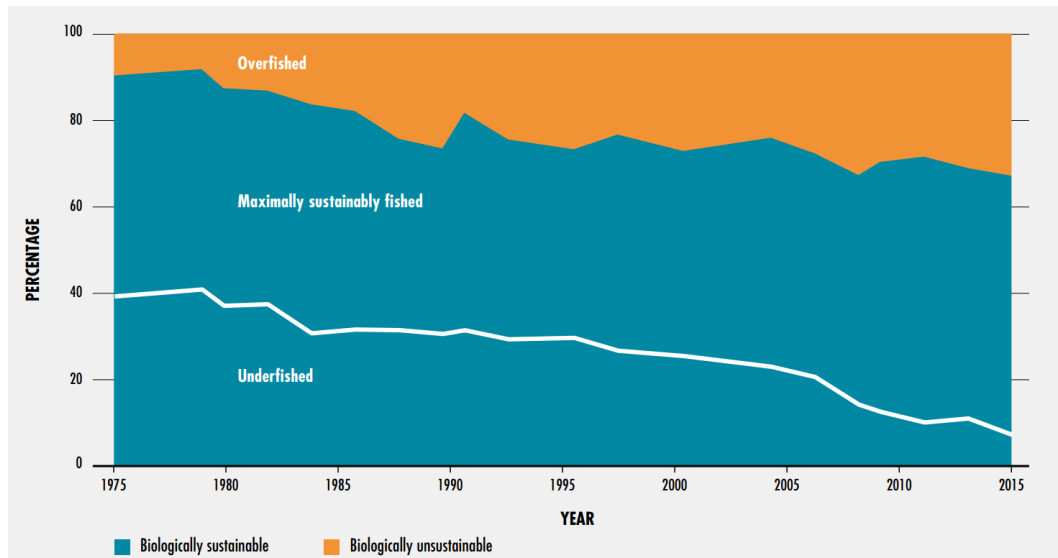


FIGURE 1.8 – Évolution de l'état des stocks mondiaux exploités de 1974 à 2015, la couleur orange montre les stocks surexploités, la couleur bleue au-dessus du trait blanc les stocks exploités à leur niveau maximal et la couleur bleue sous le trait blanc, les stocks sous-exploités. D'après [FAO, 2018].

conjointement. Les activités anthropiques affectent directement ou indirectement la presque totalité du milieu marin. Une étude récente a calculé que seulement 13.2% de l'océan était encore vierge de toute trace anthropique [Jones *et al.*, 2018]. Des chercheurs ont récemment trouvé des micro-plastiques dans des organismes micronectoniques présents jusqu'à 1000 mètres de profondeur [Choy *et al.*, 2019]. Lotze & Worm [2009] ont montré que les abondances des 256 espèces analysées avaient décliné en moyenne de 89% par rapport à leur niveau historique. A travers des modèles, Christensen *et al.* [2014] arrivent au même constat avec une division par trois de la biomasse des prédateurs à l'échelle globale ces 100 dernières années. Le niveau moyen de biodiversité est lui aussi en train de diminuer à une vitesse record [Butchart *et al.*, 2010; Pimm *et al.*, 1995]. Les menaces principales aboutissant à ces résultats alarmants peuvent être classées en trois catégories : les activités de pêche, la pollution et les destructions d'habitat et enfin le changement climatique.

Les premières traces d'apparition de la pêche remontent à plus de 40 000 ans [Thomazi, 1951], et depuis cette période les techniques de pêche n'ont fait que s'améliorer, si bien qu'aujourd'hui le rapport pression de pêche / poissons laisse peu de chance aux poissons. Petit à petit, l'amélioration des techniques de pêche et des bateaux a rendu possible la pêche de plus en plus loin du port d'attache : tous les océans ont progressivement été exploités et on a pu pêcher de plus en plus profond. L'usage grandissant des DCP (Dispositifs de Concentration de Poissons) utilisé principalement pour la pêche au thon a permis de concentrer la ressource et de pêcher de manière bien plus efficace, parfois au détriment de nombreuses captures accessoires [Escalle *et al.*, 2018]. Soixante pourcent des ressources marines seraient exploitées à leur niveau maximal et 30% surexploitées (Figure 1.8). Les espèces exploitées sont de plus en plus nombreuses, mais le niveau trophique moyen des captures est de plus en plus bas [Pauly *et al.*, 1998]. Une revue a même récemment publié une série d'articles qui évaluent le potentiel du micronecton comme ressource alimentaire [Hidalgo & Browman, 2019].

La destruction d'habitats par les engins trainant en contact avec le fond est une autre menace importante qui pèse sur les écosystèmes marins, impactant particulièrement les stades critiques de vie

comme les stades larvaires/juvéniles. Cependant, cette menace est plus présente en milieu côtier [Gibson *et al.*, 2007; Le Pape *et al.*, 2007].

Enfin, le changement climatique global menace lui aussi ces écosystèmes (Figure 1.9). Dans les écosystèmes pélagiques, l'augmentation de température de l'océan impacte majoritairement la distribution spatiale des espèces ainsi que leur métabolisme. Une étude récente a montré que les biomasses des espèces seraient de plus en plus impactées au fur et à mesure que leur niveau trophique s'élève [Lotze *et al.*, 2019]. Les nouvelles conditions environnementales peuvent être physiologiquement tolérables, permettant l'acclimatation (un ajustement de la physiologie par exemple un changement de tolérance à l'oxygène par l'individu) ou l'adaptation (une abondance et une reproduction accrues avec certains génotypes changeant au fil des générations) des espèces. Si au contraire un habitat devient inadéquat pour une population donnée, la taille de la population peut diminuer à mesure que la performance éco-physiologique (les taux métaboliques ou la croissance par exemple) diminue [Hillebrand *et al.*, 2018; Portner, 2001], les espèces peuvent également migrer vers des eaux plus froides [Pecl *et al.*, 2017] ou encore subir une extinction locale [Parmesan, 2006]. L'effet sur les changements de distribution a été étudié par un grand nombre d'études et un consensus s'accorde sur la prévision d'un grand nombre de disparitions dans les régions tropicales et subpolaires et des apparitions d'espèces en zone Arctique et Antarctique [e.g. Cheung *et al.* 2009; Pecl *et al.* 2017]. L'impact physiologique du changement climatique sur les espèces de poisson est lui encore très peu appréhendé.

Le micronecton a une faible capacité natatoire, et a donc peu de chance de pouvoir migrer à de grandes échelles spatiales pour échapper au réchauffement des températures. Il est donc plus probable que ces espèces connaissent des changements métaboliques ou des extinctions. Actuellement, l'impact sur le micronecton est encore peu compris. Bryndum-Buchholz *et al.* [2019] ont prédit une diminution de la biomasse d'environ 15% pour les organismes dont la taille varie entre 0 et 30 cm pour l'ensemble du Pacifique Sud et Lefort *et al.* [2015] une diminution d'environ 20% pour l'ensemble du Pacifique. Ces études se basent sur des modèles, et à notre connaissance, aucune étude ne mesure l'impact du changement climatique sur le micronecton à travers des données. Les impacts potentiels du changement climatique sur les prédateurs à travers des changements de micronecton sont encore, eux aussi, peu étudiés, majoritairement dû à un manque de connaissance sur le micronecton [St. John *et al.*, 2016].

### **Une prise de conscience globale place aujourd'hui ces menaces au cœur des préoccupations politiques**

Aujourd'hui la question de l'urgence climatique et de ses impacts néfastes pour les écosystèmes semble être une évidence. Pourtant, vers le début des années 1900, à l'époque des premiers travaux portant sur l'impact climatique d'une hausse du gaz carbonique (CO<sub>2</sub>) dans l'atmosphère, Walter Nernst, prix Nobel de chimie, proposa de brûler du charbon pour réchauffer l'atmosphère et ainsi améliorer le confort humain. Il avança également comme argument qu'une augmentation de CO<sub>2</sub> dans l'atmosphère allait doper la production primaire et donc l'état de santé des végétaux. En 1940, des scientifiques montrèrent pour la première fois qu'une augmentation de la concentration de CO<sub>2</sub> pouvait entraîner une augmentation de température [Plass, 1956a,b]. La première preuve d'accumulation du CO<sub>2</sub> dans l'atmosphère fut ensuite apportée en 1960 par Keeling [1960] qui mesura quotidiennement les concentrations de CO<sub>2</sub> à Hawaï et en Antarctique. Les préoccupations écologiques apparurent dans les années 1960-70,

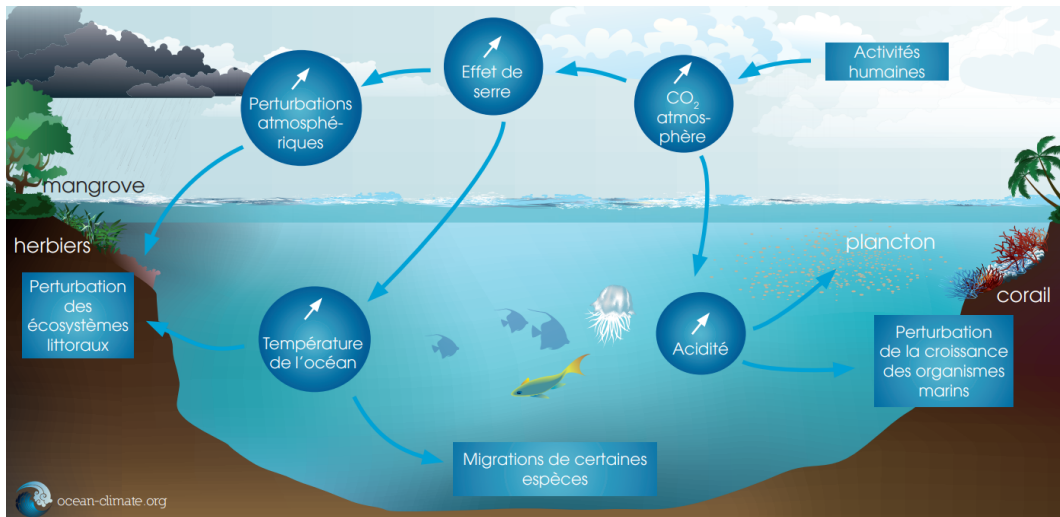


FIGURE 1.9 – Conséquences des activités humaines et de l'augmentation des concentrations en CO<sub>2</sub> sur les écosystèmes marins. Figure extraite de <https://ocean-climate.org>

avec la création des premières ONG environnementales (WWF, Greenpeace, etc.), puis avec le premier sommet de la Terre à Stockholm en 1972 qui marqua le début des préoccupations à l'échelle internationale.

En 1988 se crée le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC) (en anglais *Intergovernmental Panel on Climate Change*, IPCC), organisme intergouvernemental ouvert à tous les pays membres de l'ONU et regroupant actuellement 195 États. Il a pour objectif de fournir aux décideurs des évaluations scientifiques régulières de l'état actuel des connaissances sur le changement climatique.

En 1992, au sommet de la Terre de Rio, ces préoccupations s'étendent à l'écologie et à la conservation de la biodiversité à grande échelle. Parmi les accords signés à l'issue de cette rencontre figure la Convention sur la diversité biologique, première du genre, à l'échelle mondiale, à être consacrée au maintien et à l'utilisation durable de la biodiversité (conserver la diversité; utiliser la diversité de façon durable; partager les avantages de la diversité de façon juste et équitable). Cet accord a très vite bénéficié d'une large acceptation : il a été signé sur place par plus de 150 gouvernements et compte désormais plus de 180 états membres. Il est entré en vigueur le 29 décembre 1993. En avril 2002, la Convention des parties s'est engagée à réduire sensiblement, d'ici à 2010, le taux de perte de biodiversité au niveau mondial, régional et national afin de contribuer à la réduction de la pauvreté et au bénéfice de toute vie sur Terre (Objectif 2010). Cet objectif a ensuite été approuvé par le Sommet mondial pour le développement durable et l'Assemblée générale de l'ONU et a été intégré en tant que nouvel objectif dans les objectifs du Millénaire pour le développement [Millennium Ecosystem Assessment, 2005]. Finalement, en 2010 la 65<sup>ème</sup> session de l'Assemblée générale de l'ONU officialise la création de l'IPBES (*Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* ou Plateforme intergouvernementale sur la biodiversité et les services écosystémiques), équivalent du GIEC mais appliqué à la biodiversité et regroupant 195 états. Très récemment en juin 2019, un atelier de l'IPBES s'est déroulé à Nouméa pour proposer des pistes d'adaptation du plan global au contexte Océanien. Les discussions se sont focalisées sur les moyens d'incorporer les connaissances et savoir-faire traditionnels pour la conservation [Payri & Vidal, 2019].

En 2020, se tiendra à Marseille le Congrès mondial de la nature de l'IUCN (*International Union for*

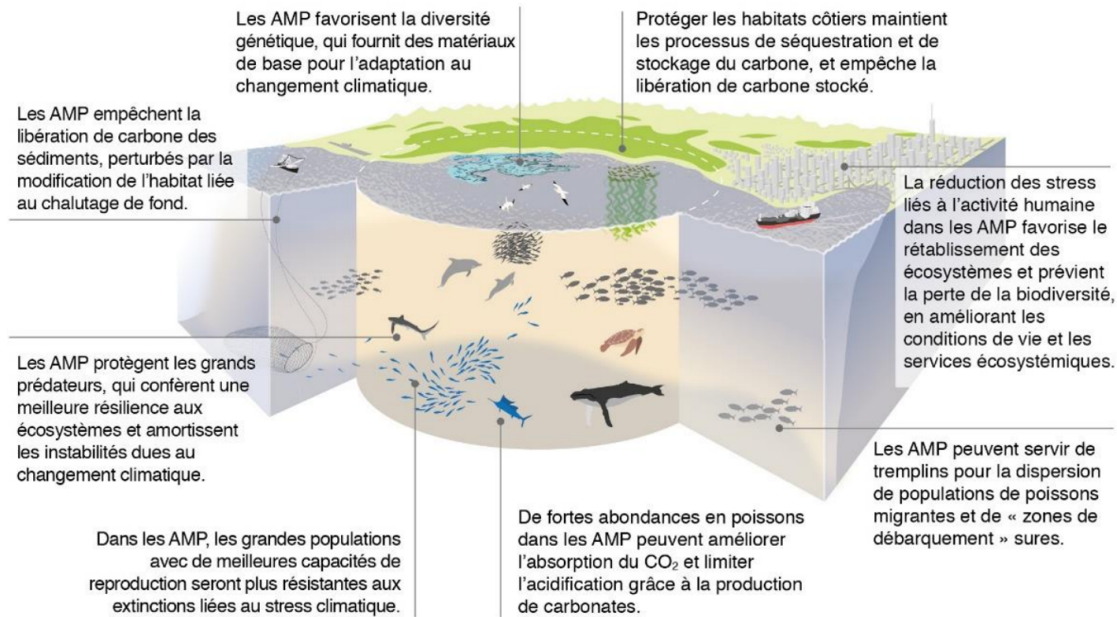


FIGURE 1.10 – schéma synthétique des avantages qu'offrent une AMP face au changement climatique. © Ivan Gromicho, KAUST

*Conservation of Nature* ou Union Internationale pour la conservation de la nature), annoncé comme le plus grand événement mondial consacré à la biodiversité. Il a pour principal objectif la mobilisation de tous les acteurs concernés par ce sujet à quelques mois de la COP15 de la biodiversité qui aura lieu en Chine et qui devrait adopter un nouveau cadre international pour la prochaine décennie. De nombreuses solutions pour préserver l'état de santé des écosystèmes marins ont été proposées au cours de ces différents sommets, nous en détaillerons deux qui incluent le micronecton : l'approche écosystémique des pêches et la mise en place d'Aires Marines Protégées (AMPs, ou *Marine Protected Areas* MPAs).

Nous avons vu précédemment que la pression de pêche affecte grandement les espèces marines, et pas uniquement les espèces exploitées, mais bien toute la structure de l'écosystème à travers les différentes interactions trophiques. La gestion écosystémique des pêches propose de minimiser les impacts de la pêche tout en maximisant la résilience des écosystèmes [Gascuel *et al.*, 2016; Worm *et al.*, 2009]. La mise en place réelle de cette approche nécessite la définition d'indicateurs concrets sur l'impact d'une pêcherie sur son écosystème. Pour cela il est nécessaire de développer des connaissances pertinentes sur les mécanismes et les processus écologiques qui façonnent les interactions prédateur-proie à l'échelle de l'écosystème [Christensen *et al.*, 1996; Koslow, 2009].

La mise en place d'AMPs est une autre solution très en vogue qui est fortement recommandée comme outil de conservation des espèces [Christie *et al.*, 2017; Davidson & Dulvy, 2017; Ehler & Douvère, 2009]. La convention sur la diversité biologique définit une AMP comme "Toute zone dans ou à proximité du milieu marin, ainsi que la flore, la faune et les caractéristiques historiques et culturelles associées, qui a été délimitée par voie législative ou par d'autres moyens comme la coutume, de sorte que sa biodiversité marine et/ou côtière bénéficie d'un niveau de protection supérieur à son environnement". Il a été avancé que les AMP pouvaient être un moyen efficace de conservation des espèces contre le changement climatique [Roberts *et al.*, 2017] à travers notamment leur rôle de stockage et de source potentielle de diversité génétique, de carbone, de prédateurs, de micronecton ... (Figure 1.10). Cependant, une AMP peut prendre des formes très différentes et la présence d'une AMP ne garantit pas forcément

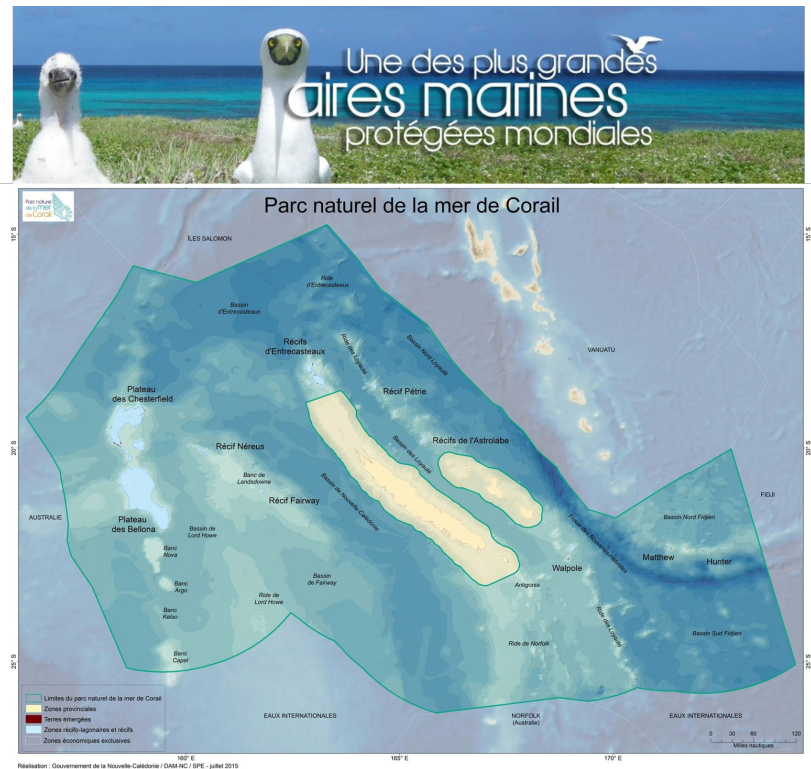


FIGURE 1.11 – Bannière et carte du parc naturel de la mer de Corail. Extrait de <https://mer-de-corail.gouv.nc/fr>.

une protection totale des espèces s’y trouvant [Horta e Costa *et al.*, 2016]. Par ailleurs, dû à un manque de connaissances des écosystèmes, il a été montré qu’à échelle globale, ces AMP ne couvraient pas les zones de fortes biodiversités [Lindgren *et al.*, 2018]. Plus récemment, des AMP pélagiques ont été mises en place pour la conservation d’espèces pélagiques telles que les thons, avec des avis scientifiques mitigés quant au niveau réel d’efficacité pour la protection [Davis *et al.*, 2012; Game *et al.*, 2009; Kaplan *et al.*, 2010].

Dans le Pacifique sud-ouest, la plus grande aire marine protégée française a vu le jour en Nouvelle-Calédonie en 2014 : le parc naturel de la mer de Corail. Sa surface recouvre toute la zone économique exclusive (ZEE) de la Nouvelle-Calédonie en dehors des eaux provinciales (Figure 1.11). Selon la définition donnée plus haut dans cette section, la zone est en effet délimitée par voie législative et représente donc bien, en ce sens, une Aire Marine Protégée. Cependant, le niveau de protection qui s’y applique est très variable, aujourd’hui seules de petites zones sont classées en réserve intégrale.

## 1.2 Le parc marin de la mer de Corail, un écosystème riche dans une région oligotrophe

Les paragraphes qui suivent s’attacheront à décrire de manière succincte le milieu physique et les espèces du parc de la mer de Corail. Nous décrirons notamment les connaissances scientifiques manquantes et qui sont nécessaires pour développer une bonne gestion de ce milieu.

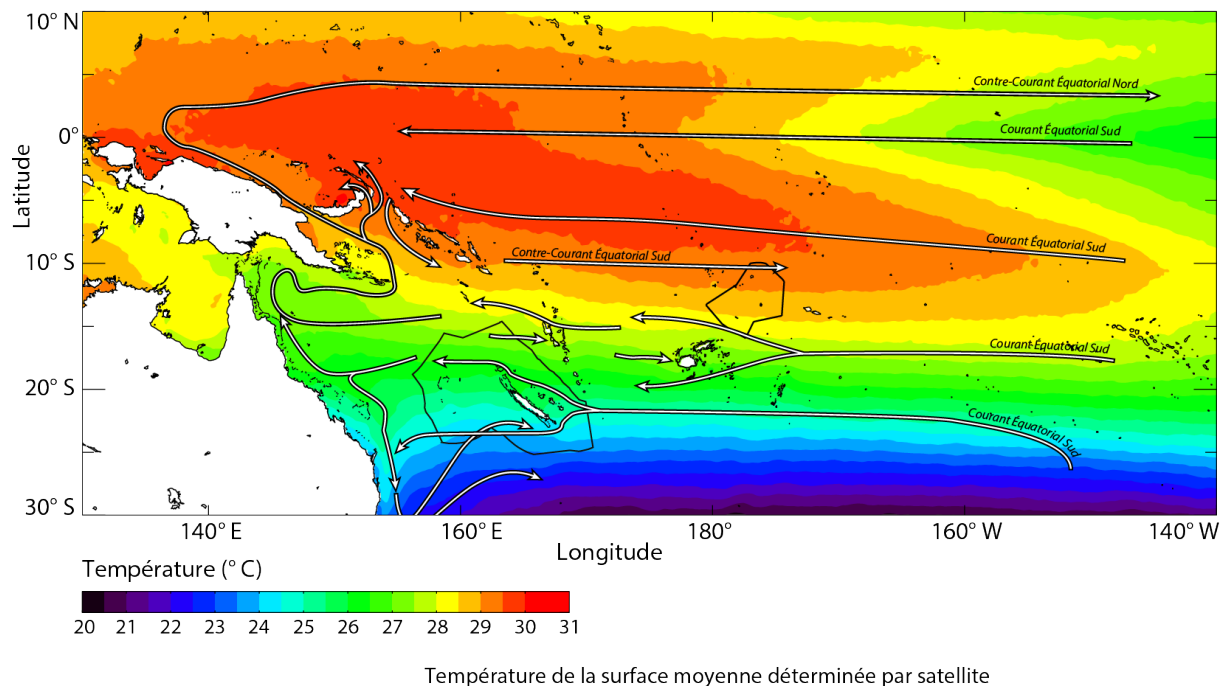


FIGURE 1.12 – Température de surface moyenne (1998-2015) du Pacifique et principaux courants de surface. Les zones en noir matérialisent les ZEE de Nouvelle-Calédonie (dans l'ouest) et de Wallis et Futuna (au centre). Figure © CPS.

### 1.2.1 La circulation océanique du Pacifique sud

A l'échelle du Pacifique les eaux de surface sont plus chaudes dans l'ouest et plus froide dans l'est, créant ainsi un gradient longitudinal de température. La *warm pool* ou encore piscine d'eau chaude qui se situe au large des côtes de Papouasie-Nouvelle-Guinée est la région où l'on retrouve les eaux les plus chaudes (29-30°C), tandis que le long des côtes du Pérou la température moyenne est d'environ 17-18°C. On observe également un gradient latitudinal, avec des températures de l'ordre de 30°C au niveau de l'équateur, de 25°C au niveau de la Nouvelle-Calédonie et de 18°C au niveau de la Nouvelle-Zélande (Figure 1.12). La circulation de surface dans l'océan Pacifique est principalement générée par les vents d'est communément appelés « alizés » [Gasparin *et al.*, 2011]. La circulation océanique de grande échelle du Pacifique sud est dominée par un courant de surface le courant équatorial sud (SEC en anglais) qui s'écoule d'est en ouest, avec des contre-courants qui s'écoulent dans le sens inverse (Figure 1.12). À l'ouest du bassin, au contact des côtes australiennes, le courant équatorial sud se divise en deux branches, une branche dirigée vers le sud, appelée courant est australien, et une branche qui remonte vers le nord vers la Papouasie-Nouvelle-Guinée.

L'ensemble de ces courants du Pacifique Sud délimitent le Gyre du Pacifique sud, en rotation anticyclonique ce qui maintient des thermocline et nutricline profondes (Figure 1.13). Ainsi, les concentrations en nutriments dissous sont très faibles, à tel point que le Pacifique sud est connu pour être le grand désert biogéochimique des océans avec des concentrations en nutriments les plus faibles du monde [Claustre *et al.*, 2008], ce qui contraste avec les zones plus riches en bordure de Gyre (Figure 1.13). Dans ce grand Gyre du Pacifique Sud, une gradation se fait entre des eaux ultra-oligotrophes, avec des productions < 50 gC/m<sup>2</sup>/jour telles que trouvées dans la ZEE de Wallis et Futuna au centre du Gyre, et des eaux plus riches sur les bords du Gyre telles que les eaux Néo-Calédonienne.

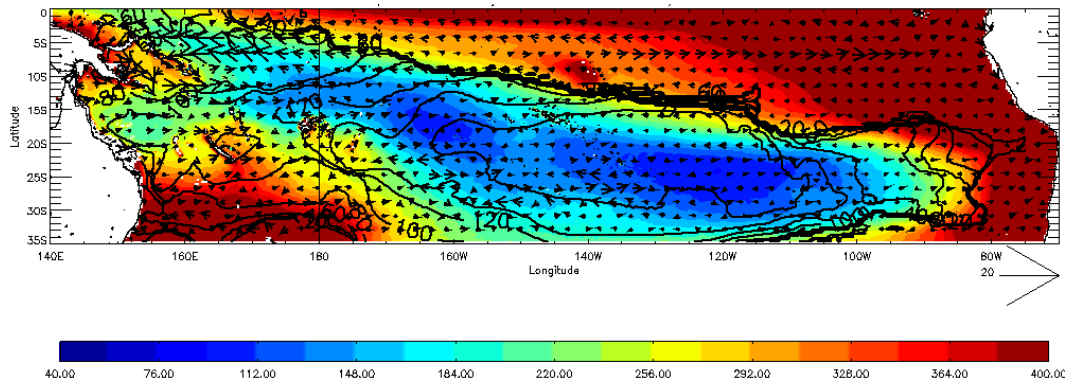


FIGURE 1.13 – Production primaire nette de surface moyenne du Pacifique Sud en couleurs. Les flèches représentent les courants géostrophiques et les traits pleins, la profondeur de la nitracline (ligne de concentration en nitrates égale à  $1 \text{ gC/m}^2/\text{jour}$ ). La partie bleue matérialise la position du Gyre. Production primaire extraite de <https://www.science.oregonstate.edu/ocean.productivity/>.

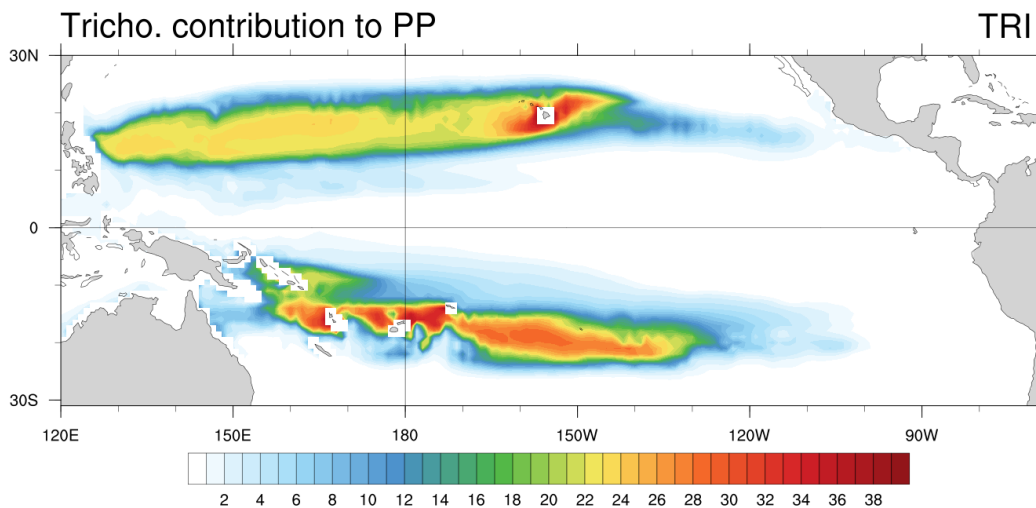


FIGURE 1.14 – Contribution relative (en pourcentage) du *Trichodesmium* sp. à la production primaire totale. Figure extraite de [Dutheil et al. \[2018\]](#).

Le Pacifique sud-ouest reste une région oligotrophe où la croissance du phytoplancton est majoritairement limitée par l'azote. La présence de nombreuses espèces de phytoplancton diazotrophes permet néanmoins d'enrichir légèrement ce milieu naturellement pauvre [[Berthelot et al., 2015a, 2017](#); [Bonnet et al., 2016](#)]. En effet, les espèces diazotrophes fixent le diazote ( $\text{N}_2$ ) atmosphérique dissous dans l'océan et excrètent en retour de l'azote bio-assimilable (principalement sous forme d'ammonium  $\text{NH}_4^+$ , essentiel dans la croissance du phytoplancton [[Berthelot et al. \[2015b\]](#)]) par les autres espèces phytoplanctoniques. La multitude d'îlesensemencent le milieu en fer, élément essentiel aux espèces diazotrophes [[Dutheil et al., 2018](#); [Shiozaki et al., 2014](#)]. Ainsi, cette partie du Pacifique sud, la mer de Corail, est moins oligotrophe que les eaux situées plus à l'est dans le centre du grand gyre [[Ceccarelli et al., 2013](#); [Menkes et al., 2015](#)]. Une étude de modélisation a permis d'estimer à 30% la part de production primaire due à la présence de ces diazotrophes (Figure 1.14) [[Dutheil et al., 2018](#)]. Dans le même temps [Bonnet et al. \[2017\]](#) ont montré que les plus forts taux de fixation mesurés à l'échelle du globe se situaient dans le Pacifique sud-ouest. C'est dans ce contexte biogéochimique que se situe la Nouvelle-Calédonie.

TABLEAU 1.3 – Caractéristiques des masses d'eau autour de la Nouvelle-Calédonie, avec  $\sigma$  la densité relative définie comme la densité absolue moins 1000, T la température, S la salinité, O<sub>2</sub> l'oxygène et la profondeur moyenne de la couche dans la ZEE. TSW : *Tropical Surface Water*; SPTWS : *South Pacific Tropical Water South*; SPTWN : *South Pacific Tropical Water North*; WSPCW : *Western South Pacific Central Water*; AAIW : *Antarctic Intermediate Water*. Tableau adapté de Gasparin *et al.* [2014].

|   | Surface | Upper Thermocline |       | Lower Thermocline | Intermediate |
|---|---------|-------------------|-------|-------------------|--------------|
|   | TSW     | SPTWN             | SPTWS | WSPCW             | AAIW         |
| $\sigma$ (kg.m <sup>-3</sup> )          | >24     | ~24.5             | ~25.3 | ~26.3             | ~27          |
| T (°C)                                  | 28      | 22                | 19.5  | 14.5              | 5.5          |
| S                                       | 34.5    | 35.9              | 35.65 | 35.25             | 34.45        |
| O <sub>2</sub> (μmol.kg <sup>-1</sup> ) | 200     | 120               | 175   | 180               | 180          |
| Profondeur (m)                          | 40      | 220               | 130   | 360               | 530          |

### 1.2.2 Le milieu physique autour de la Nouvelle-Calédonie

La Nouvelle-Calédonie se situe dans le Pacifique sud-ouest entre l'Australie et le Vanuatu, dans le sud de la mer de Corail. Un zoom autour de la Nouvelle-Calédonie fait apparaître une circulation océanique plus complexe qu'à grande échelle (Figure 1.15). Les eaux superficielles de la ZEE sont sous l'influence de deux grands systèmes de courants très distincts. Au sud, le STCC (*Sub Tropical Counter Current*), branche du Courant Est Australien (EAC), amène de l'eau froide et salée tandis que de l'eau d'origine équatoriale, chaude et peu salée, pénètre au nord de la ZEE par le biais du Courant Equatorial Sud (SEC) [Bonvallet *et al.*, 2013; Cravatte *et al.*, 2015; Kessler & Cravatte, 2013]. Ce dernier se divise en deux en arrivant sur la grande terre (voir Figure 1.16 pour la localisation de la grande terre) : une branche monte vers le nord et crée le NCJ (*North Caledonian Jet*) et possiblement une branche part vers le sud : le SCJ (*South Caledonian Jet*). Sur la côte est, une zone de *downwelling* (plongée des eaux chaudes de surface) est associée à la convergence géostrophique des eaux à la côte [Cravatte *et al.*, 2015; Marchesiello *et al.*, 2010]. Sur la côté ouest, les courants, associés à des forts alizés ponctuels, créent parfois une zone d'*upwelling* (remontée d'eaux froides et riches en nutriments) dans la partie sud de la côte [Alory *et al.*, 2006; Cravatte *et al.*, 2015; Marchesiello *et al.*, 2010]. L'*upwelling*, particulièrement présent pendant la saison chaude entre novembre et avril est visible sur la température de surface et pourrait enrichir localement le milieu pélagique en nutriments jusqu'à une centaine de kilomètre au large de la barrière de corail mais de façon intermittente [Hénin & Cresswell, 2005].

On retrouve principalement 5 masses d'eau dans la ZEE qui se différencient par leur densité et par leur concentration en oxygène (Table 1.3). En surface, on retrouve majoritairement la TSW (*Tropical Surface Water*) qui est chaude et oxygénée et qui arrive de l'est. Aux alentours de la thermocline, deux masses d'eau aux caractéristiques bien différentes sont présentes : la SPTWN (*South Pacific Tropical Water North*) qui est une masse d'eau chaude, salée et relativement peu oxygénée venant du Pacifique est, vers la Polynésie; et la SPTWS (*South Pacific Tropical Water South*) qui est plus froide, moins salée et plus oxygénée. Cette dernière masse d'eau provient de la zone de convergence subtropicale qui est proche de la Nouvelle-Zélande [Gasparin *et al.*, 2014]. En dessous, entre 300 et 400 mètres, les eaux de "basse thermocline" sont composées majoritairement par la WSPCW (*Western South Pacific Central Water*), masse d'eau froide arrivant du sud. Enfin, sous la thermocline la masse d'eau AAIW (*Antarctic Intermediate Water*) est majoritaire et est composée d'eau froide et peu salée arrivant d'Antarctique.

Enfin, la zone économique de Nouvelle-Calédonie est également sujette à une forte activité tour-



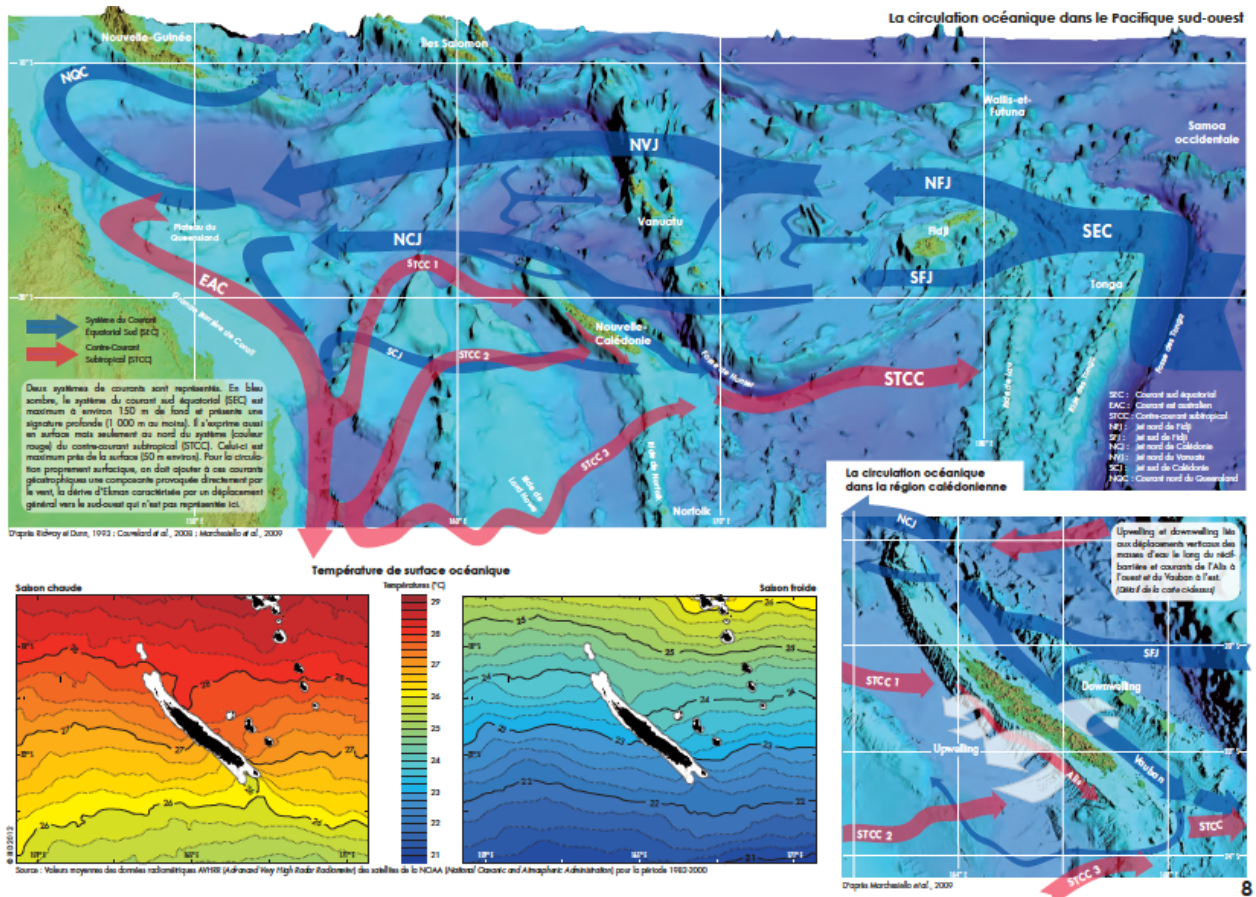


FIGURE 1.15 – Cartes de référence du Pacifique sud-ouest (haut) et de la Nouvelle-Calédonie (bas) extraite de [Bonvallet et al. \[2013\]](#). Les flèches bleues représentent la circulation des eaux situées entre la surface et la thermocline (environ 120m) et les flèches rouges représentent la circulation de surface lorsque cette dernière est différente des flèches bleues. Les abréviations sont : SEC (*South Equatorial Current*), NVJ (*North Vanuatu Jet*), NCJ et SCJ (*North and South Caledonian Jet*), STCC (*Sub Tropical Counter Current*) et EAC (*East Australian Current*). Les deux cartes en bas à gauche représentent la température moyenne de surface en saison chaude (décembre à mai, gauche) et en saison froide (juin à novembre, droite).

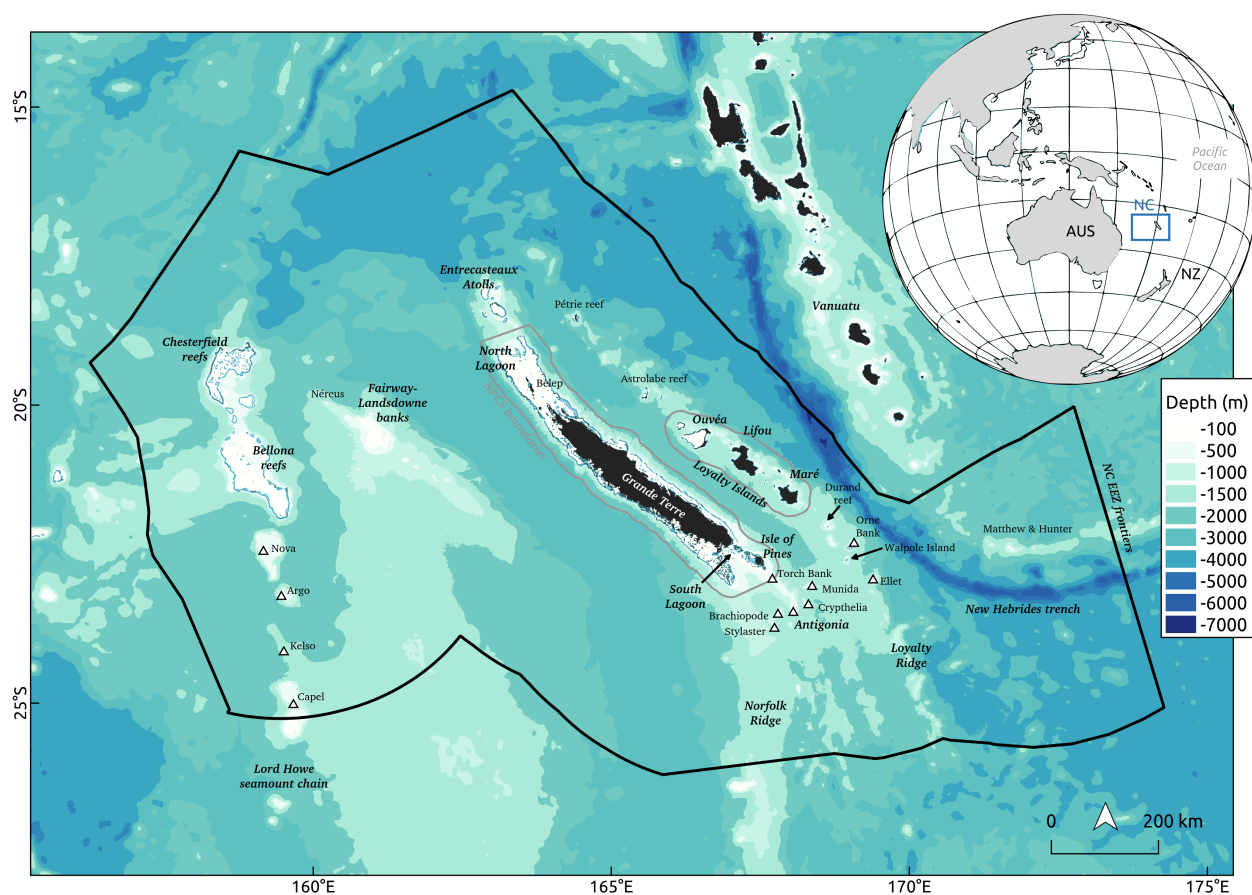


FIGURE 1.16 – Carte de la zone économique de Nouvelle-Calédonie. Les zones discutées au cours de cette thèse sont localisées, et les triangles gris représentent certains monts sous-marins. Carte extraite de la thèse de Solène Derville [2018].

billonnaire [Keppeler *et al.*, 2018]. Au nord de la zone, ces tourbillons dits de méso-échelle, de l'ordre de la centaine de kilomètres, sont épars et de courte durée, et n'affectent que les 200 premiers mètres de la colonne d'eau. Au sud de la zone par contre, le cisaillement latéral entre le STCC et SCJ, crée des tourbillons plus nombreux et plus énergiques. Les tourbillons de méso-échelle sont omniprésents, avec des durées de vie d'environ 5 mois et affectent les propriétés de l'eau jusqu'à une profondeur d'au moins 500 mètres et contribuent au mélange des eaux comprises entre la thermocline et la surface.

Comme décrit en section 1.2.1, la température moyenne de l'eau de surface est d'environ 25°C, mais oscille entre 27°C l'été (entre décembre et mai) et 22°C l'hiver (entre juin et novembre) (Figure 1.15). La grande terre joue un rôle de barrière physique à la circulation des masses d'eau, et un décalage des températures de surface est présent entre la côte est et la côte ouest avec des températures en moyenne plus chaude sur la côte est. C'est pendant la saison froide et dans le sud que la concentration en chlorophylle est plus forte en lien avec la structure verticale des eaux de surface. En hiver, la colonne d'eau est peu stratifiée et donc plus homogène avec probablement plus de nutriments dans la couche euphotique. En été, elle est fortement stratifiée avec des eaux globalement plus pauvres sauf durant les événements ponctuels d'*upwelling* du sud-ouest calédonien.

Tous ces paramètres océanographiques sont influencés par le phénomène ENSO (*El Niño Southern Oscillation*) même si son influence est moins forte qu'à l'équateur. Les effets d'ENSO en Nouvelle-Calédonie sont inversés par rapport au niveau du Pacifique équatorial. Les eaux sont globalement plus froides et plus productives pendant *El Niño* et inversement pendant *La Niña* [Dandonneau & Gohin, 1984; Delcroix & Lenormand, 1997; Radenac *et al.*, 2012]. Le signal reste cependant limité avec des baisses de température de surface d'en moyenne 0.5°C dans la ZEE et des vents légèrement accru durant *El Niño*.

La bathymétrie de la ZEE de Nouvelle-Calédonie est complexe, avec une grande variété de formations. On y retrouve notamment trois rides continentales (la ride de Lord Howe et la ride de Fairway à l'ouest de la grande terre, et la ride de Norfolk qui est dans le prolongement de la grande terre) des rides volcaniques et des bassins sédimentaires (comme le grand bassin de la Nouvelle-Calédonie juste à l'ouest de la grande terre). Dans ces trois formations, de nombreux monts sous-marins sont présents (Figure 1.16). On retrouve enfin une fosse de subduction dans l'est de la grande terre : la fosse des Nouvelles Hybrides qui descend jusqu'à 7000 mètres. Des récifs isolés sont présents en grand nombre dans le milieu océanique, on notera notamment : les récifs de Chesterfield dans le nord-ouest, le plateau de Bellona au sud de ces derniers, les atolls d'Entrecasteaux au nord de la Grande Terre, le récif Pétrie juste à l'est de ces derniers, et les récifs d'Astrolabe au nord des îles Loyautés.

### 1.2.3 Un point de rencontre de nombreuses espèces

La bathymétrie complexe ainsi que les nombreux récifs éloignés offrent un nombre incroyable d'habitats différents pour les espèces évoluant dans ce milieu pélagique. Par ailleurs, le lagon de Nouvelle-Calédonie est le plus grand lagon fermé au monde et est également très diversifié [Garcia *et al.*, 2018]. Les échanges entre ce milieu lagunaire et le milieu pélagique sont nombreux, avec par exemple un apport de nutriments du lagon vers l'océan, ou un passage des larves de poissons récifaux par une phase pélagique [Allain *et al.*, 2012] (Figure 1.17). La "neige pélagique" permet également d'enrichir le milieu benthique. Les nombreux monts sous-marins abritent également des communautés encore mal-connues.

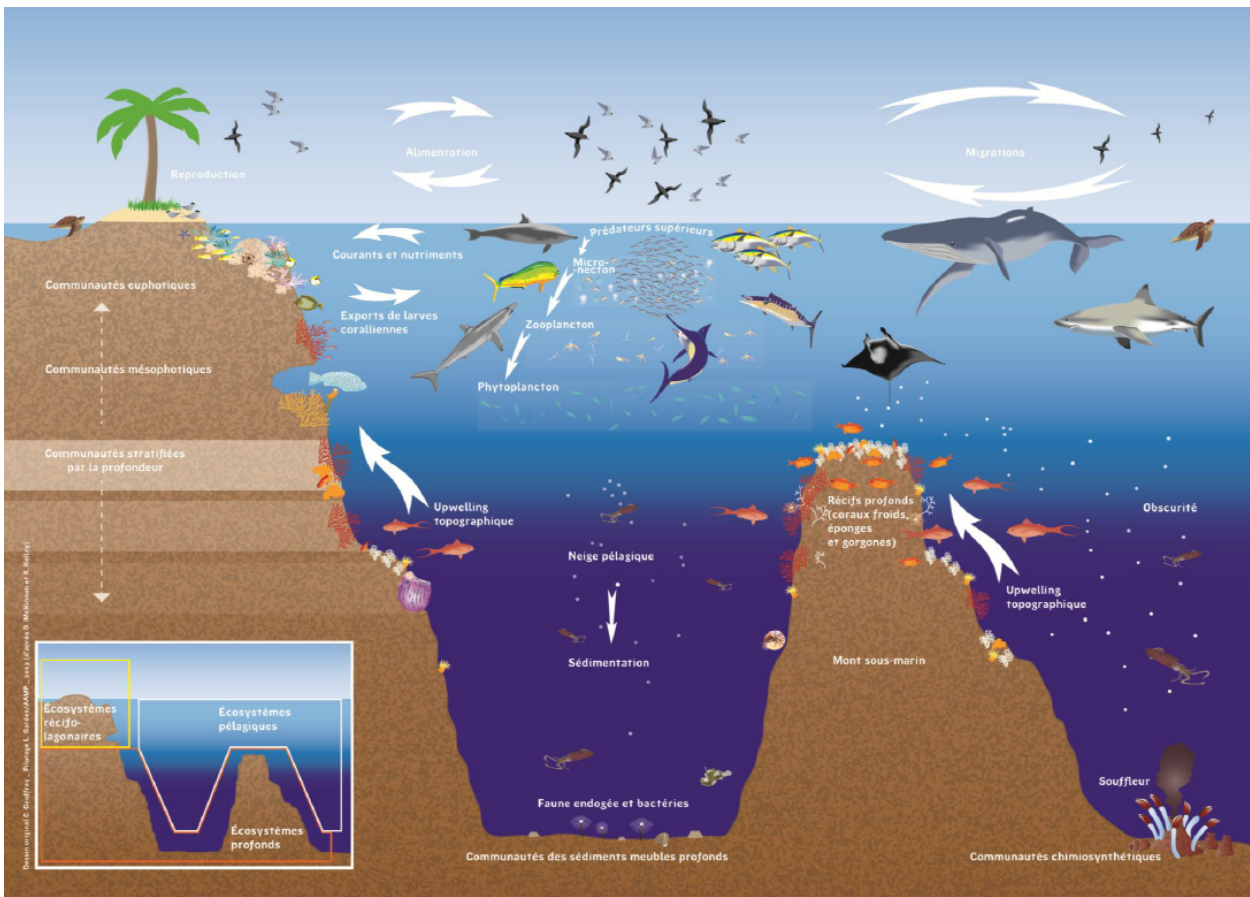


FIGURE 1.17 – Schéma montrant les écosystèmes récifo-lagonaire, pélagique et profonds et les échanges autour de la Nouvelle-Calédonie. Figure extraite de l'Analyse Stratégique Régionale de Nouvelle-Calédonie [Gardes *et al.*, 2014].

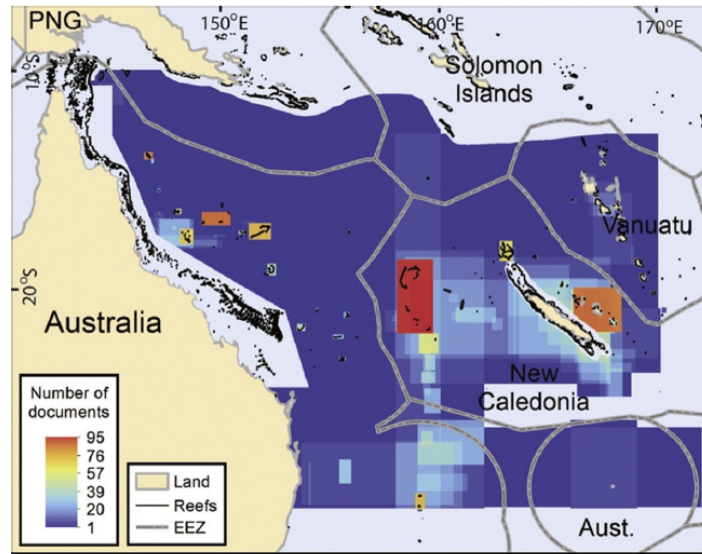


FIGURE 1.18 – Carte montrant spatialement le nombre d'études publiées dans la mer de Corail. Extraite de [Ceccarelli et al. \[2013\]](#).

La méga faune est particulièrement riche dans la zone [[Laran et al., 2016b](#); [Tittensor et al., 2010](#); [Worm et al., 2003](#)]. On y retrouve de nombreuses espèces emblématiques comme les oiseaux marins [[Borsa et al., 2010, 2014, 2015](#); [Weimerskirch et al., 2017](#)], raies, requins [[Bakker et al., 2017](#); [Boussarie et al., 2018](#); [Ceccarelli et al., 2013](#)], tortues et cétacés [[Derville et al., 2018](#); [Garrigue et al., 2015](#)]. Les ressources marines exploitées sont majoritairement composées du thon blanc et du thon jaune, complétées par le thon obèse, la bonite à ventre rayée, la dorade coryphène, les poissons à rostre pour en citer quelques-unes [[WCPFC, 2018](#)]. Certaines espèces comme le puffin Fouquet ou la baleine à bosse ne sont présentes que pendant leur saison de reproduction, stade critique du cycle de vie, alors que d'autres espèces sont présentes toute l'année. Globalement, la mer de Corail reste relativement peu étudiée en comparaison d'autres zones, et les études existantes se concentrent sur des petites régions comme les Chesterfields, comme le montre le répartition spatiale des articles sur la zone (Figure 1.18).

Toutes ces espèces se partagent les ressources alimentaires disponibles dans la zone. Les espèces de micronecton sont elles aussi très diversifiées d'après des études de contenus stomacaux de leurs prédateurs [[Allain et al., 2012](#); [Olson et al., 2014](#); [Williams et al., 2014](#); [Young et al., 2010](#)] et de chalutages pélagiques [[Grandperrin et al., 1999](#); [Menkes et al., 2015](#); [Young et al., 2011](#)]. Une étude globale a classé le milieu mésopélagique de la mer de Corail comme une région dominée par les poissons lanternes [[Sutton et al., 2017](#)], en accord avec les précédents résultats [[Grandperrin, 1975](#); [Vourey et al., 2017](#)] qui avaient identifié les Gonostomatidae, Sternoptychidae, Myctophidae (poissons lanternes) et Scopelarchidae comme les familles dominantes dans la mer de Corail (Figure 1.19). Globalement, les espèces présentes dans la région sont relativement bien caractérisées, cependant deux synthèses regroupant toutes les connaissances de la région sur le milieu pélagique ont identifié le micronecton comme le maillon tropique le plus méconnu [[Ceccarelli et al., 2013](#); [Gardes et al., 2014](#)]. Ce constat local rejoint un constat global sur le manque crucial de connaissances concernant le micronecton [[Hidalgo & Browman, 2019](#); [St. John et al., 2016](#)].

Une première étude sur la dynamique du micronecton en Nouvelle-Calédonie a émis l'hypothèse

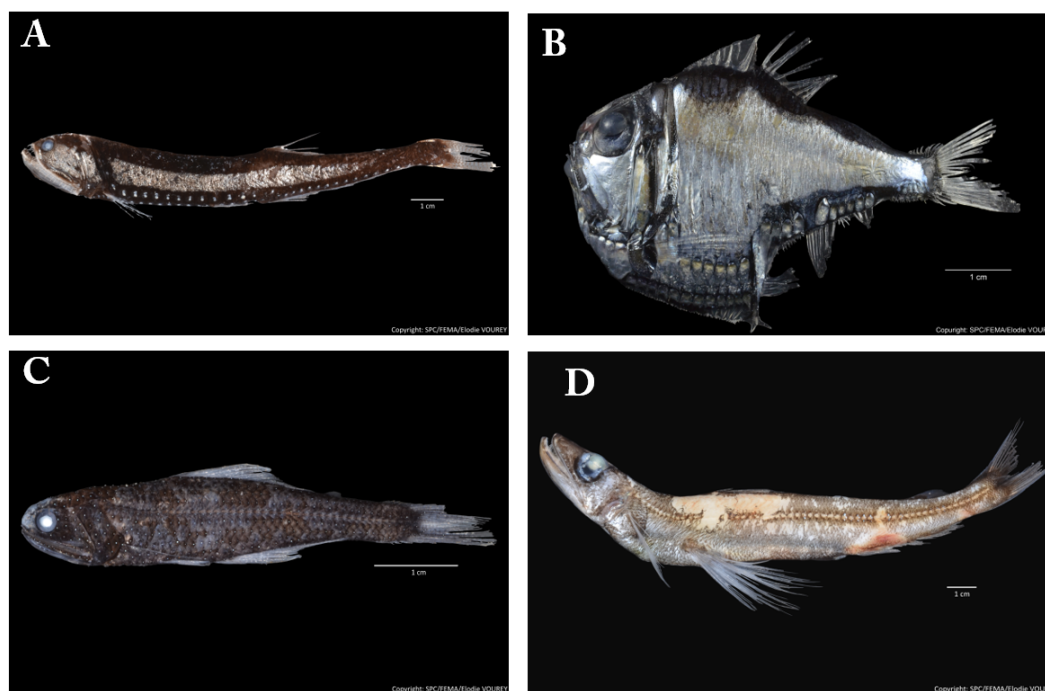


FIGURE 1.19 – Illustration des différentes familles présentes dans la zone avec une espèce exemple par famille : Gonnostomatidae (A, *Sigmops elongatus*), Sternoptychidae (B, *Argyropelecus aculeatus*), Myctophidae (C, *Scopelopsis multipunctatus*) et Scopelarchidae (D, *Benthalbella linguoidens*). Toutes les photos sont © Elodie Vourey/CPS.

d'une plus forte abondance de micronecton dans le sud que dans le nord mais n'a pas pu conclure sur la saisonnalité avec des réponses contradictoires entre les différentes méthodes d'échantillonnages [Menkes *et al.*, 2015]. Une compréhension de la dynamique spatiale et temporelle du micronecton est donc manquante dans la ZEE de Nouvelle-Calédonie, connaissance essentielle pour mieux appréhender la dynamique de tous les prédateurs supérieurs qui en dépendent. Une description plus détaillée des espèces présentes, notamment avec une quantification de leur abondance, est également importante pour comprendre les changements de communauté qui pourraient influencer les prédateurs et aider à la gestion du milieu.

Par ailleurs, la profondeur de migration du micronecton pendant le jour a été mesurée entre 500 et 600 mètres par deux études globales [Bianchi & Mislán, 2016; Proud *et al.*, 2018a]; une étude plus fine de la dynamique journalière de ces migrations serait également intéressante. Enfin, comme identifié en section 1.1.4, l'impact que le changement climatique pourrait avoir sur le micronecton est pour le moment très peu étudié, majoritairement dû à un manque de données d'observation. Il est donc nécessaire de regrouper au maximum les données disponibles pour avoir des séries temporelles aussi longues que possible et ainsi avoir une idée de l'évolution temporelle de ce groupe.

#### 1.2.4 La gestion actuelle

Comme annoncé en section 1.1.4, la zone pélagique de la Nouvelle-Calédonie est entièrement intégrée dans le parc marin naturel de la mer de Corail depuis 2014. Depuis 2018, des réserves intégrales ont été mises en place autour de certains récifs éloignés : récif des Chesterfields, récif de Pétrie, récif d'Astrolabe et dans les atolls d'Entrecasteaux (voir Figure 1.16 pour la localisation). Les zones protégées intégralement s'étendent jusqu'à l'isobathe des 1000 mètres. Cependant, les zones pélagiques protégées

intégralement sont encore relativement limitées spatialement. Des informations scientifiques solides sont maintenant nécessaires pour délimiter d'autres zones d'intérêt prioritaire pour la conservation des espèces et de tout l'écosystème pélagique en général.

### 1.3 Les questions scientifiques de la thèse

Comme nous l'avons vu tout au long de cette introduction, les écosystèmes pélagiques ont un fonctionnement très complexe, notamment au niveau des interactions trophiques. La variabilité des échelles spatio-temporelles auxquelles ces processus interviennent rajoute une complexité difficile à appréhender. Cependant, une bonne compréhension des processus contrôlant le milieu et les espèces est nécessaire pour la mise en place de moyens de gestion efficace quant à la protection des espèces. Dans le monde et autour de la Nouvelle-Calédonie, le maillon du réseau trophique pélagique le moins connu est le micronecton. Dans un objectif de compréhension du fonctionnement de l'écosystème, nous avons donc choisi dans cette thèse de nous concentrer majoritairement sur son rôle en répondant aux questions suivantes :

- Quelle est la dynamique spatiale et temporelle du micronecton dans la ZEE de Nouvelle-Calédonie?
- Quels facteurs environnementaux contrôlent cette dynamique?
- Quelles sont les espèces qui composent le micronecton?
- Est-il possible de quantifier les dynamiques spatiotemporelles au niveau spécifique?
- Est-il possible de prédire le devenir du micronecton dans un contexte de changement climatique?
- Comment le micronecton influence par sa dynamique temporelle et sa distribution spatiale les prédateurs supérieurs?
- Comment les informations collectées peuvent servir pour la gestion du parc marin de la mer de Corail?

Pour répondre à ces 7 questions, plusieurs outils d'observation et d'analyse ont été utilisés, les deux parties suivantes ont pour objectif de les décrire succinctement. Nous finirons cette introduction générale par présenter le plan de la thèse.

### 1.4 Les moyens d'étude du micronecton

Comprendre le fonctionnement et estimer la diversité du micronecton dépend fortement de notre capacité à accéder aux espèces. Comme décrit au cours de cette introduction, le domaine pélagique est vaste spatialement et verticalement et les capacités d'étude du micronecton dépendent fortement de l'échantillonnage *in situ*. Pour étudier ce micronecton plusieurs méthodes s'offrent à nous, qui se séparent en deux grands groupes : méthodes d'observation directes dans leur milieu et modélisations. L'observation permet d'accéder à un certain nombre de paramètres *in situ*, aux résolutions spatiale et temporelle accessibles par la méthode utilisée. Ces observations sont limitées par la technique qui peut être biaisée comme nous le verrons plus loin, par leur coût et le temps nécessaire pour les réaliser. Ces observations peuvent se faire avec prélèvement (méthode intrusive) ou sans prélèvement biologique

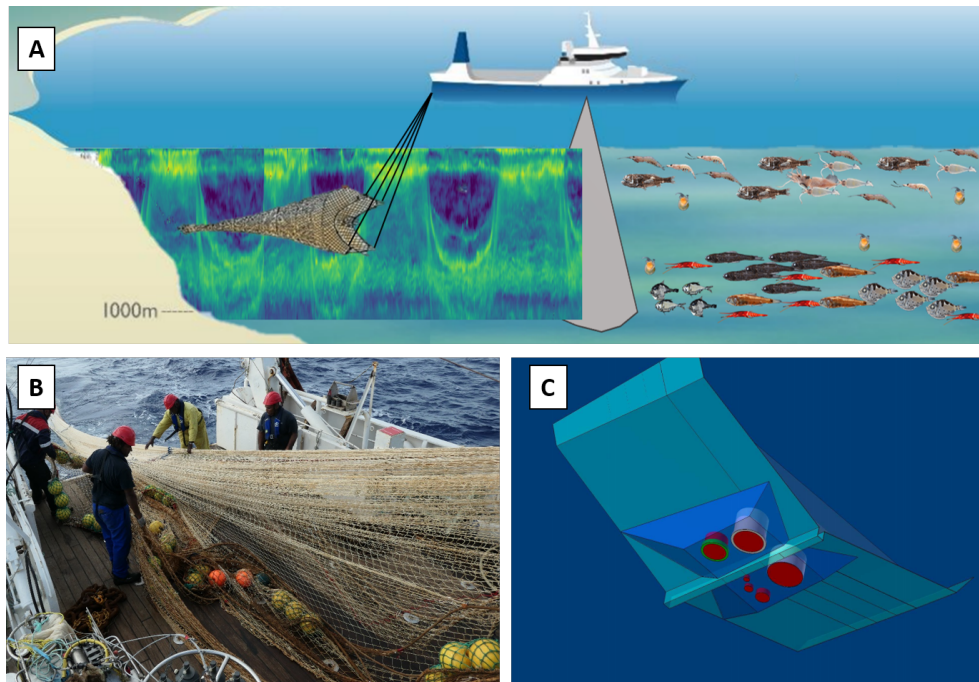


FIGURE 1.20 – Figure illustrant les moyens d’échantillonnage du micronecton avec (A) schématiquement la position d’un chalut et d’un cône d’enregistrement acoustique par rapport aux couches d’organismes micronectoniques inspirée d’une figure du projet MESOPP [Proud & Brierley 2018, <http://www.mesopp.eu/project-details/>]; (B) une photo du chalut pélagique du navire océanographique de l’IRD : l’Alis; et (C) un schéma du positionnement des bases acoustiques (émetteur+transducteur) sous la coque de l’Alis.

(méthode non intrusive). Ces données d’observation à la mer sont ponctuelles dans le temps et dans l’espace. Elles présentent un certain nombre de biais et d’incertitudes que nous allons présenter.

Par contraste, la modélisation permet d’accéder à des données prédites en continu spatialement et temporellement. Cependant, ces données reposent sur de multiples hypothèses de modélisation. Par ailleurs, les données prédites ont une erreur associée difficile à estimer car souvent les prédictions ne sont pas directement comparables aux observations. Nous allons voir pourquoi dans les paragraphes qui suivent. Nous ne présenterons que les outils qui ont servi dans cette thèse, sans faire une description exhaustive de tous les moyens d’observation et de modélisation du micronecton qui existent.

### 1.4.1 Les chaluts

La méthode traditionnelle d’échantillonnage du micronecton est le chalut pélagique (Filet schématisé sur la Figure 1.20A et photo sur la Figure 1.20B). Cette méthode a pour grand avantage de permettre l’identification taxonomique des individus capturés, ainsi qu’un dénombrement direct de l’abondance et de la biomasse par espèce. Cependant, le chalutage a également plusieurs inconvénients. Le phénomène d’évitement peut créer un fort biais, avec une surreprésentation des espèces à faible capacité natatoire et une sous-représentation des espèces capables d’éviter le chalut. En moyenne, le phénomène d’évitement a pour conséquence une sous-estimation de la biomasse [Kaartvedt *et al.*, 2012; Kloser *et al.*, 2009]. Par ailleurs, le maillage choisi sélectionne également certaines espèces et surtout une gamme de tailles, ce qui biaise l’estimation de biomasse. Enfin, le chalutage est un processus pouvant être long à mettre en place, notamment pour chaluter à des profondeurs dépassant les 200 mètres. A titre d’exemple,



sur le navire océanographique de l'IRD basé à Nouméa, l'Alis, un chalutage à 500 mètres de 30 minutes prend plus de deux heures de mise en œuvre. Cette complexité de mise en place rend le nombre de chaluts limités dans le temps et dans l'espace, cela rend difficile également la capture d'organismes repérés à un temps  $t$ , qui peuvent se disperser ou changer de profondeur au cours de l'opération. Pour toutes ces raisons, avoir une vue d'ensemble de la distribution de l'abondance du micronecton reste compliqué avec l'aide du chalut seul.

### 1.4.2 L'acoustique active

L'acoustique est l'outil essentiel utilisé dans cette thèse pour comprendre les dynamiques du micronecton. Pour bien comprendre les forces et faiblesses des différents résultats, il est nécessaire de comprendre les bases de son fonctionnement. Ces dernières sont décrites succinctement dans les paragraphes suivant, en se basant sur l'ouvrage de référence : [Simmonds & MacLennan \[2005\]](#).

On distingue deux types d'acoustique : les systèmes acoustiques actifs qui émettent des ondes sonores et reçoivent les signaux réfléchis, et l'acoustique passive qui écoute (via un hydrophone) les sons émis naturellement dans le milieu, comme par des mammifères marins ou par des phénomènes physiques (pluie, séisme) ou des sons anthropiques (passage d'un sous-marin...). On ne parlera dans ce document que d'acoustique active et ce ne sera plus précisé dans la suite du manuscrit. L'acoustique est aujourd'hui un outil largement répandu pour l'étude du milieu pélagique, mais son histoire débute dans les années 1830 avec les premières mesures de célérité du son dans l'eau. Cent ans plus tard, le premier échogramme de poissons est enregistré avec une seule fréquence et un seul faisceau. Aujourd'hui, les sonars ont plusieurs fréquences voire sont large bande, ils peuvent être multi faisceaux et leur capacité à mettre en évidence aussi bien les structures physiques, les échelons trophiques intermédiaires que les prédateurs en font des outils clefs pour les approches écosystémiques.

### Principes généraux

Le principal avantage de l'acoustique est sa large couverture spatiale avec une résolution fine : le signal acoustique émis par un sonar (pour *sound navigation and ranging*) est enregistré en continu le long du trajet des bateaux, avec une cadence d'émission élevée (typiquement, toutes les secondes). La portée verticale maximale du signal dépend de l'engin acoustique et de sa fréquence, du navire et de la météo, mais on peut atteindre de l'ordre de 1000 mètres à 38 kHz avec une résolution verticale de la donnée brute d'une dizaine de centimètres. De plus, l'échantillonnage se fait de manière non intrusive, c'est-à-dire sans déranger les espèces présentes. La couverture totale temporelle dépend, elle, de la durée de la campagne. L'inconvénient majeur de l'acoustique réside dans notre incapacité à identifier les espèces responsables de l'écho acoustique, particulièrement dans des milieux complexes avec de grands mélanges d'espèces comme le sont les milieux hauturiers où l'on rencontre essentiellement du micronecton. Dans des cas relativement simple (*i.e.* composé d'un faible nombre d'espèces), on peut différencier des organismes (2 tailles d'euphausiacés ou de myctophidés, séparation poissons/crustacés/méduses, par exemple) à partir de méthodes basées sur une approche multi fréquentielle [[De Robertis et al., 2010](#); [Kloser et al., 2002](#); [McQuinn et al., 2013](#)]. Mais dans la majorité des cas, une estimation exhaustive des espèces présentes nécessite de compléter l'échantillonnage acoustique par des méthodes intrusives de

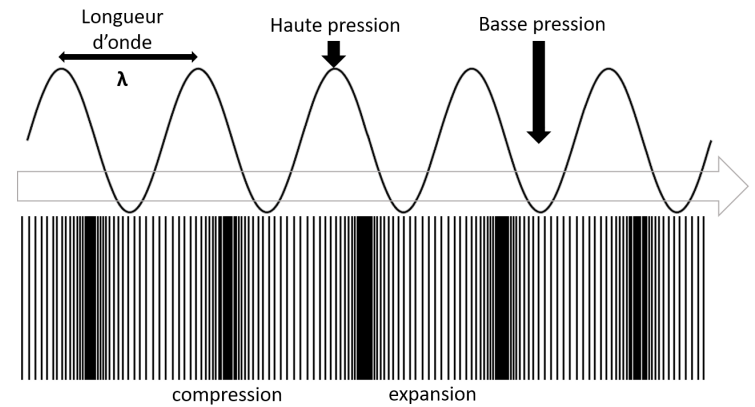


FIGURE 1.21 – Illustration d'une onde sonore se propageant. La pression varie cycliquement comme une onde sinusoïdale (haut); déplacement des particules en déphasage par rapport à la pression (bas). Figure inspirée de Simmonds & MacLennan [2005].

collecte d'organismes. De ce fait, l'estimation d'une biomasse reste très compliquée avec l'usage seul de l'acoustique.

### Propagation d'une onde acoustique

La vitesse de propagation (ou célérité) d'une onde dépend de la densité du milieu dans lequel elle se propage, soit de la cohésion entre ses particules, de leur capacité à se transmettre les petites compressions/dilatations que produit l'onde en se propageant (Figure 1.21). Une onde sonore se déplace donc plus rapidement dans les milieux denses : elle se déplace à environ 1 500m/s dans l'eau de mer et à environ 340m/s dans l'air. Le produit de la densité et de la célérité du son, dans un milieu, s'appelle son impédance. La densité du milieu océanique n'est pas constante et varie avec la température ou la pression. Une relation simplifiée permet de calculer la célérité du son dans l'eau en fonction des caractéristiques du milieu de propagation ( $c$  en m/s) :

$$c = 1449.2 + 4.6T - 0.055T^2 + 0.00029T^3 + (1.34 - 0.01T) * (S - 35) + 0.016z$$

Avec  $T$  la température (°C),  $S$  la salinité (ppm) et  $z$  la profondeur (m).

La longueur d'onde  $\lambda$  (m) (Figure 1.21) se calcule ainsi :  $\lambda = c/f$ , avec  $f$  la fréquence (Hz) de l'onde (Figure 1.21). Pour une vitesse donnée, plus la fréquence est élevée et plus la longueur d'onde est faible.

Les variations locales de pression créées dans le milieu par le déplacement d'une onde sonore (Figure 1.21) correspondent à un flux d'énergie par unité de temps, appelée intensité de l'onde. L'intensité  $I$  est proportionnelle au carré de la pression locale  $p$  :  $I = \frac{p^2}{\rho \cdot c}$ , avec  $\rho$  la densité et  $c$  la célérité de l'onde dans le milieu de propagation. Lorsque l'onde incidente  $I_1$  rencontre un obstacle ayant une impédance différente de celle de l'eau, elle se réfléchit en partie et le récepteur mesure l'intensité réfléchie  $I_2$ . La mesure réalisée s'exprime en termes de ratio de l'intensité réfléchie sur l'intensité incidente. Ce rapport est exprimé en décibels, c'est-à-dire dans une échelle logarithmique qui facilite la manipulation de données dans une très grande dynamique, qui peut être de plus d'une dizaine d'ordres de grandeurs en acoustique :  $r(\text{dB}) = 10 \log_{10} \left( \frac{I_2}{I_1} \right)$

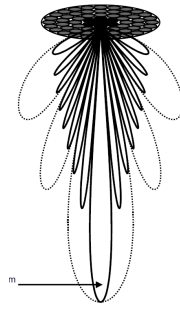


FIGURE 1.22 – Exemple de représentation tridimensionnel d'un faisceau : le lobe principal du centre (indiqué par une flèche) a la plus grande énergie acoustique et cette énergie décroît au fur et à mesure que l'on s'éloigne du lobe principal. Plus la surface d'émission est grande, plus le faisceau est étroit. Figure extraite de [Simmonds & MacLennan \[2005\]](#).

### Fonctionnement d'un échosondeur

L'échosondeur est un cas particulier de sonar avec un faisceau acoustique dirigé verticalement (Figure 1.20C). Un échosondeur est composé d'un émetteur, d'un récepteur, d'un transducteur, d'une horloge de synchronisation et d'un système d'enregistrement et de visualisation. L'émetteur envoie un signal électrique avec une certaine fréquence de tir et durée d'impulsion au transducteur. Le transducteur converti le signal électrique en signal acoustique, il transmet l'onde acoustique en faisant légèrement vibrer le milieu. Le transducteur a également le rôle inverse, il transforme le signal acoustique reçu en signal électrique à destination du récepteur.

Le transducteur est directionnel, il concentre l'onde acoustique selon une direction principale : les ondes émises se propagent selon un faisceau acoustique principal qui concentre le maximum de l'énergie et dont l'axe est perpendiculaire au plan du transducteur, et des lobes secondaires dans des directions latérales qui concentrent des niveaux d'énergie beaucoup plus bas (Figure 1.22). L'ouverture du faisceau, les niveaux et orientations des lobes latéraux, dépendent de la surface du transducteur et de la fréquence émise : (i) à une fréquence donnée, plus le transducteur est grand, plus il est directif; et (ii) pour une taille de transducteur donnée, sa directivité est d'autant plus grande que la fréquence est haute.

Lors de la propagation de l'onde acoustique dans l'espace et dans le temps, la forme conique du faisceau principal induit une augmentation du volume échantillonné et une diminution de l'intensité acoustique qu'il faut corriger. L'absorption moléculaire du milieu transmetteur (liée à la viscosité et conduction thermique) diminue également l'intensité acoustique avec la profondeur. Ces deux effets de perte d'intensité du signal acoustique sont compensés par l'application d'un gain proportionnel à la distance de la cible détectée par le transducteur (*Time Variable Gain*, TVG). La mesure du temps que met l'onde à revenir au récepteur permet de calculer cette distance de la cible à l'émetteur.

L'onde émise par le transducteur est rétrodiffusée par des cibles (*i.e.* tout objet dont la densité est différente de celle de l'eau). Lorsqu'une seule cible est présente dans le faisceau acoustique, on mesure un écho de cible individuelle (ou *backscattering cross-section*  $\sigma_{bs}$ ) en  $m^2$  [[MacLennan et al., 2002](#)]. Elle représente l'aire d'un réflecteur standard qui produirait un signal équivalent au signal reçu et est plus souvent exprimée en échelle logarithmique (*Target Strength* ou *TS*). Lorsque les cibles sont agrégées selon diverses structures (couches, bancs) ou qu'elles sont trop nombreuses pour être seules dans le faisceau, il y a dans le volume échantillonné un ensemble de cibles que l'on ne peut pas séparer les

unes des autres dans le signal. L'analyse des données acoustiques est basée sur un principe de linéarité : on considère que l'écho provenant d'un volume échantillonné résulte de la combinaison linéaire des contributions des cibles individuelles qui s'y trouvent. La somme des  $\sigma_{bs}$  des cibles individuelles incluses dans le volume  $V_0$ , divisée par ce volume, fournit le  $s_v$ , le coefficient de rétrodiffusion volumique (ou *volume backscattering coefficient* en  $m^2/m^3$ ) : c'est la surface totale réfléchissante par unité de volume. Comme le  $\sigma_{bs}$ , le  $s_v$  s'exprime surtout sous sa forme logarithmique  $S_v$ . On peut également intégrer les valeurs de  $s_v$  sur une gamme de profondeurs  $z_1$  et  $z_2$ , pour mesurer le coefficient de rétrodiffusion ou surface totale réfléchissante par unité de surface, le  $s_a$  (ou *area backscattering coefficient*, en  $m^2/m^2$ ) et son équivalent logarithmique  $S_a$  [MacLennan *et al.*, 2002]. Le NASC (*Nautical Area Scattering Coefficient*, ou  $S_A$ , en  $m^2/nm^2$ ) enfin, est l'expression du  $s_a$  pour un carré d'un mile nautique de côté. C'est cette grandeur qui est utilisée comme indicateur de biomasse dans la plupart des études.

Toutes ces valeurs sont reliées les unes aux autres selon les formules suivantes :

$$\sigma_{bs} = \frac{I_2}{I_1}; TS = 10 * \log_{10}(\sigma_{bs})$$

$$s_v = \frac{\sum \sigma_{bs}}{V_0}; S_v = 10 * \log_{10}(s_v)$$

$$s_a = \int_{z_1}^{z_2} s_v dz; S_a = 10 * \log_{10}(s_a)$$

$$NASC = 4\pi(1852)^2 * s_a$$

Ces équations montrent que l'intensité acoustique mesurée est proportionnelle au nombre de cibles échantillonnées et donc qu'elle peut être utilisée comme un indicateur linéairement lié au nombre de cibles détectées, c'est-à-dire à leur abondance. Afin que ces mesures soient comparables d'une campagne à l'autre ou d'un navire à l'autre et deviennent indépendantes du sondeur scientifique utilisé, il faut en début de chaque campagne réaliser une calibration des sondeurs suivant le protocole décrit dans Foote *et al.* [1987]. Une telle procédure n'est pas encore réalisable pour les ADCP (Acoustic Doppler Current Profiler).

### Rétrodiffusion d'une onde acoustique

En cas de réflexion sur une cible, la part de l'onde qui est réfléchiée en direction de l'émetteur-récepteur est la part rétro-diffusée. L'intensité de l'onde rétrodiffusée par une cible individuelle est fonction de son impédance et du rapport entre la longueur  $L$  de la cible et la longueur  $\lambda$  de l'onde, donc de la fréquence  $f$  de l'onde incidente.

Si la cible est très petite par rapport à la longueur d'onde acoustique incidente ( $L \ll \lambda$ ), elle se comporte comme un point source pour l'onde diffusée et la diffusion est omnidirectionnelle, limitant sa détection dans la direction du récepteur. L'énergie de l'écho est déterminée par le volume et non par la forme de la cible et suit la loi de diffusion de Rayleigh : elle est proportionnelle à  $(\frac{d}{\lambda})^4$  avec  $d$  la racine cubique du volume de la cible et  $d \ll \lambda$  (Figure 1.23 dans la partie linéairement croissante des courbes pour les crustacés, méduses, céphalopodes).

Si au contraire la cible est très grande en comparaison de la longueur d'onde ( $L \gg \lambda$ ), seule la portion de l'objet présente dans le volume de l'onde réfléchit le signal, dans une direction privilégiée. L'onde est

alors rétrodiffusée par la surface plutôt que par son volume. Si la surface est plate, la diffusion se fait avec un angle de réflexion égal à celui d'incidence. Par exemple, une onde qui arrive perpendiculaire à une surface plane, est entièrement rétrodiffusée de manière perpendiculaire vers le récepteur (cas le plus simple). L'énergie rétrodiffusée ne dépend pas directement de la fréquence, mais de la taille et surtout de la forme de la cible. On parle de diffusion géométrique (zone où la courbe devient indépendante de la fréquence sur la Figure 1.23), elle survient à des fréquences plus hautes que la figure pour les copépodes, euphausiacés, ptéropodes : à partir d'environ 40kHz par exemple pour les calmars (courbe verte, Figure 1.23).

Pour résumer, l'énergie rétrodiffusée par une cible de petite taille augmente rapidement avec la fréquence, alors que pour les cibles de grande taille la forme de la cible a de l'importance et par là même son orientation vis-à-vis de l'onde incidente. La fréquence d'acquisition doit être choisie en fonction du type et de la taille des organismes recherchés (Figure 1.23). Dans cette thèse nous avons uniquement utilisé la fréquence 38kHz qui est la fréquence avec une portée verticale la plus grande (800 mètres en moyenne). De plus, cette fréquence permet de cibler les espèces micronectoniques [Davison *et al.*, 2015a; Proud *et al.*, 2018b]. Les autres fréquences disponibles (70kHz, 120kHz et 200kHz) ciblent également des organismes d'intérêt, mais leurs portées verticales sont plus faibles (respectivement 450, 250 et 120 mètres).

Les cibles gazeuses (*e.g.* organismes gélatineux, poissons à vessie natatoire...) génèrent une diffusion de forte intensité à une fréquence spécifique du fait d'un phénomène de résonance. A l'état d'équilibre, la pression du gaz de la cible a une pression équivalente à la pression environnante, mais lorsque l'onde acoustique perturbe la cible gazeuse en la faisant osciller, la pression se met à varier. Le changement de pression induit un état oscillatoire de la cible gazeuse autour de son état d'équilibre selon la fréquence de l'onde; c'est la résonance.

La Figure 1.23 montre bien l'importance de la fréquence dans l'intensité de la réponse acoustique ( $S_v$ ) mesurée pour un type d'organisme donné. La réponse en fréquence obtenue en enregistrant plusieurs fréquences en même temps, est donc une information importante pour la détermination de la nature de la cible. Des sondeurs 'large bande' ont d'ailleurs été développés afin de passer de mesures à plusieurs fréquences ponctuelles à des mesures continues dans des plages de fréquences afin de mieux localiser les fréquences de résonance, les fréquences de transition entre zone de Rayleigh et zone géométrique, espacements des maximums et minimums locaux lorsqu'il y a des ondulation [Blanluet *et al.*, 2019]. Ceci devrait aider à la reconnaissance des organismes mais c'est un champ de recherches en plein développement. Les données présentées dans cette thèse sont uniquement des données à 38kHz, mais la Figure 1.23 met bien en évidence des biais dans les données acoustiques : à une fréquence unique, certains organismes sont bien détectés mais d'autres ne le sont pas ou mal; si la fréquence d'enregistrement correspond au pic de résonance d'un type d'organisme, le signal rétrodiffusé sera dominé par cet organisme qui masquera les autres. Toutefois de faibles diffuseurs peuvent tout de même être détectés s'ils sont seuls dans une zone. Ainsi et malgré les limites que l'on vient de mentionner, l'acoustique est un outil précieux en écologie pour déterminer les densités et les distributions spatiales des divers organismes qui sont présents dans le milieu, étudier leurs interactions et leurs comportements à différentes échelles spatiales et temporelles.

La figure 1.24 donne un exemple d'enregistrement acoustique à une fréquence donnée (38kHz) : l'axe vertical matérialise la profondeur, entre 0 et 800 mètres et l'axe horizontal le temps. Les fortes in-

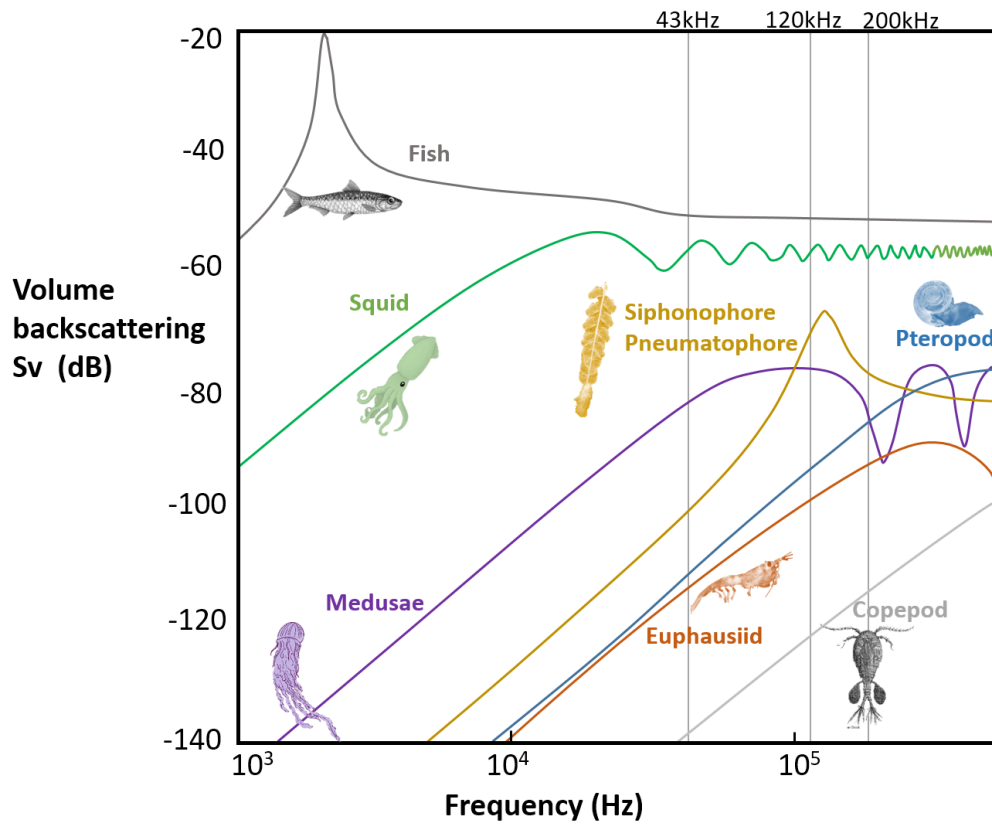


FIGURE 1.23 – Réponse acoustique théorique des grandes catégories de réflecteurs en fonction de la fréquence. Figure inspirée de Lavery *et al.* [2007].

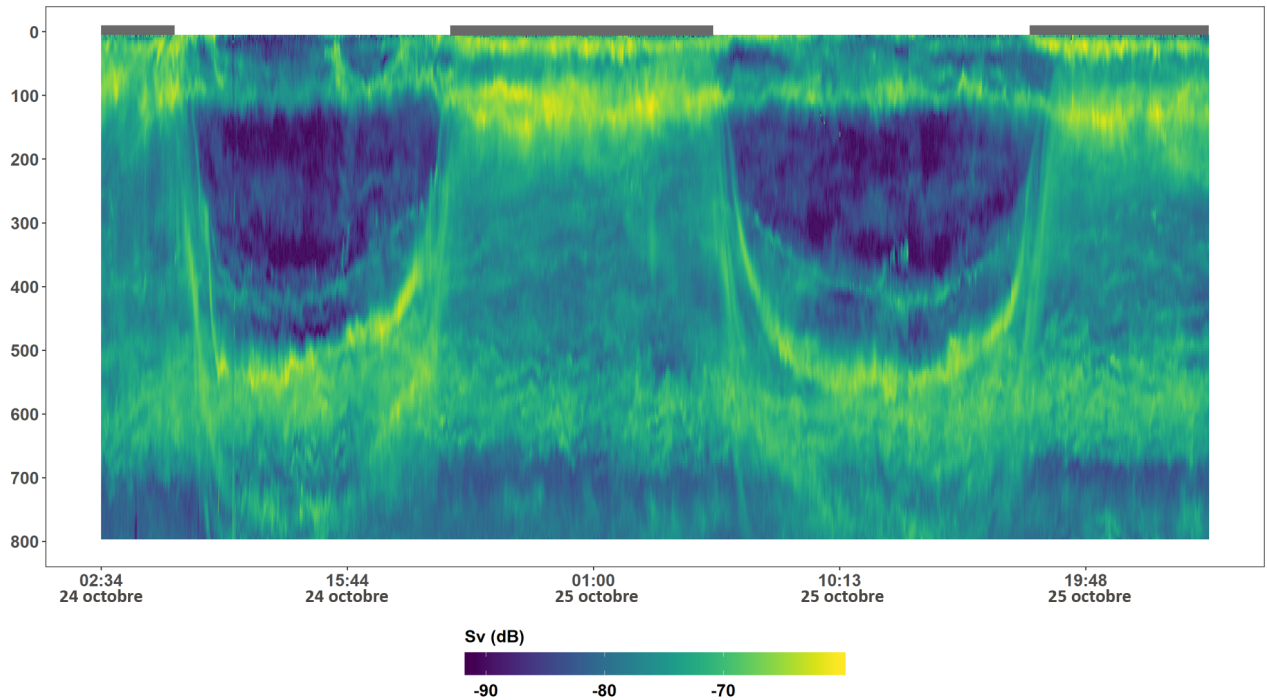


FIGURE 1.24 – Exemple d'enregistrement acoustique, aussi appelé échogramme. Les données ont été extraites de la campagne Nectalis 4, réalisée en 2015 sur l'Alis. L'axe horizontal représente le temps et l'axe vertical la profondeur entre 0 et 800 mètres. Les barres grises au dessus de l'échogramme représentent les périodes de nuit.

tensités acoustiques sont en jaune, les moyennes en vert et le bleu foncé traduit un vide acoustique. Les migrations nyctémérales abordées en section 1.1.3 sont bien visibles sur cet enregistrement : de nuit, les fortes densités de micronecton sont concentrées entre 0 et 200 mètres (périodes identifiées par les barres grises au dessus de l'échogramme) alors que de jour les densités sont plus diffuses et le maximum plutôt autour de 600mètres. On peut voir que pendant la journée, les couches ne s'arrêtent pas toutes à la même profondeur : une fine couche se retrouve à 400 mètres, une deuxième vers 500 mètres, une autre rejoint la couche présente de nuit également à 600 mètres, une dernière couche descend jusqu'à 780 mètres et une dernière couche reste dans les 200 premiers mètres.

### 1.4.3 Les modèles

Une autre méthode d'étude du micronecton est l'utilisation de modèles déterministes. Les modèles sont nombreux et leurs fonctionnements très divers (basés sur les interactions trophiques, basés sur la taille des organismes, individu-centré ou non ...). Les modèles spatiaux de dynamique des écosystèmes et des populations permettent de prédire des processus dans l'espace et le temps qu'il est difficile d'observer directement. Nous ne détaillerons ici que le modèle utilisé dans cette thèse : SEAPODYM pour "Spatial Ecosystem And POpulation DYnamics Model" [Lehodey *et al.*, 2008]. Il comporte plusieurs composantes, chacune modélisant un échelon trophique particulier : le zooplancton, le micronecton [Lehodey *et al.*, 2015, 2010] et les prédateurs supérieurs (majoritairement les thons) [Lehodey, 2001; Lehodey *et al.*, 2013]. SEAPODYM est composé d'un ensemble de modèles eulériens qui décrit l'évolution temporelle de variables en tous points d'un domaine spatial, avec une composante verticale. Il n'est pas individu-centré car on ne suit pas des cohortes ou des individus. Il est basé sur un ensemble d'équations (eulériennes) d'advection-diffusion-réaction qui codent les différents processus de dynamique spatiale

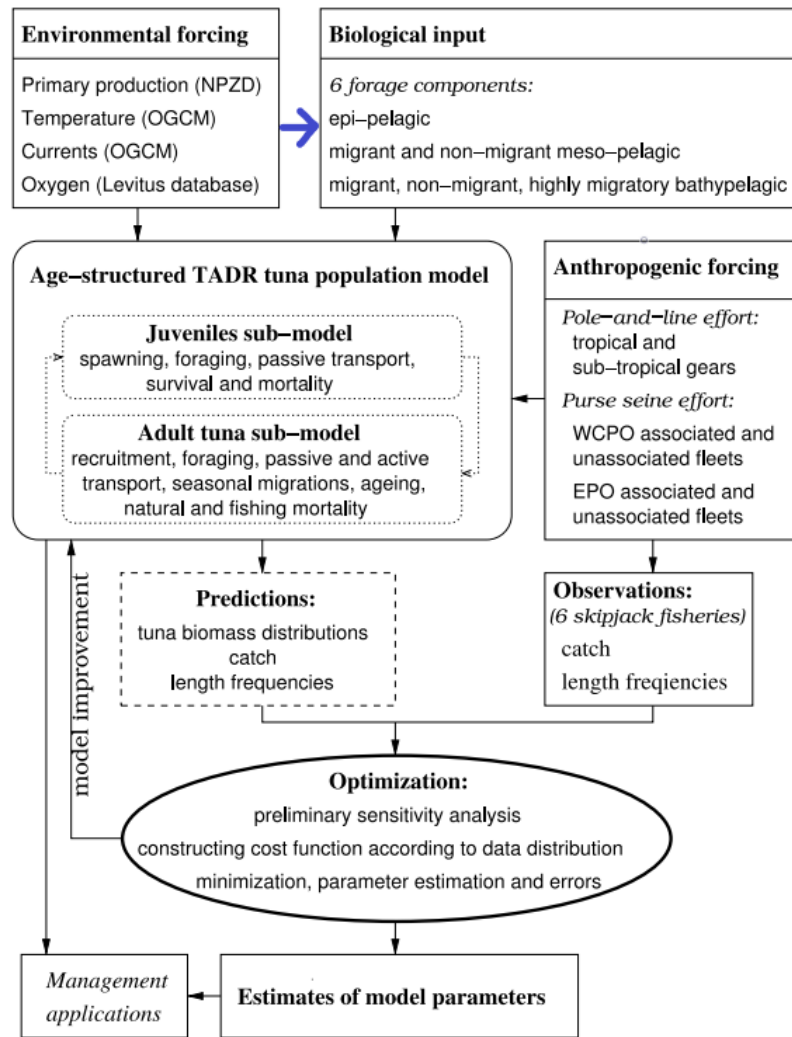


FIGURE 1.25 – Schéma explicatif de SEAPODYM extrait de Senina *et al.* [2008].

et temporelle des populations. Le modèle de diffusion saisit la dispersion aléatoire d'une population ; le modèle d'advection sert à conditionner les mouvements en fonction des courants et du gradient de qualité de l'habitat. Les données hydrodynamiques (température et courants) et biogéochimiques (oxygène et production primaire) sont utilisées pour simuler la distribution du micronecton. Ensuite, cette distribution de micronecton ainsi que les variables environnementales sont utilisées pour estimer l'habitat de reproduction et le transport de larves et de juvéniles pour des prédateurs supérieurs comme les thons. Le modèle crée un indice d'habitat avec des formules empiriques basées sur la densité de micronecton et l'environnement puis simule la biomasse et le mouvement du thon dans l'espace et le temps (Figure 1.25) pour différentes cohortes d'âge. Il est donc important de simuler avec précision le micronecton afin d'avoir une bonne représentation des prédateurs supérieurs. Les prédictions de biomasse et de captures des prédateurs sont ensuite comparées aux données observées de captures et cette comparaison sert à optimiser les différents paramètres du modèle de thon. La validation du modèle de micronecton est plus compliquée due à l'absence de données de comparaison.

Le modèle micronectonic (SEAPODYM-MTL pour Mid Tropic Level) sépare le micronecton en 6 groupes basés sur leurs comportements verticaux. La colonne d'eau est divisée en trois couches verticales selon la profondeur de la couche euphotique (*Zeu*) : la couche épipelagique (entre la surface et 1.5\*



$Z_{eu}$ ), la couche haute mésopélagique (entre  $1.5 * Z_{eu}$  et  $4.5 * Z_{eu}$ ), et la couche basse mésopélagique (entre  $4.5 * Z_{eu}$  et  $10.5 * Z_{eu}$ ). Les groupes de micronecton sont ensuite divisés selon leur couche de résidence pendant la nuit et le jour (Figure 1.26). On retrouve les trois groupes résidents dans chacune des couches (1.1, 2.2, et 3.3 sur la Figure 1.26), le groupe qui migre de la couche haute mésopélagique à la couche épipélagique (2.1), le groupe qui migre de la couche basse mésopélagique à la couche épipélagique (3.1) et enfin le groupe qui migre de la couche basse à la couche haute mésopélagique (3.2). Ce modèle de micronecton simule des biomasses, et comme nous l'avons vu dans les deux paragraphes précédents, il est très compliqué d'obtenir des biomasses de micronecton qui ne sont pas biaisées par l'outil d'échantillonnage. Il est donc très compliqué d'optimiser le modèle de micronecton en fonction de données observées et également de valider ses prédictions.

En 2015, [Lehodey et al. \[2015\]](#) propose une méthode d'optimisation de SEAPODYM-MTL basée sur les données acoustiques, notamment pour optimiser les transferts d'énergie. Le paramètre  $E$  définit le pourcentage d'énergie qui est transféré de la production primaire au micronecton, et ne peut donc pas être optimisé car il nécessiterait une biomasse absolue. Les autres paramètres sont les paramètres  $E'n$  qui définissent la redistribution de  $E$  aux différents compartiments de micronecton, la somme des  $E'n$  vaut 1. Comme ces paramètres sont relatifs les uns aux autres, ils peuvent être estimés en comparant les valeurs acoustiques intégrées dans les couches verticales les unes aux autres : les coefficients de transfert d'énergie sont optimisés pour s'adapter aux rapports relatifs de biomasse en micronecton (via les valeurs de NASC) entre les couches qui changent pendant les périodes diurnes et nocturnes. La part d'organismes migrant est ainsi optimisée avec des valeurs d'acoustique mais la biomasse absolue des couches et sa distribution spatiale ne l'est pas.

Au cours de cette thèse, nous comparerons les prédictions de biomasse micronectonic faites par SEAPODYM et les informations tirées de l'acoustique. Pour cela, le signal acoustique sera analysé par des méthodes statistiques qui sont présentées succinctement dans le paragraphe suivant.

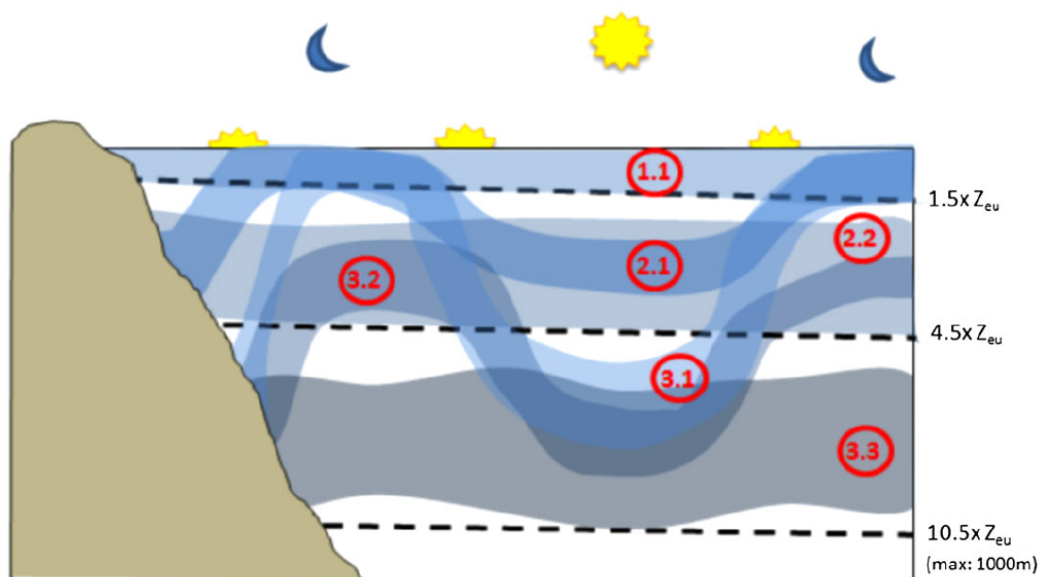


FIGURE 1.26 – Identification des groupes fonctionnels de micronecton sur un schéma conceptuel. Figure extraite de [Lehodey et al. \[2015\]](#). De la surface vers la profondeur, les couches verticales sont la couche épipélagique (couche '1', entre la surface et  $1.5 * Z_{eu}$ ), la couche haute mésopélagique (couche '2', entre  $1.5 * Z_{eu}$  et  $4.5 * Z_{eu}$ ), et la couche basse mésopélagique (couche '3', entre  $4.5 * Z_{eu}$  et  $10.5 * Z_{eu}$ ). Les chiffres rouge indiquent les groupes fonctionnels de micronecton basés sur leur distribution verticale et leur migration : par exemple le groupe 3.2 se situe dans la couche '3' de jour (basse mésopélagique) puis dans la couche '2' de nuit (haute mésopélagique)...

## 1.5 Les outils mathématiques d'analyse

Les modèles déterministes/empiriques comme SEAPODYM offrent une couverture spatio-temporelle extensive pouvant être adaptée à la question posée, ils fonctionnent en mettant en équation des processus écologiques connus et quantifiables. Les modèles statistiques, eux, ajustent une relation entre une quantité mesurée et des variables explicatives. [Dormann et al. \[2012\]](#) résume cette dualité : il écrit que dans les modèles statistiques, les paramètres n'ont pas de signification écologique définie à priori et les processus sont implicites. En revanche, les modèles empiriques basés sur des processus mécanistes sont formalisés mathématiquement avec des paramètres explicitement énoncés qui ont une interprétation écologique claire définie à priori. Dans un modèle statistique, il n'y a pas à priori de lien de causalité entre la quantité mesurée et les variables explicatives mais la mise en évidence de relations statistiques. Ces relations doivent ensuite être appuyées par des processus écologiques pour être vérifiées. La Figure 1.27 montre par exemple une excellente relation (corrélation de 0.79) entre le nombre de thèses par an et les taxes collectées par l'état sur les paris hippiques. Peut-on pour autant en conclure que les taxes sur les paris hippiques financent les thèses en France ? Toute relation statistique identifiée, pour être validée, doit donc s'appuyer sur des concepts fondamentaux écologiques ou sur un grand nombre d'études faites sur une autre espèce ou dans un autre endroit.

La définition d'un modèle statistique est « une description mathématique approximative de la réalité, c'est-à-dire du mécanisme qui a généré les observations, sans description à priori de ces mécanismes. Un modèle statistique permet d'ajuster des relations entre paramètres sans que ces relations soient connues à priori.

Dans la grande majorité des cas, les modèles statistiques impliquent une variable de réponse (ou

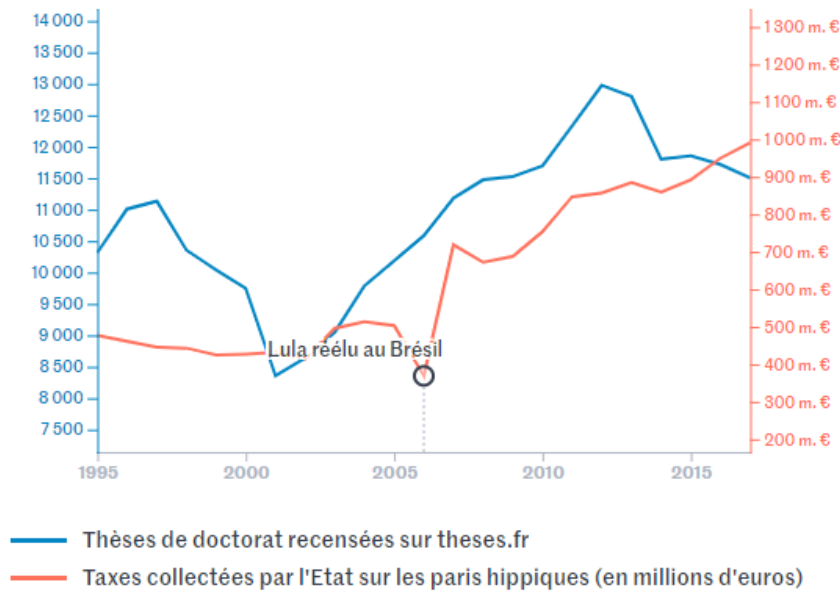


FIGURE 1.27 – Relation en le nombre de thèses en France et les taxes collectées sur les paris hippiques. Figure extraite de [https://www.lemonde.fr/les-decodeurs/article/2019/01/02/correlation-ou-causalite-brillez-en-societe-avec-notre-generateur-aleatoire-de-comparaisons-absurdes-5404286\\_4355770.html](https://www.lemonde.fr/les-decodeurs/article/2019/01/02/correlation-ou-causalite-brillez-en-societe-avec-notre-generateur-aleatoire-de-comparaisons-absurdes-5404286_4355770.html).

variable aléatoire à expliquer) notée  $Y$ , et des variables explicatives (ou covariables) notées  $X_p$ .  $Y$  est la mesure dont nous cherchons à expliquer les variations en fonction des variables explicatives. Dans les modèles paramétriques, la variable de réponses ( $Y_i$  pour un individu  $i$ ) peut s'écrire comme une combinaison des  $p$  variables explicatives ( $X_{ip}$ ) avec l'utilisation de paramètres ( $\theta_n$ ). On peut écrire pour chaque individu  $i$ :

$$Y_i = \theta_1 + \theta_2 * X_{i1} + \theta_3 * X_{i2} + \dots + \epsilon$$

Cette formulation (ou équation) est vraie pour un modèle linéaire : la variable de réponse dépend linéairement des variables explicatives de manière additive. Le terme  $\epsilon$  représente les résidus : ils sont les différences entre les valeurs observées ( $Y_i$ ) et les valeurs prédites par le modèle ( $\theta_1 + \theta_2 * X_{i1} + \theta_3 * X_{i2} + \theta_3 * X_{i2} + \dots$ ) et représentent la part de variabilité des données n'ayant pas été capturée par le modèle.

Les paramètres  $\theta$  sont à priori inconnus et il faut donc les estimer. Pour cela, dans la majorité des cas, la minimisation des moindres carrés et le principe du maximum de vraisemblance sont utilisés (*maximum likelihood*). La méthode des moindres carrés consiste à estimer  $\theta$  en minimisant la somme des carrés des résidus (SSR). La vraisemblance d'un modèle par rapport aux données doit être elle maximisée, car elle peut être vue comme la probabilité qu'un échantillon observé (les données) provienne bien d'un tirage aléatoire. La fonction de vraisemblance est calculée à partir du vecteur des paramètres  $\theta_i$  et des valeurs des données observées. Sur un jeu d'observations ( $x_1, x_2, \dots x_n$ ), la fonction de vraisemblance est la suivante :

$$L(\theta; x) = \prod_{i=1}^n f(x_i; \theta)$$

où  $f(x_i; \theta)$  est la densité de la loi Normale sur  $x$ . L'objectif sera de trouver un estimateur de  $\theta$  (noté  $\hat{\theta}$ ) qui maximise la fonction de vraisemblance à partir du jeu d'observations de départ. Pour maximiser cette fonction, on trouve des valeurs de  $\theta$  pour lesquels la dérivée de la fonction de vraisemblance est nulle. On peut ainsi ajuster une relation statistique, basée sur des paramètres estimés par cette méthode, entre une variable de réponse et des variables explicatives. Les différentes manières d'ajuster cette relation sont détaillées ci-dessous, sans en faire une liste exhaustive, mais en mettant l'accent sur les outils utilisés pendant cette thèse. On retrouve deux grands groupes d'analyses : uni-variés (une seule variable de réponse) et multi-variés (plusieurs variables de réponse).

### 1.5.1 Analyses univariées

**Le modèle linéaire (gaussien) de base.** À la fois le plus simple, le plus ancien et le plus connu des modèles statistiques, il englobe essentiellement la régression linéaire, l'analyse de variance et l'analyse de covariance. Dans ce modèle, les variables explicatives (qualitatives ou quantitatives) sont liées à la variable de réponse de manière linéaire et additive. Il se base sur une hypothèse de distribution Gaussienne de ses résidus.

**Le modèle linéaire généralisé.** Il généralise le précédent à deux niveaux : d'une part, la loi des erreurs n'est plus nécessairement gaussienne, mais doit appartenir à l'une des lois de la famille exponentielle; d'autre part, la liaison linéaire entre l'espérance de la variable réponse et les variables explicatives se fait à travers une fonction particulière appelée fonction de lien (spécifiée à priori).

**Les modèles non linéaires.** De façon très générale, il s'agit de modèles permettant d'expliquer la variable réponse au moyen des variables explicatives à travers une fonction quelconque inconnue, souvent non paramétrique. Les GAM (pour *Generalized Additive Models*) font partis de cette famille et modélisent la variable réponse avec une somme de fonctions de lissage non-linéaires des variables explicatives [Hastie & Tibshirani, 1995; Wood, 2006]. Les fonctions de lissage (ou *spline* en anglais) sont découpées en parties et les points de jonctions entre les parties sont des nœuds (le nombre maximal de nœuds est souvent un paramètre à renseigner à priori). Entre chaque nœud, des fonctions souvent polynomiales, sont ajustées.

**Les modèles mixtes.** Les modèles mixtes, comme leur nom l'indique, mixent plusieurs types de modèles. Dans notre cas, le modèle GAM est combiné avec un autre modèle qui prend en compte la colinéarité [Wood *et al.*, 2012]. Dans le cas où la variable de réponse a une dimension spatiale ou temporelle, sa répétition  $n$  est liée à sa répétition  $n-1$  car elle est proche de cette dernière temporellement ou spatialement. Il faut prendre en compte cette autocorrélation mathématiquement avant d'ajuster la relation aux variables explicatives. On dit parfois qu'un autre modèle est emboîté dans le premier pour gérer l'autocorrélation.

**Les modèles par arbre de régression et de classification.** Ces méthodes consistent à découper une population en plusieurs groupes en fonction des variables explicatives qui discrétisent au mieux la variable

de réponse. Ces modèles sont non linéaires. On parle d'arbre de régression en présence d'une variable réponse quantitative et d'arbre de classification en présence d'une variable réponse qualitative.

### 1.5.2 Analyses multivariées

**L'analyse en composante principale (ACP).** L'ACP consiste à transformer des variables corrélées en nouvelles variables décorrélées les unes des autres dans un nouvel espace. Ces nouvelles variables sont nommées « composantes principales », ou axes principaux et sont orthogonales entre elles. Elle est majoritairement utilisée pour réduire le nombre de variables et rendre l'information moins redondante. On dit aussi qu'on projette l'ensemble des variables dans un nouvel espace réduit. Le meilleur ajustement des axes est trouvé en utilisant la vraisemblance. Souvent, une classification basée sur une minimisation des distances est réalisée dans cet espace réduit.

**Les modèles multivariés.** Contrairement à l'ACP, les modèles multivariés ne vont pas simplement réduire l'espace mais réduire cet espace en fonction d'autres variables comme pour les modèles linéaire, GLM et GAM. Dans ce cas, la variable de réponse est multivariée, c'est-à-dire que la variable mesurée pour un individu est composée d'un vecteur de valeurs (contre une seule valeur en analyse uni-variée) [Foster *et al.*, 2013; Ward *et al.*, 2015].

### 1.5.3 Et le *machine learning* dans tout ça ?

Le *machine learning* est de plus en plus présent dans le monde de l'analyse de données. Malgré ça, il n'est pas simple d'en trouver et d'en donner une définition claire. On pourrait le définir comme un ensemble de méthodes heuristiques (*i.e.* vraies dans les faits mais qu'on ne peut pas démontrer) permettant d'approximer des observations par apprentissage. Concrètement, les statistiques « classiques » sont basées sur des hypothèses de distribution des données relativement à des lois de probabilités sur lesquelles on peut calculer des seuils de significativité, alors que les méthodes de machine learning fonctionnent uniquement avec de l'apprentissage. Par exemple en 2017, un algorithme de *machine learning* (*AlphaGo*, propriété de Google) a battu le champion du monde du jeu de Go. La version suivante de ce programme (*AlphaGo Zero*) a ensuite battu 100 parties à zéro *AlphaGo*. *AlphaGo Zero* a appris tout seul à jouer au jeu de Go, sans intervention humaine, en s'entraînant contre lui même [Silver *et al.*, 2017]. Ces algorithmes sont plus puissants que les algorithmes classiques mais souvent vus comme des boîtes noires souffrant d'un manque de compréhension.

### 1.5.4 Validation et utilisation des modèles

Une fois le modèle ajusté, il existe une relation statistique capable de calculer une valeur de la variable réponse pour tout vecteur des variables explicatives. En prédisant sur la base des valeurs explicatives observées, on obtient une valeur prédite comparable à la valeur observée. La différence de l'une à l'autre est appelée résidu. C'est la part de la variance que le modèle ne peut expliquer, due à du bruit et/ou à un lien avec une variable qui n'a pas été incluse dans le modèle. Tout modèle statistique nécessite

de faire des hypothèses sur la distribution de ses résidus qu'il faut donc vérifier ensuite. On y retrouve surtout : l'indépendance des résidus 2 à 2, la bonne distribution des résidus, l'indépendance des résidus vis-à-vis des valeurs prédites (appelée hétéroscédasticité), l'absence de sur-dispersion pour les lois discrètes (*e.g.* Poisson, binomiale). Une fois que le modèle est validé, il peut être utilisé comme outils de prédiction. Dans le cas où les valeurs des variables explicatives sortent des gammes échantillonnées, on parle d'extrapolation.

## 1.6 Le plan de la thèse

Nous avons analysé des données d'acoustique et de chaluts avec les outils présentés précédemment pour répondre aux questions scientifiques de la thèse. Pour mémoire ces questions portaient sur la compréhension de la dynamique spatiotemporelle du micronecton; des paramètres environnementaux contrôlant cette dynamique, de la description des espèces de micronecton et enfin du rôle joué par le micronecton dans son écosystème. Ce manuscrit s'articule autour de 5 chapitres (Figure 1.28) :

Le travail du **chapitre 2** se concentre sur la distribution spatiale et temporelle du micronecton dans une couche superficielle entre 20 et 120 mètres. Pour cela, 19 ans de données acoustiques d'un échosondeur non calibré largement répandu ont été analysées dans un premier modèle pour estimer l'évolution de l'abondance du micronecton entre 1999 et 2017 dans la ZEE calédonienne. L'influence du phénomène ENSO a également été étudiée ainsi que le cycle nyctéméral jour/nuit. Un deuxième modèle statistique nous a ensuite permis d'analyser l'influence de paramètres environnementaux sur la valeur moyenne acoustique de nuit uniquement. Nous nous sommes servis de ce modèle pour prédire une valeur acoustique moyenne dans la zone que nous avons comparé avec les prédictions de biomasse de micronecton de SEAPODYM-MTL sur la même couche verticale.

Au cours du **chapitre 3**, nous nous sommes focalisés sur la distribution verticale du micronecton. Pour cela, les données de six campagnes acoustiques utilisant un échosondeur calibré ont été analysées. Une méthodologie statistique relativement complexe a permis de décrire la variabilité de la distribution verticale du micronecton et également de la relier à certains paramètres environnementaux. Encore une fois, des prédictions de distribution verticale ont été faites sur toute la zone.

Dans le **chapitre 4**, nous avons analysé des données de chaluts réalisés dans la zone entre 2011 et 2017. Cette étude a permis d'identifier et de décrire les assemblages dominants d'espèces de micronecton. L'influence de quelques paramètres environnementaux sur la probabilité de présence de ces assemblages a été également investiguée. Enfin, la distribution spatiale des assemblages a été prédite dans la zone, de nuit et de jour et à différentes profondeurs.

Pour le **chapitre 5**, nous avons utilisés le cadre statistique du chapitre 3 pour prédire ce que pourrait devenir les distributions verticales dans un contexte de changement climatique en se basant sur une simulation régionale d'un modèle biogéochimique. Nous avons également étudié quels seraient les facteurs environnementaux les plus influents. Les prédictions acoustiques en changement climatique ont été encore une fois comparées aux prédictions issues du modèle SEAPODYM-MTL.

Enfin, le cadre statistique du chapitre 2 a de nouveau été utilisé pour le **chapitre 6**. Nous en

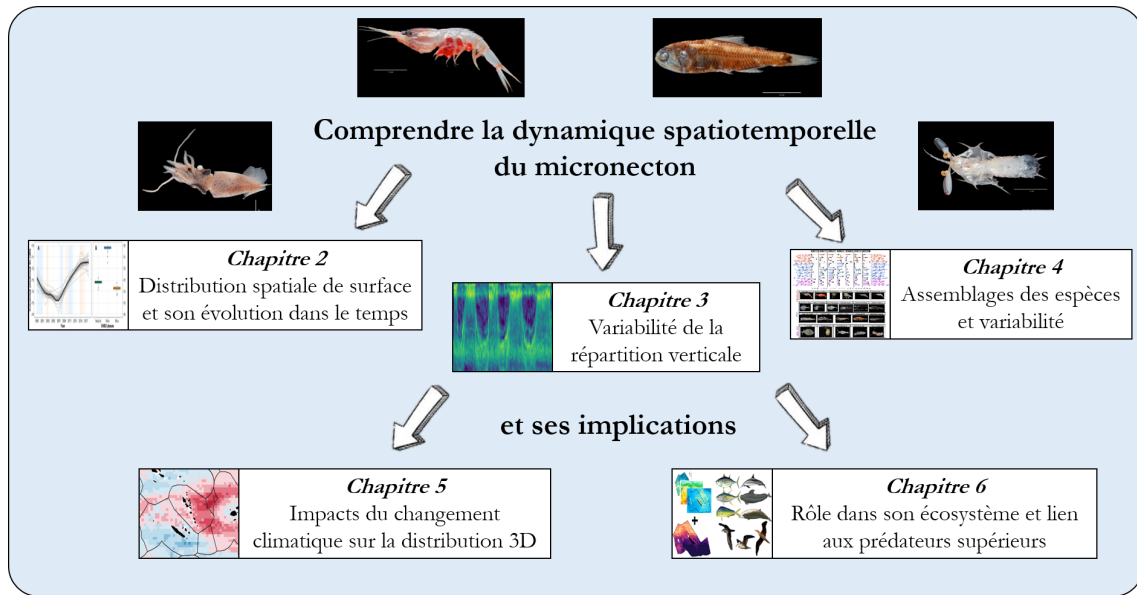


FIGURE 1.28 – Schéma descriptif de l'articulation de la thèse.

avons utilisé les prédictions spatio-temporelles, conjointement avec des variables environnementales, pour comprendre les facteurs contrôlant la dynamique de neuf prédateurs supérieurs (trois espèces de poissons pélagiques, trois guildes de cétacés et trois espèces d'oiseaux marins). Des modèles statistiques ont permis de mesurer l'influence de la distribution du micronecton par rapport à l'influence de facteurs abiotiques sur la distribution de ces prédateurs. Les prédictions spatiales des neuf prédateurs ont ensuite été combinées en un indice unique pour identifier des zones d'intérêt en matière de conservation et potentiellement utiles aux gestionnaires du parc marin.

Les résultats majeurs de la thèse sont résumés et discutés dans le **chapitre 7** et plusieurs pistes de recherches futures sont avancées.

## Chapitre 2

# Micronekton distribution in the southwest Pacific (New Caledonia) inferred from Shipboard-ADCP backscatter data

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## Abstract

Acoustic data is an invaluable data source for characterizing the distribution and abundance of mid-trophic level organisms (micronekton). These organisms play a pivotal role in the ecosystem as preys of top predators and as predators of low-trophic level organisms. Though it cannot provide an absolute biomass estimate, the Shipboard ADCP (Acoustic Doppler Current Profiler) acoustic backscatter signal intensity may be a useful proxy to investigate variability in distribution and relative density of micronekton. This study uses data from 19 years (1999 - 2017) across 54 cruises of acoustic recording from ADCP in the New-Caledonia oceanic sub-tropical EEZ (Exclusive Economic Zone) to assess micronekton seasonal and interannual variabilities and spatial distribution. The dataset is composed of two different ADCPs with a 150 kHz for the first period followed by a 75 kHz ADCP for the latest years. We examine the 20-120m averaged scattering layer. Using a few cruises with concurrent EK60 measurements, we propose that the backscatters from the ADCPs and 70 kHz EK60 are closely linked allowing to use the backscatter signal of both ADCPs in a combined dataset over the full time series. We then design a GAMM (Generalized Additive Mixed Model) model that takes into account the two ADCP devices as well as the temporal variability. After accounting for the device effect, we show that the acoustic signal is mainly driven by diel vertical migration, season, year as well as ENSO (El Niño-Southern Oscillation). In a second step, a consensus model between two statistical approaches (GAMM and SVM) (Support Vector Machine) is constructed linking the night 20-120m backscatter to the oceanographic and geographic environment. The model shows that sea-surface temperature is the main factor driving the backscatter variability in the EEZ with enhanced backscatter during austral summer in the northern part of the EEZ. We show that such acoustic density differs significantly spatially and temporally from micronekton biomass predicted for the same period by the SEAPODYM-MTL (Mid Trophic Level) ecosystemic model. The seasonal cycle given by ADCP data lags the SEAPODYM-MTL seasonal cycle by around 3 months. Reasons to explain these differences and further needs in observation and modelling are explored in the discussion. In addition to providing new insights for micronekton dynamics in the EEZ needed for ecosystem-based fisheries management, the data may also help improving our ability to model that key trophic compartment.

**Keywords :** *Micronekton; southwest Pacific Ocean; SEAPODYM; acoustic; ecosystem*

## 2.1 Introduction

In the western Pacific, marine pelagic predators, in particular tuna, are a major food and economic resource for small island developing states [Bell *et al.*, 2015]. Tuna distribution variability in space and time has been linked to oceanographic factors (*e.g.* temperature, depth and oxygen) or to biological factors (*e.g.* age and reproduction) [Brill *et al.*, 2005; Young *et al.*, 2011]. However, the presence and the availability of forage fauna remains a key driver of tuna distribution [Bertrand *et al.*, 2002a; Duffy *et al.*, 2017; Olson *et al.*, 2014].

Tuna forage fauna is mostly composed of micronekton, which are mid-trophic level organisms comprising crustaceans, molluscs, gelatinous organisms and fish measuring between 1 and 20cm [Bertrand *et al.*, 2002a; Young *et al.*, 2015]. Distributed in the upper 1000m of the water column [Gjøsaeter & Ka-

waguchi, 1980), micronekton is layer-distributed [Burgos & Horne, 2008]. Layer vertical positions are influenced by physical-chemical properties of the water mass such as oxygen or temperature [Klevjer *et al.*, 2016], or by the presence of predators [Benoit-Bird *et al.*, 2017]. Micronekton abundance is also influenced by environmental conditions such as primary production [Escobar-Flores *et al.*, 2013; Irigoien *et al.*, 2014] or the presence of eddies or fronts [Behagle *et al.* 2016, Sabarros *et al.* 2009]. A large proportion of micronekton organisms undertakes diel vertical migrations (DVM), moving from the mesopelagic zone (200-1000m), where they stay during the day, to the more productive surface layer (0-200m) during the night [Pearre, 2003]. Diel vertical migrations are observed across all the oceans [Bianchi & Mislan 2016, Klevjer *et al.* 2016] and are recognized today as the biggest biomass movement on earth [Hays, 2003]. In addition to their pivot role between low trophic-level organisms and top predators [Bedford *et al.* 2015, Giménez *et al.* 2018], micronekton actively contribute to the downward flux of nutrients and particulate organic matter by their diel vertical migration [Ariza *et al.*, 2016; Drazen & Sutton, 2017; Kiko *et al.*, 2017].

Understanding the dynamics of micronekton in the water column and its horizontal spatial distribution at different scales remains challenging. Net trawling is the traditional sampling approach [Potier *et al.*, 2014]. However, trawl data are size and species dependent and because of net avoidance behavior of organisms, obtaining an unbiased quantitative estimate with trawls is challenging [Heino *et al.*, 2011; Kaartvedt *et al.*, 2012]. Further, trawl data are temporally and spatially discrete data, which complicates their use in attempting to have an overview of the area considered. For the last fifty years, net sampling has been complemented by the use of underwater sound measurement [Benoit-Bird & Lawson, 2016] as micronekton layers scatter sound. Scientific echosounders are a powerful tool to study the distribution and behavior of pelagic biota [Cade & Benoit-Bird, 2015; Kloser *et al.*, 2002]. For all echosounders, organisms' biomass estimation needs the knowledge of community species composition with net sampling and their target strength. The use of several frequencies is recommended to achieve a better discrimination between species or group of species [Davison *et al.*, 2015b]. Calibrated echosounders are widely used to study the organisms' distribution through the water column.

Compared to the sampling coverage by scientific echosounders, the one available from shipboard un-calibrated Acoustic Doppler Current Profiler (hereafter ADCP) is potentially huge. Given that the ADCP, initially devoted to measuring current velocities, has been used routinely for several decades to sample currents, the data provided by these instruments are potentially useful over relatively long periods and large spatial scale. Since Flagg & Smith [1989] proposed a method to use ADCP echo intensity and convert it as a proxy of abundance, a number of subsequent studies have investigated the distribution, the dynamic and the variability of scattering layers in the pelagic ocean using ADCP records [Chereskin & Tarling 2007; Radenac *et al.* 2010; Smeti *et al.* 2015]. Due to the lack of calibration, ADCP data must be numerous to overcome the potential device biases such as the temperature dependence. Several studies have successfully compared ADCP and calibrated echosounder [Brierley *et al.*, 1998; Fiedler *et al.*, 1998; Gostiaux & van Haren, 2010; Griffiths, 2010; Lee *et al.*, 2004]. They suggest that ADCP provides a proxy of relative density of combined zooplankton and micronekton [Flagg & Smith, 1989; Lee *et al.*, 2004; Radenac *et al.*, 2010].

Net sampling and acoustic data provide critical information to calibrate and validate ecosystem models including a representation of mid-trophic functional groups [Handegard *et al.*, 2013]. Such models allow for estimating, at regional to global scales, the biomass of micronekton based on key biological processes and ecological principles such as growth and mortality rates with temperature. SEAPODYM is

a Spatial Ecosystem and Population Dynamics Model where both micronekton groups and predator fish (*e.g.* tuna) population dynamics are described [Lehodey *et al.*, 2008, 2010]. A method has been developed to assimilate biomass observations in this model for the estimation of energy transfer efficiency coefficients between micronekton groups, *i.e.* migrant and resident. It has been demonstrated using acoustic data directly, assuming for the sake of simplicity that acoustic signal and biomass are directly proportional [Lehodey *et al.*, 2015]. To explore the interest of using existing abundant archived ADCP data in a future data assimilation ecosystem modeling framework, we investigate a 19-year time series of ADCP data, collected through 54 oceanographic cruises in the New Caledonian EEZ.

New Caledonian Exclusive Economic Zone is located in the Coral Sea, at the southwestern edge of the Pacific Ocean. New Caledonia and the nearby Vanuatu Archipelago create an obstacle to the westward South Equatorial Current (SEC), the dominant feature of water circulation for the surface, thermocline and intermediate waters. The SEC is divided into zonal jets when encountering the New Caledonian islands and finally, waters above the thermocline diverge into two branches around 15°S when reaching the Australian coast [Cravatte *et al.*, 2015]. In this region, the general circulation models are prone to shear instabilities and high eddy kinetic energy is observed [Qiu *et al.*, 2009; Rousselet *et al.*, 2016] that may influence on deep-living organisms distribution [Behagle *et al.*, 2014; Tew Kai & Marsac, 2010]. On the western barrier reef of New Caledonia's main island, strong wind episodes during Austral summer also create upwelling conditions cooling the sea surface temperature and creating vertical movement of nutrients [Alory *et al.*, 2006; Ganachaud *et al.*, 2010; Marchesiello *et al.*, 2010]. Excluding the very coastal areas, the New Caledonian EEZ is regarded as oligotrophic with a higher productivity zone south of 22°S [Ceccarelli *et al.*, 2013; Dandonneau & Gohin, 1984].

The active management of the recently created Coral Sea Natural Park (Decree 2014-1063/GNC) creates a need for robust information on the productivity and functioning of this remarkable ecosystem, including micronekton dynamics and its pivotal role in food webs. Micronekton taxonomy, distribution and biomass are still poorly known in the Coral Sea [Ceccarelli *et al.*, 2013] and in the New Caledonian EEZ [Gardes *et al.*, 2014]. Top predator diet studies [Allain *et al.*, 2012; Olson *et al.*, 2014; Williams *et al.*, 2014; Young *et al.*, 2010] and trawl data analyses [Grandperrin *et al.*, 1999; Menkes *et al.*, 2015; Young *et al.*, 2011] emphasized a high diversity level of macro-zooplankton and micronekton with a dominance of Gonostomatidae, Sternoptychidae, Myctophidae, Scopelarchidae and Phosichthyidae [Ceccarelli *et al.*, 2013; Grandperrin, 1975; Sutton *et al.*, 2017; Vourey *et al.*, 2017].

Behind this diversity description, the amount of data collected specifically to study micronekton together with co-located oceanographic conditions are still rare [Menkes *et al.*, 2015; Smeti *et al.*, 2015]. In the New Caledonian EEZ, the poor data coverage prohibits a comprehensive description of the pelagic ecosystem, including the main seasonal patterns of micronekton and their relationships with its oceanographic drivers. In the present paper, we focus on the analysis of the spatial and seasonal variability of acoustic backscatter collected around New Caledonia and its relationships with oceanographic conditions, assuming that backscatter values are a relevant proxy for micronekton relative abundance. Our objectives are four-fold. Firstly, we propose a simple approach of inter-calibration between various instruments. We describe diel vertical migration, seasonal cycles and multi-year trends in backscatter data. Then, the effect of environmental variables (bathymetry, distance to the closest coast, sea surface temperature, chlorophyll-a and depth of the thermocline) on backscatter values is investigated through statistical models providing backscatter predictions at the scale of the EEZ. Finally, we compare acous-

tic data from the ADCP model to micronekton outputs of SEAPODYM simulations. In the discussion, pathways are proposed to progress on the observation, understanding and modelling of micronekton.

## 2.2 Material and Methods

Micronekton dynamics are usually studied with calibrated echosounder devices such as the SIMRAD EK60 echosounder. Therefore, EK60 backscatter values are comparable to any other backscatter value from other EK60 survey. The un-calibrated ADCP is usually switched-on for current measurements on-board oceanographic vessels : for the New Caledonian region, only 6 cruises have collected acoustics data using the EK60, while 54 cruises have recorded ADCP data. Hence, despite the lack of calibration, ADCP offers longer time series and wider spatial coverage than calibrated acoustic data for our zone.

### 2.2.1 Acoustic data

TABLEAU 2.1 – Number of 10km transects per season, warm season : DJF (December, January, February) and MAM (March, April, May) ; and cold season : JJA (June, July, August) and SON (September, October, November) and per year. Italic numbers are with the ADCP 75 kHz plain numbers are for the ADCP 150 kHz.

|      | DJF | MAM | JJA     | SON |
|------|-----|-----|---------|-----|
| 1999 | 0   | 0   | 0       | 71  |
| 2000 | 0   | 79  | 0       | 0   |
| 2001 | 17  | 68  | 0       | 39  |
| 2002 | 7   | 59  | 0       | 0   |
| 2003 | 100 | 0   | 213     | 290 |
| 2004 | 244 | 68  | 77      | 96  |
| 2005 | 19  | 35  | 0       | 0   |
| 2006 | 0   | 0   | 0       | 60  |
| 2007 | 0   | 64  | 117     | 0   |
| 2008 | 0   | 262 | 110     | 0   |
| 2009 | 0   | 0   | 0       | 0   |
| 2010 | 0   | 124 | 0       | 0   |
| 2011 | 135 | 0   | 192     | 78  |
| 2012 | 0   | 83  | 50 + 56 | 148 |
| 2013 | 30  | 1   | 40      | 72  |
| 2014 | 70  | 0   | 0       | 94  |
| 2015 | 0   | 0   | 0       | 90  |
| 2016 | 51  | 134 | 50      | 170 |
| 2017 | 0   | 0   | 62      | 217 |

We gathered historical ADCP data from 54 cruises on board the R/V Alis in the New-Caledonia EEZ between 156°E–174°E and 14°S–27°S, from 1999 to 2017 (Figure 2.1, Table 2.1 and Appendix 2.4.5). Two profilers were used : a 150 kHz BroadBand ADCP (BBADCP), from 1999 to May 2012, and an Ocean Surveyor 75 kHz NarrowBand ADCP (NBADCP) from October 2012 to 2017.

All ADCP data were processed using the freely available CODAS software (<http://currents.soest.hawaii.edu>), applying the procedure described in Hummon & Firing [2003]. The echo intensity ( $E_a$ ), in counts, recorded by the ADCP was converted to backscatter coefficient ( $S_v$  in dB.re.m<sup>2</sup>) using the stan-

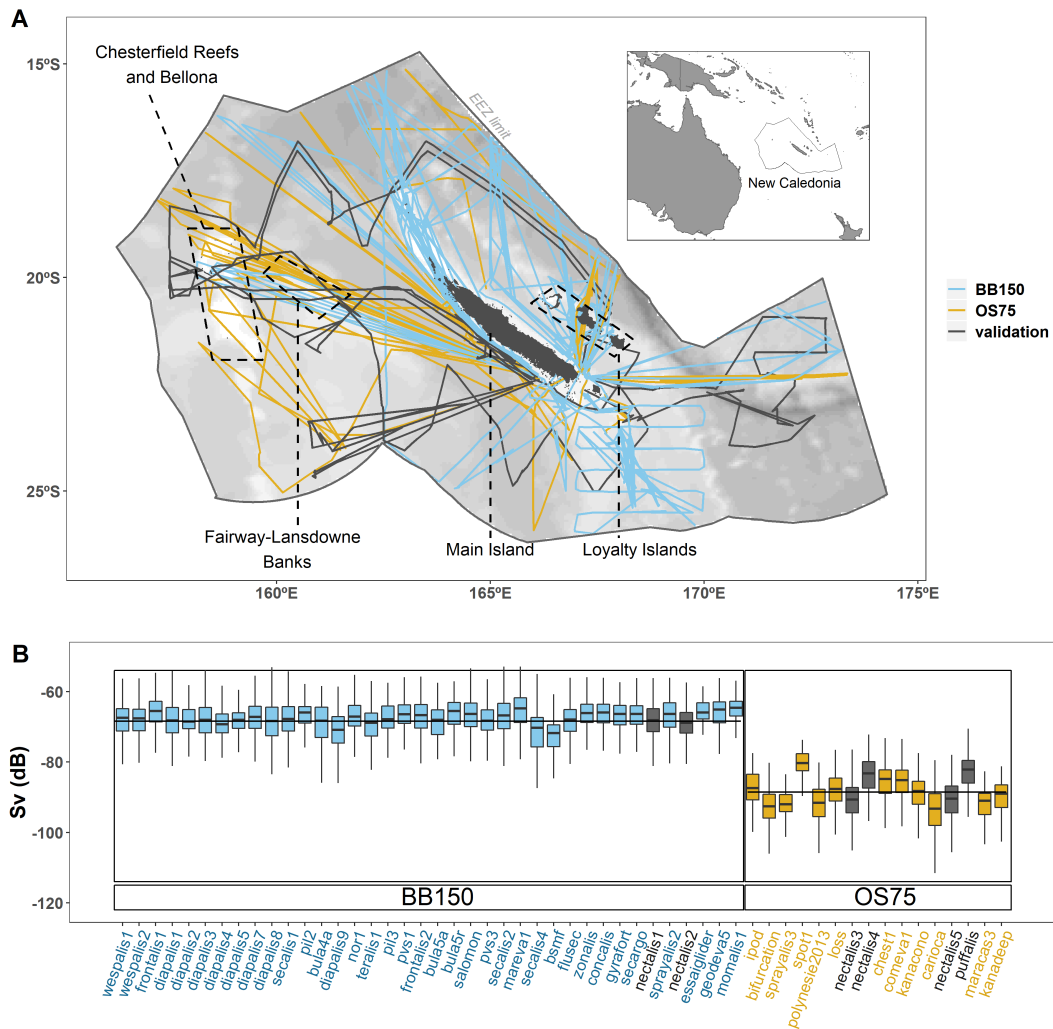


FIGURE 2.1 – Map showing cruise tracks of the R/V Alis (solid lines) with SADCPC device (blue line for 150 kHz, yellow line for 75 kHz and grey line for cruises used for ADCP validation) in the New Caledonian Exclusive Economic Zone. The background grey colors represent the seabed depth (where lighter colors are shallower). Important areas discussed in the paper are indicated in grey dashed line (panel A). Boxplot of ADCP backscatter values per cruises with the same color code than for the map (panel B).

standard equation of sonar given by RDI [1998] for a NB-ADCP. Deines [1999] transformed this equation for a BB-ADCP, subsequently rearranged by Gostiaux & van Haren [2010] (Appendix 2.4.5). 150 kHz ADCP backscatter data also had to be corrected due to a technical bias : due to two technical interventions, the mean level of backscatter values changed abruptly two times. Cruises were grouped in order to have constant mean Sv across groups (i.e. Group1 : Wespalis1 to Mareva1 ; Group2 : Secalis4 to Secargo ; and Group3 : Nectalis1 to Momalis) (Appendix 2.4.5). The maximum depth reached between these cruises groups are statistically different according to a Wilcoxon test ( $p$ -value  $< 0.05$  for Group1-Group2, Group1-Group3 and Group2-Group3) showing that backscatter values changes are due to technical bias and not due to some environmental changes. We adjusted backscatter values on a similar mean level across groups by adding offsets (Appendix 2.4.5). The final vertical resolution (bin) was 8m for the 150 kHz and 16m for the 75 kHz, both starting at 16m depth and ending on at 300m for the 150 kHz and at 700m for the 75 kHz, with a time resolution of 5 min.

We selected the surface layer (20-120 m) only, because of the limited vertical range of the 150 kHz

ADCP : its initial vertical range was 300 m, but the depth actually reached after several years was limited to 120 m due to a decrease in the power of the device. Analyses were done on a thicker layer (20-200 m) with fewer cruises and conclusions were similar, so the 20-120 m layer was kept and considered representative of the epipelagic zone (0-200 m).  $S_v$  data were transformed into a linear scattering measure ( $s_v = 10 \frac{S_v}{10}$ ) before to be depth-averaged over 20-120 meters. In order to remove phenomena happening at high spatiotemporal scales [Escobar-Flores *et al.*, 2018], the linear scattering measure was also averaged along survey traces every 10km that corresponds approximately to 10 initial points with a vessel speed around 7 knots (13km.h<sup>-1</sup>). Sensitivity studies with different spatial resolution (5, 10 and 20 km) as well as by analyzing the median value rather than the mean, and all results lead to the same conclusions (not shown). Then, the logarithmic value ( $S_v = 10 \log(s_v)$ ) was calculated and used for all following analysis ( $S_{v\_ADCP}$ , in dB.re.m<sup>2</sup>) (Appendix 2.4.5).

To analyze the complete time series (from 1999 to 2017), the two ADCP frequencies needed to be analyzed together to look for a potential long temporal trend. For that purpose, we offered a method to replace the two ADCP signals on a similar mean level by comparing to the EK60 data. Both instruments, were used simultaneously during six cruises : Nectalis 1 through 5 and Puffalis (cruises numbers 33, 35, 45, 46, 51, 52 in Appendix 2.4.5). During these cruises, EK60 calibration was performed according to the Foote *et al.* [1987] method at the beginning of each cruise. As for ADCP, the mean value of EK60  $S_v$  of the 70 kHz frequency was calculated in the 20-120m layer, with a 10km resolution. Two linear regressions were fitted between the  $S_{v\_ADCP}$  values (one regression for each device : 150 kHz and 75 kHz) and the  $S_{v\_EK60}$  values (70 kHz). By comparing the two ADCP frequencies to the same EK60 frequency, we assumed that a part of each ADCP signal was correlated to the EK60. Based on the assumption that backscatter echo-intensities of EK60 70 kHz were comparable between the 6 cruises due to calibration step, an 'ADCP corrected value' relative to the EK60 70 kHz value could be calculated. For the rest of the text, the 'corrected backscatter' ( $S_{v\_ADCP\_corrected}$ ) corresponded to the  $S_{v\_ADCP}$  corrected with one of the two linear regressions with EK60 values. These regressions were used to adjusted on the same mean backscatter level the two ADCP frequencies and therefore to average predictions (Figure 2.2).

The comparison with the EK60 data made it possible to treat together the two groups of cruises carried out with the two ADCPs. The adjustment from  $S_{v\_ADCP}$  to  $S_{v\_EK60}$  was made globally for each group, assuming that the 38 cruises (150 kHz) on the one hand and the 16 others (75 kHz) on the other were comparable. Indeed, in a group, it is considered that variations in  $S_v$  values between cruises are due solely to biological and environmental effects and not to a "device effect" such as technical dependence on temperature. The influence of ambient temperature on the backscatter calculation (Appendix 2.4.5) was tested and found to be negligible (not shown). Many previous studies have used a similar approach [e.g. Ashjian *et al.* 2002, Bianchi & Mislán 2016, Blanc *et al.* 2008, Chereskin & Tarling 2007, Kaneda *et al.* 2002, Liljebladh & Thomasson 2001, Radenac *et al.* 2010, Tarling *et al.* 2001].

## 2.2.2 Environmental data

A suite of available environmental variables was selected to explore the physical drivers of backscatter data. For each backscatter location, environmental variables were obtained at the matching sampling position and date when data were available. Where real date data were not available, climatologic data were used (Table 2.2).

The bathymetry was extracted from a 500m resolution dataset [ZoNéCo, 2013], and the Euclidean distance to the closest coastline or shallow reef (0-30m) was calculated from a coastline-reef shapefile [Andréfouët *et al.*, 2008]. Sun elevation was calculated for all points with an adapted version [Blanc & Wald, 2012] of the formula given by Michalsky [1988], a function of spatial position and date. Sun elevation negative value are for Night period (from -90° to 0°) and positive value for Day (from 0° to 90°).

Several products were tested for zonal and meridional currents : a mean absolute geostrophic current climatology, based on 1000m-Argo floats combined with geostrophic currents computed from the CSIRO Atlas of the Regional Sea (CARS2009) [Kessler & Cravatte, 2013], a seasonal ADCP current climatology [Cravatte *et al.*, 2015], the ARMOR3D gridded weekly velocities derived from satellite and *in situ* observations [Guinehut *et al.*, 2004, 2012; Mulet *et al.*, 2012] and the MERCATOR-OCEAN GLORYS ocean reanalysis. Other oceanographic physical parameters used were the sea level anomaly [Pujol *et al.*, 2016], the sea surface temperature [Reynolds *et al.*, 2007], and the depth of the 20°C isotherms calculated from the ARMOR3D dataset. We used surface vector winds from Cross-Calibrated Multi-Platform (CCMP-v2), produced using satellite, moored buoy, and model [Wentz *et al.*, 2015]. One biological parameter was extracted from GlobColour project : surface chlorophyll-a [Saulquin *et al.*, 2009]. These geographic parameters and environmental dataset are detailed in Table 2.2.

To assess ENSO effect, the Oceanic Niño Index (ONI) [3 month running mean of ERSST.v5 SST anomalies in the Niño 3.4 region (5°N-5°S, 120°-170°W)] ([http://origin.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ONI\\_v5.php](http://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php)) was used. ENSO phases were defined with a 0.7 threshold on : months with an ONI above 0.7 were classified as El Niño and months with an ONI below -0.7 as La Niña.

TABLEAU 2.2 – Environmental variable summary with unit, source and resolutions detailed for each variable. Variables with an asterisk (\*) were downloaded via the Copernicus portal, CMEMS (Copernicus Marine Environment Monitoring Service) (<http://copernicus.eu/main/marine-monitoring>). Variables with (C) are climatologic.

| Variable name  | Unit  | Source  | Temporal resolution | Spatial resolution |
|--|-------|---|---------------------|--------------------|
| Bathymetry   | km    | ZoNeCo, 2013  | -                   | 500 m              |
| Distance to the closest land or reef                       | km    | from coastline and reef shapefiles  | -                   | ¼°                 |
| Sun elevation  | °     | Calculated from position and date   | -                   | -                  |
| 3D geostrophic zonal and meridional currents 30-100m mean  | cm/s  | ARGO floats and CSIRO Atlas of the Regional Sea (CARS2009)                        | Annual (C)          | ¼°                 |
| SADCP zonal and meridional currents 25-100m mean           | cm/s  | Large ADCP dataset  | Quarter (C)         | ¼°                 |
| Surface zonal and meridional seawater velocity (*)         | m/s   | MERCATOR GLORYS2V4  | Day                 | ¼°                 |
| Zonal and meridional geostrophic currents 20-110m mean (*) | m/s   | ARMOR3D   | Week                | ¼°                 |
| Sea Surface Temperature (SST) (*)                          | °C    | Advanced Very High Resolution Radiometer (AVHRR) infrared satellite               | Day                 | ¼°                 |
| Chlorophyll-a (*)  | mg/m3 | GlobColour-Processors versions : MODIS 2014.0.1/VIIRS 2014.0.2                    | Day                 | ¼°                 |
| Sea Level Anomaly (SLA) (*)                                | m     | DT all-sat-merged Global Ocean Gridded SSALTO/DUACS Sea Surface Height L4 product | Day                 | ¼°                 |
| Zonal and meridional winds (*)                             | m/s   | Cross-Calibrated Multi-Platform (CCMP-v2)   | Week                | ¼°                 |
| Depth of the 20 degrees isotherm (D20) (*)                 | m     | ARMOR3D   | Week                | ¼°                 |

### 2.2.3 Statistical model and analysis

GAM (Generalized Additive Models) [Hastie & Tibshirani, 1995] and SVM (Support Vector Machine) [Cortes & Vapnik, 1995] statistical models were used to investigate variability of backscatter echo-intensities in the New Caledonian EEZ. We studied the temporal variability (daily, monthly, multi-annually variability) in a first step and the relationships between backscatter values and environmental variables in a second step to avoid collinearity problems (*e.g.* between SST and month) (Figure 2.2). Each model used has specific advantages : GAM allows to rank the variables by relevance and to highlight the relationships between the response variables and the predictors (explanatory variables), which is interesting from an ecological point of view. However, GAM is difficult to tune while respecting strong assumptions (*e.g.* absence of autocorrelation in residuals, error distributed normally). SVM, as the state-of-the-art classification and regression algorithm, has been applied in various scientific domains and especially in ecological niche modeling [Drake *et al.*, 2006; Palialexis *et al.*, 2011]. For this method there is no requirement concerning predictors' distributions or autocorrelation [Hegel *et al.*, 2010]. Yet, it remains difficult to interpret the SVM results and there is no straightforward method for explaining the results and rank the predictors by relevance. To interpret ecological phenomena, partial dependence plots were produced by environment variables to visually explore the marginal effect of a given variable on the backscatter value while other variable are fixed to their mean values [Friedman, 2001]. SVM partial dependence plots were not presented as strong interactions exist between predictors [Goldstein *et al.*, 2015]. Subsequent models were fitted both GAMM and SVM, excluding each of the remaining terms, one at a time, to assess percentage of variation explained by predictor and we classified predictors, according to their importance in the model.

To account for autocorrelation between consecutive backscatter values we used a Generalized Additive Mixed Model (GAMM). We nested an autocorrelation structure of order 1 (*i.e.* a 10km autocorrelation structure, Ménard & Marchal, 2003), with a random effect fitted by cruises dealing with the correlation structure [Dormann *et al.*, 2007; Wood, 2006]. The absence of collinearity was checked in residuals. We used a Gaussian family with an identity link function and adopted restricted maximum likelihood (RML) as the smoothness selection criteria [Wood, 2011]. All splines were fitted with a maximum knot number of 10 to keep a relatively simple relationship. SVM uses a functional relationship to map data onto a new hyperspace in which complex patterns can be more simply represented [Drake *et al.*, 2006; Muller *et al.*, 2001]. SVM parameters were tuned (Gaussian kernel, gamma = 0.1 and cost = 10) by cross validation [Browne & Cudeck, 1989]. We calculated the root mean square error (RMSE) on the evaluation dataset by removing data from each of the 54 cruises one by one.

To account for the potential difference between the two ADCP devices, we included an ADCP device effect in all models (GAMM and SVM). Therefore, backscatter values were predicted for each ADCP device, BB150 and OS75 respectively. We then corrected the predicted  $S_v$  using the corresponding EK60 linear regressions, and finally averaged the corrected predicted values from the two devices (Figure 2.2). The effect of the ADCP device included in the each models is different. For the GAMM, it is a 'fixed effect', meaning that relationships between backscatter and covariates have the same shape but with an offset function of the ADCP device. For the SVM approach, ADCP effect is included as a binary variables (-1/1) and fitted relationships linked to ADCP device have different shapes.

We explored visually the temporal dynamic over the entire time series (1999-2017) with GAMM out-



puts. In a first step, GAMM1 allowed us to investigate relationships between  $S_{v\_ADCP}$  values and a set of temporal and spatial predictors. Six predictors were tested : the ADCP effect (BB150 or OS75) and the ENSO phase (Neutral, Niño or Niña) as qualitative variables and sun elevation (proxy for the moment of the day), year, month, latitude and longitude as quantitative variables (Figure 2.2, step 1). Year variable was smoothed with a cubic spline and month with a cyclic cubic spline. Latitude and longitude were fitted inside the same isotropic spline [Wood *et al.*, 2012] with a Gaussian process model smoothing basis [Golding & Purse, 2016; Miller *et al.*, 2013]. This spatial term was added to fit the mean spatial distribution pattern to account for difference in surveys spatial localisation across years (Appendix 2.10).

In a second step, environmental variables described in Table 2.2 (*i.e.* bathymetry, distance to the coast/reef, sun elevation, 4 currents sources, SST, chlorophyll-a, SLA, winds and d20) and a fix effect of the ADCP device were included in GAMM2 and SVM (Figure 2.2, step 2) independently of a month or year variables. All variables were smoothed with cubic splines. Predictions were done on climatological environmental variables with a  $\frac{1}{4}^\circ$  resolution grid (explicative variables resolution) and then averaged between models leading to a hybrid GAMM2-SVM prediction. A measure of the coherence between the two models was estimated through the variation coefficient (*i.e.* standard deviation divided by mean), which ranged from 0 to 7%. We applied two different standard deviation thresholds (6%, 2%) : the lower the variation coefficient threshold is, the higher the confidence is in the prediction, but the lower the number of cells predicted is. We used two statistical models to compare large spatial predictions, combine common patterns [Oppel *et al.*, 2012] and to ensure that conclusions are robust to the underlying statistical assumptions. Before constructing models, we confirmed that collinearity was not apparent among the predictors using variance inflation factors (VIF) [O'brien, 2007] and Spearman correlations between each pair of covariates. We considered covariates were not collinear when both Spearman correlations were inferior to 0.5 and VIF were inferior to 3.

The GAMM1 assesses the seasonal cycle by fitting a 'month' variable as a continuous variable. GAMM2-SVM does not use a temporal variable to explicit seasonality but use relationships with environmental variables (such as SST) in which seasonality is inherent to predict backscatter values at each point and finally the seasonal cycle is assessed by averaging all EEZ predicted values by month.

All statistical analyses were performed with R (version 3.5.0, R Core Team 2016). GAMMs were fitted using the *gamm* function of R package *mgcv* [Wood, 2017]. SVM was fitted using the *svm* function of R *e1071* package [Meyer *et al.*, 2017].

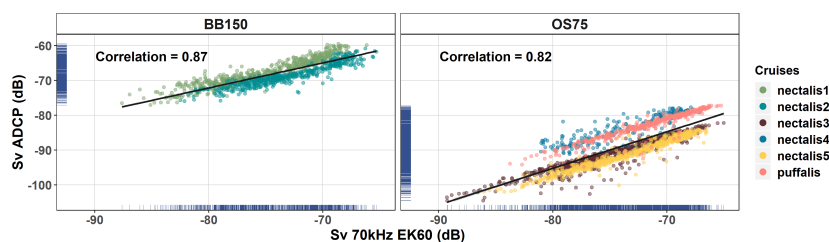


FIGURE 2.2 – Diagram explaining the different steps of the analysis. For models GAMM1, GAMM2 and SVM, purple variables are numerical and orange variables are qualitative.

## 2.2.4 SEAPODYM simulation

The sub-model of SEAPODYM for mid-trophic levels (MTL) simulates several functional groups of micronekton for the oceanic epi- and mesopelagic layers [Lehodey *et al.*, 2015, 2010]. The spatial and temporal dynamics of production and biomass are modelled with a system of advection-diffusion-reaction equations driven by ocean temperature, horizontal currents, primary production and euphotic depth. Currently, there are six groups of micronekton defined according to the Diel Vertical Migration (DVM) patterns of mesopelagic organisms between three broad epipelagic, upper and lower mesopelagic vertical layers. The euphotic depth  $Z_{eu}$  is used to define the depth boundaries of the vertical layers :  $0-1.5*Z_{eu}$  for the epipelagic layer,  $1.5-4.5*Z_{eu}$  for the mesopelagic layer and  $4.5-10.5*Z_{eu}$  for the bathypelagic layer. In New Caledonia,  $Z_{eu}$  is around 70-75m hence the epipelagic layer in the model occupies the top 110m. During the day, only the epipelagic group inhabits the epipelagic layer, but during the night, it also includes the migrant upper-mesopelagic and highly migrant lower mesopelagic groups.

We compared the predicted backscatter to SEAPODYM-MTL modelled micronekton biomass. We used SEAPODYM-MTL micronekton simulation for the 1999-2017 period. The biomass of micronekton groups inhabiting the epipelagic layer at night was extracted at the date and places of the ADCP data. Values were centered (the mean was subtracted) and scaled (divided by the standard deviation) for both SEAPODYM and acoustics models. Biomass values were compared along the tracks by calculating correlations, and distribution patterns compared over the whole New Caledonian EEZ.

## 2.3 Results

A total of 89530km of survey track across 435 days (288 days for the 150 kHz and 147 for the 75 kHz ADCP) over 19 years were analyzed in this study. All quarters were sampled at least nine times during the study period (Table 2.1 and Appendix 2.4.5) and the whole Exclusive Economic Zone was surveyed at least once except a small area in the south east corner of the EEZ, and an area in the south west below Chesterfield Reefs (Figure 1.1).

### 2.3.1 Comparison to EK60 values

We compared the un-calibrated ADCP acoustic data to the calibrated EK60 echosounder data. Two cruises were available with concomitant 150 kHz  $S_{V\_ADCP}$  and  $S_{V\_EK60}$  records (1110 paired values) and four cruises with 75 kHz  $S_{V\_ADCP}$  and  $S_{V\_EK60}$  (1955 paired values). For both ADCP frequencies, correlations between mean 20-120m  $S_{V\_ADCP}$  and  $S_{V\_EK60}$  were significant and higher than 0.8 (Figure 2.3). The two regressions were significant (p-values <0.01) and had different slopes : 1.05 (standard error 0.017) for the 75 kHz ADCP and 0.72 (standard error 0.012) for the 150 kHz ADCP (Table 2.3). For the 75 kHz, the data scatterplot from Nectalis 4 and Puffalis on one side, and from Nectalis 3 and Nectalis 5 on the other side, could warrant the estimation of different intercepts (Figure 2.3).

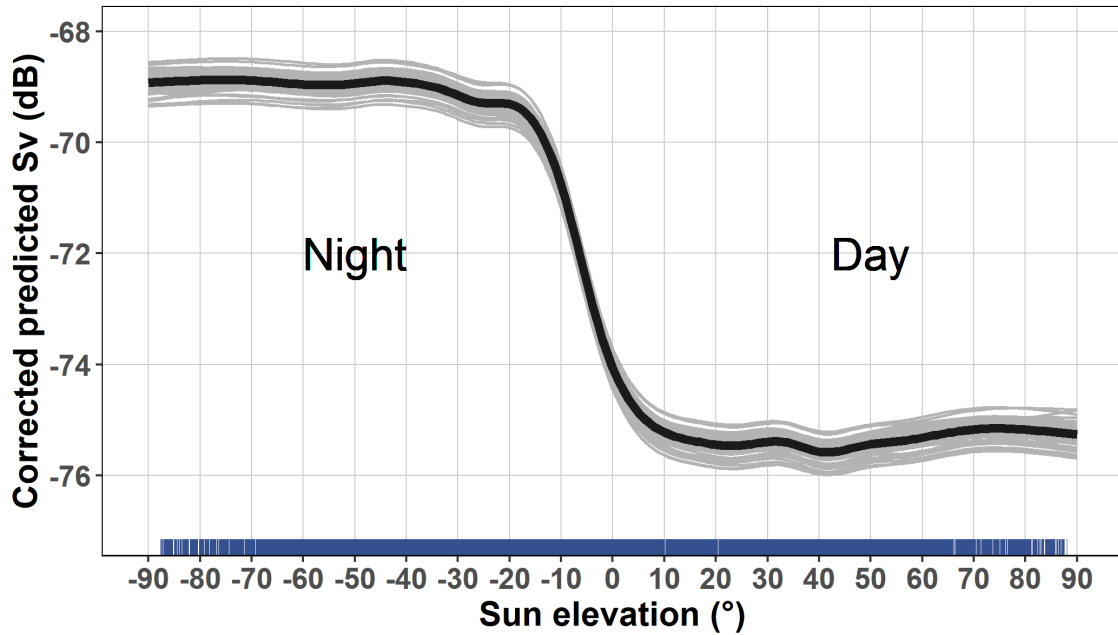


FIGURE 2.3 – ADCP backscatter ( $S_v$ ) as a function of the 70 kHz EK60 echosounder  $S_v$  and the associated linear regressions (black line) for the 150 kHz ADCP device (BB150, Nectalis 1 and 2) (left) and the 75 kHz ADCP (OS75, Nectalis 3, 4, 5 and Puffalis) (right). Blue ticks on both axis show the distribution of the observations.

TABLEAU 2.3 – Linear regression analysis outputs including the intercept, the slope, the slope standard error and p-value, the deviance explained (or  $R^2$ ) and the number of observations for each ADCP device.

| ADCP device | Intercept | Slope | Slope standard error | Slope p-value | Deviance explained | n    |
|-------------|-----------|-------|----------------------|---------------|--------------------|------|
| OS75        | -11.32    | 1.05  | 0.017                | <2e-16        | 67                 | 1955 |
| BB150       | -14.64    | 0.72  | 0.012                | <2e-16        | 76                 | 1110 |

### 2.3.2 Temporal variability of backscatter

Temporal variability of backscatter micronekton was analyzed at three scales : daily, monthly and yearly using a GAMM including all  $S_{v\_ADCP}$  values (night and day) as a function of ADCP device, sun elevation, year, ENSO phase, month and location (latitude and longitude) with a nested auto-correlative model (Figure 2.2, left part). In this model, the largest part of the variance was explained by the sun elevation (Table 2.4).  $S_{v\_ADCP}$  in the 20-120m layer was higher during the night than during the day (respectively -69dB and -75dB) (Figure 2.4), with a 6dB difference. The usual value used as a density proxy is the linear value ( $s_v$ ), so a 6dB difference meant that the micronekton density was about 4 times higher during the night than during the day in the 20-120m layer.  $S_{v\_ADCP}$  values were constant during the night, but started to decrease at dawn when the sun elevation exceeds  $-20^\circ$ . The variance explained by the sun elevation demonstrated the important impact of the diel vertical migration in the 20-120m layer. The second most important variable was the effect of the ADCP device (Table 2.4).

Month was the third variable explaining the variance of  $S_{v\_ADCP}$  (Table 2.4). The seasonal cycle displayed a maximum in March (-70.8dB), and a minimum in September (-74.3dB), with two superimposed relative maxima in July and November (-71.8dB and -72.8dB respectively) (Figure 2.5). The difference between extreme values was about 3.5dB, meaning there was in average 2 times more biomass during March than during September, 1.6 more in July and 1.4 more in November compared to September. The

54 cross-validation simulations (Figure 2.5) confirmed the robustness of the seasonal cycle.

The variance explained putted the year variable at the 5<sup>th</sup> rank and ENSO at the 6<sup>th</sup> rank (Table 2.4). The relationship between the  $S_{V\_ADCP}$  and the year was non-linear with a minimum and a maximum (Figure 2.6 A). Predicted  $S_{V\_ADCP}$  were about -73dB in 1999, decreased to a minimum of -75dB in 2007 and reached a maximum of -71.5dB in 2017. So, on average the acoustic density decreased by 1.6% between 1999 and 2007 and then increased by 2.2% between 2007 and 2017. The ENSO phase effect was significant in the GAMM1 :  $S_{V\_ADCP}$  was twice as high during El Niño phase than during a neutral phase (Figure 2.6B), and the  $S_{V\_ADCP}$  during La Niña phase was not significantly different from the value during the neutral phase.

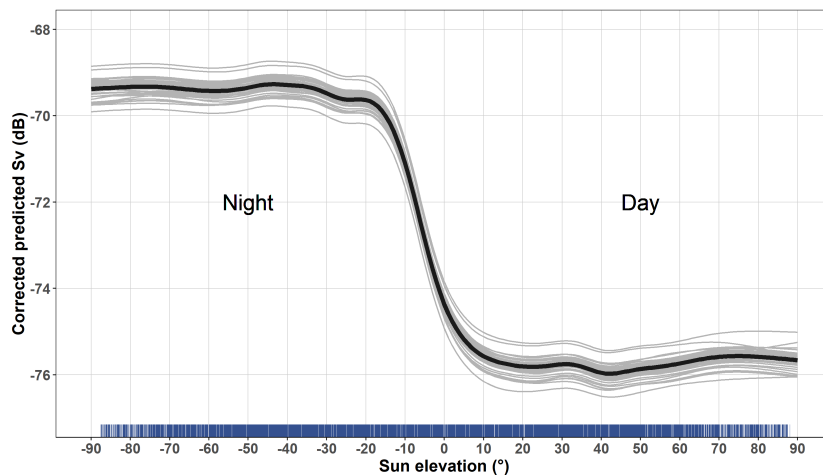


FIGURE 2.4 – GAMM1 partial dependence plot showing the effect of the sun elevation on corrected backscatter values ( $S_v$ ). The solid grey lines are the estimates of the smooths for the 54 simulations from cross-validation and the black line is the average smooth. Blue ticks on the inner X-axis show the distribution of the observations.

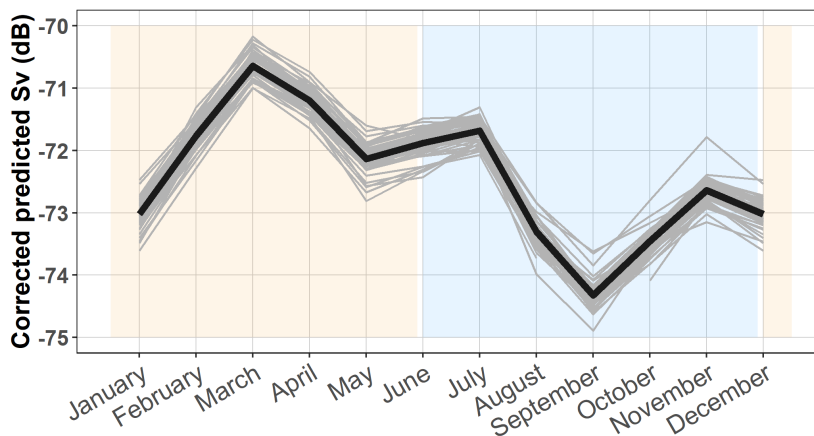


FIGURE 2.5 – GAMM1 partial dependence plot showing the effect of the month on corrected backscatter values ( $S_v$ ). The solid grey lines are the estimates of the smooths for the 54 simulations from cross validation and the black line is the average smooth. Cold season is indicated in blue and warm season in orange.

### 2.3.3 Estimating ecological relationships

To investigate the impact of environmental variables on  $S_{V\_ADCP}$ , values during the night only ( $S_{V\_ADCP\_night}$ ) were fitted through both a GAMM2 (with a nested auto-correlative model) and a SVM with environmen-

TABLEAU 2.4 – Model summary with the model name, the response variable, the explicative variables, the total deviance explained (or  $R^2$ ) and the rank of importance by variable. All predictors were significant in the GAMMs output (p-values < 0.05). An asterisk (\*) indicates that an auto-correlative model is nested into the GAMM.

| Model     | Response variable    | Explicative variables | Deviance explained | Rank of importance by variable |
|-----------|----------------------|-----------------------|--------------------|--------------------------------|
| GAMM1 (*) | $S_{v\_ADCP}$        | Sun elevation         | 63.9               | 1                              |
|           |                      | year                  |                    | 5                              |
|           |                      | month                 |                    | 3                              |
|           |                      | Lat * lon             |                    | 4                              |
|           |                      | ENSO_phase            |                    | 6                              |
|           |                      | ADCP_device           |                    | 2                              |
| GAMM2 (*) | $S_{v\_ADCP\_NIGHT}$ | SST                   | 58.1               | 2                              |
|           |                      | D20                   |                    | 4                              |
|           |                      | Log_chloro            |                    | 3                              |
|           |                      | Bathy                 |                    | 5                              |
|           |                      | Dist_coast            |                    | 6                              |
|           |                      | ADCP_device           |                    | 1                              |
| SVM       | $S_{v\_ADCP\_NIGHT}$ | SST                   | 77.9               | 2                              |
|           |                      | D20                   |                    | 3                              |
|           |                      | Log_chloro            |                    | 6                              |
|           |                      | Bathy                 |                    | 4                              |
|           |                      | Dist_coast            |                    | 5                              |
|           |                      | ADCP_device           |                    | 1                              |

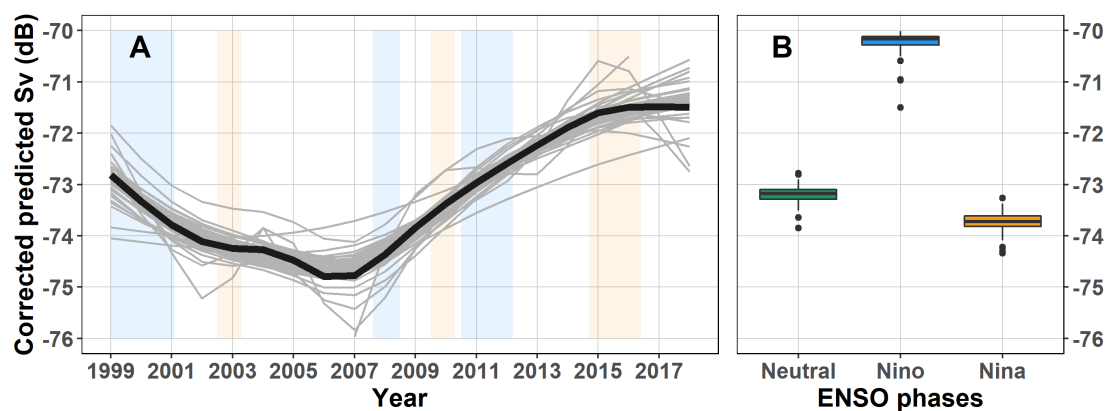


FIGURE 2.6 – GAMM1 partial dependent plot terms showing the effect of year (A) and ENSO phases (B) variables on corrected backscatter values ( $S_v$ ). The solid grey lines are the estimates of the smooths for the 54 simulations from cross validation and the black line is the average smooth. El Niño events are indicated in blue on panel A, and La Niña events in orange.

tal variables and an effect on ADCP device (150 kHz or 75 kHz) (Figure 2.2, right part). We focused this part of the study on nighttime values to reveal the potential influence of environmental parameters that could have been masked by the strong impact of the sun elevation on backscatter. The night signal was preferred over the day signal as in the layer 20-120m it better represents the micronekton community by accumulating both permanent epipelagic organisms and migrating organisms coming from deeper layers.

Based on Spearman correlation tests and VIF, depth of isotherm 20°C (d20) and SLA were correlated, which required selecting only one of those variables to be included in the model. As SLA was not significant for the GAMM2, we chose to keep d20 in the final model. The zonal and meridional currents and

wind data were un-significant in the GAMM2; relationships were flat thus they were not considered further in the models (GAMM2 and SVM). The final models included SST, chlorophyll-a, depth of the 20°C isotherm, distance to the coast/reef, bathymetry and the effect of the ADCP device for both SVM and GAMM2.

After considering the ADCP device effect, the two statistical methods mostly agreed on the relative contribution of variables (Table 2.4) with SST demonstrating the main effect among the oceanographic variables. The contribution rank of the chlorophyll-a was different between the GAMM2 and the SVM : chlorophyll-a was the second most important variable for the GAMM2 and the last (6<sup>th</sup>) for the SVM. Then, in descending order of importance, we found the 20°C isotherm depth, the bathymetry and the distance to the closest coast/reef.

The relationship between backscatter value and distance to the closest reef/coast was linearly decreasing, with higher values closer to the coast (Figure 2.7A). The influence of the bathymetry was not linear, but an optimum of the 20-120m backscatter value was observed over a sea floor at 1800m depth (Figure 2.7B). Relationship with SST was increasing non-linearly, with a first optimum around 24°C and a rise from 26 to 31°C (Figure 2.7C). The chlorophyll-a concentration relationship was also increasing; the backscatter value was higher with higher chlorophyll-a concentration (Figure 2.7D). The relationship with the 20°C isotherm depth was decreasing : the mean backscatter value was higher when the isotherm was shallower (Figure 2.7E). All relationships were significant according to GAMM outputs and the variability through cross validation was small over almost all the variable ranges showing robustness of the model (Figure 2.7).

### 2.3.4 Predicted spatial distribution

Predicted distribution patterns of the GAMM2-SVM hybrid-model backscatter during the four quarters are shown on Figure 2.8. We defined the austral summer or the warm season as the DJF (December, January and February) and MAM (March, April and May) quarter periods and the austral winter or the cold season as JJA (June, July and August) and SON (September, October and November) quarters. This definition was chosen relative to the common knowledge of these seasons in New Caledonia [Cravatte *et al.*, 2015]. Spatial predictions were highly homogenous across one season (DJF is very similar to MAM and identically for JJA and SON) (Figure 2.8A).

Generally, values were higher during the warm season. During this season the distributions showed aggregations of high values in the central part of the EEZ in a wide strip area with a south-east to north-west orientation encompassing the main island and the Loyalty islands where there was a high confidence in the predictions (refer to Figure 2.1 for islands and reefs names). The values were particularly high north of 22°S (Figure 2.8A, DJF and MAM) and around the Chesterfield Reefs. There were lower values in the southeastern corner of the EEZ. The channel between the group made of Chesterfield Reefs, Bellona, Fairway-Landsdowne, and the main island was also predicted to have lower values.

During the cold season, there were lower values in the north close to the coast of the main island and in the south along the edges of the EEZ (Figure 2.8A, JJA and SON). Highest values during the cold season were located south of 20°S, south of the main island, south of the Chesterfield Reefs and north of the southeast corner of the EEZ where there was a higher prediction divergence between the GAMM2 and

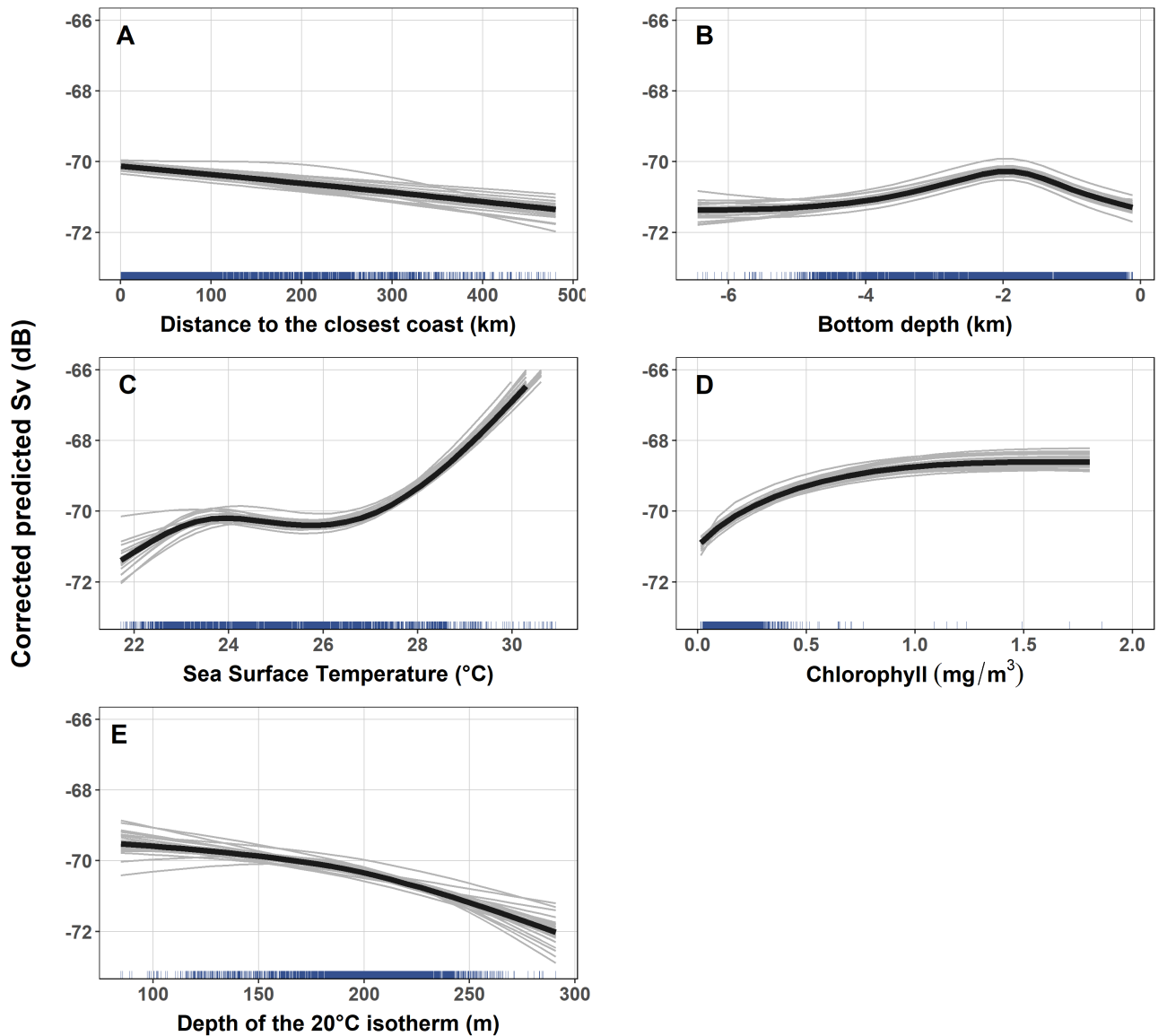


FIGURE 2.7 – GAMM2 partial dependent plot terms showing the effect of various continuous variables on corrected backscatter values (Sv). The solid grey lines are the estimates of the smooths for the 54 cross-validation simulations and the black line is the average smooth. Blue ticks on the X-axis show the distribution of the observations.

SVM and thus less confidence was given to results in this area. Along the southwest main island coast, high values were farther to the coast than during the warm season.

There was good agreement between the predictions of the two models (variation coefficient ranges from 0 to 7 %) for most of the New Caledonian EEZ (Figure 2.8B). However, discrepancies between the GAMM2 and SVM were observed in some areas, with relatively high model variation coefficients in the north of the EEZ, in the north of the southeastern corner of the EEZ and the Fairway-Landsdowne Bank for the cold season; and, the north of the main island for the warm season. Using a 6% threshold for the variation coefficient removed only 0.17% of the cells (0.084% for DJF, 0.034% for MAM, 0.53% for JJA and 0.042% for SON) whereas 28% of cells were removed for a 2% threshold for the variation coefficient (31% for DJF, 30% for MAM, 27% for JJA and 22% for SON).

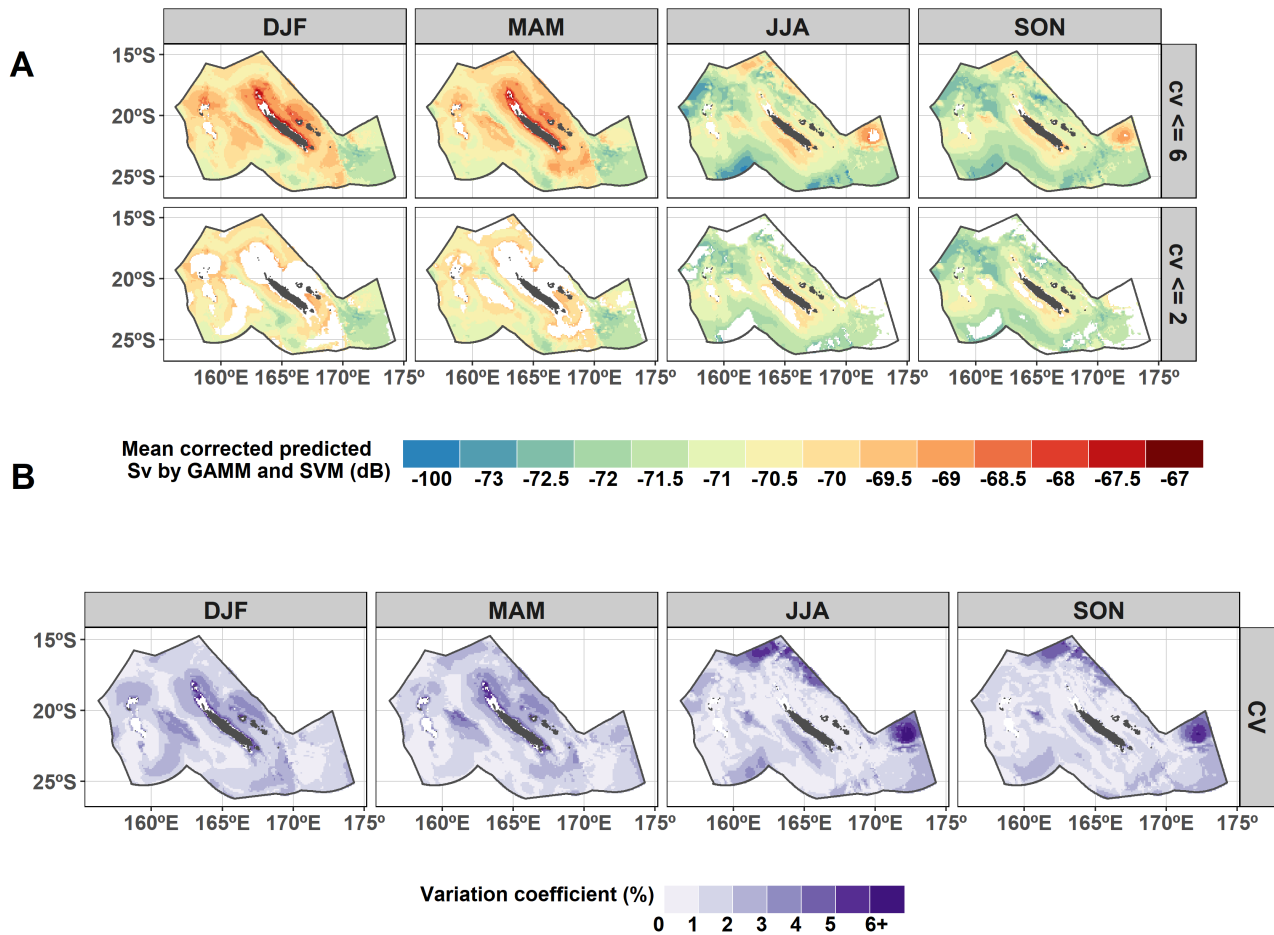


FIGURE 2.8 – Corrected backscatter values at night predicted on average by GAMM2 and SVM1 in New Caledonia Exclusive Economic Zone by quarter with two different thresholds applied to variation coefficient (panel A, top row : 6%, bottom row : 2%), and the associated variation coefficient (panel B). Warm season : DJF (December, January, February) and MAM (March, April, May) and cold season : JJA (June, July, August) and SON (September, October, November).

### 2.3.5 Comparison with SEAPODYM-MTL

Correlation between the observed 20-120m backscatter and the SEAPODYM-MTL values, extracted at the dates and locations of the cruise tracks was close to zero and non-significant, suggesting an absence of direct coherence between the two sources. We then compared the seasonal patterns of the output of the GAMM2-SVM gridded predicted model of backscatter to the seasonal SEAPODYM-MTL outputs. The warm and cold seasons were calculated as the averages of the two quarters composing each season. Within each season, we kept the data with CV ≤ 6% to keep the largest dataset in the hybrid model.

During the cold season (June to November) the GAMM2-SVM and the SEAPODYM-MTL models showed different spatial patterns (Figure 2.9A). In SEAPODYM-MTL simulations, high values were located in the southern part of the EEZ in oceanic waters close to the EEZ boundary while in the GAMM2-SVM, this area was characterized by low values, and high values were close to the main island southern coast. However, in the two cases, values were low in the northern part. During the warm season (December



to May), SEAPODYM-MTL spatial distribution pattern was similar to the SEAPODYM-MTL austral winter pattern with enhanced values. The difference between SEAPODYM-MTL and the GAMM2-SVM predictions based on observed acoustic data was stronger during the warm season than during the cold season with higher values around islands and reefs in the GAMM2-SVM predictions. For the two seasons, SEAPODYM-MTL spatial distribution showed a north-south gradient that the acoustic data does not show. The spatial structures provided by the GAMM2-SVM predictions were spatially more detailed than in SEAPODYM-MTL. For the two seasons, the Spearman correlations were very low ( $< 0.2$ ). In SEAPODYM-MTL, the predicted biomass level changed but the spatial distribution staid similar over seasons, whereas in the GAMM2-SVM predictions, a spatial distribution change over the seasonal cycle was observed as well as a change in the mean level.

The seasonal cycle coming from our GAMM2-SVM hybrid model showed increased acoustic density during austral summer and decreased density during austral winter (Figure 2.9B). The seasonal cycle showed a 3 months lag between the GAMM2-SVM predictions and the SEAPODYM-MTL and seasonal variability was much weaker in SEAPODYM-MTL than in the GAMM2-SVM predictions. The peak was in December for SEAPODYM-MTL (averaged scaled values over the EEZ) while the highest peak was in February on average for the GAMM2-SVM outputs (Figure 2.9B). The seasonal cycle from acoustic data was mainly driven by change in the North of the EEZ while the SEAPODYM seasonal cycle seemed to be due to change in the biomass level in both the north and the south (Figure 2.9A).

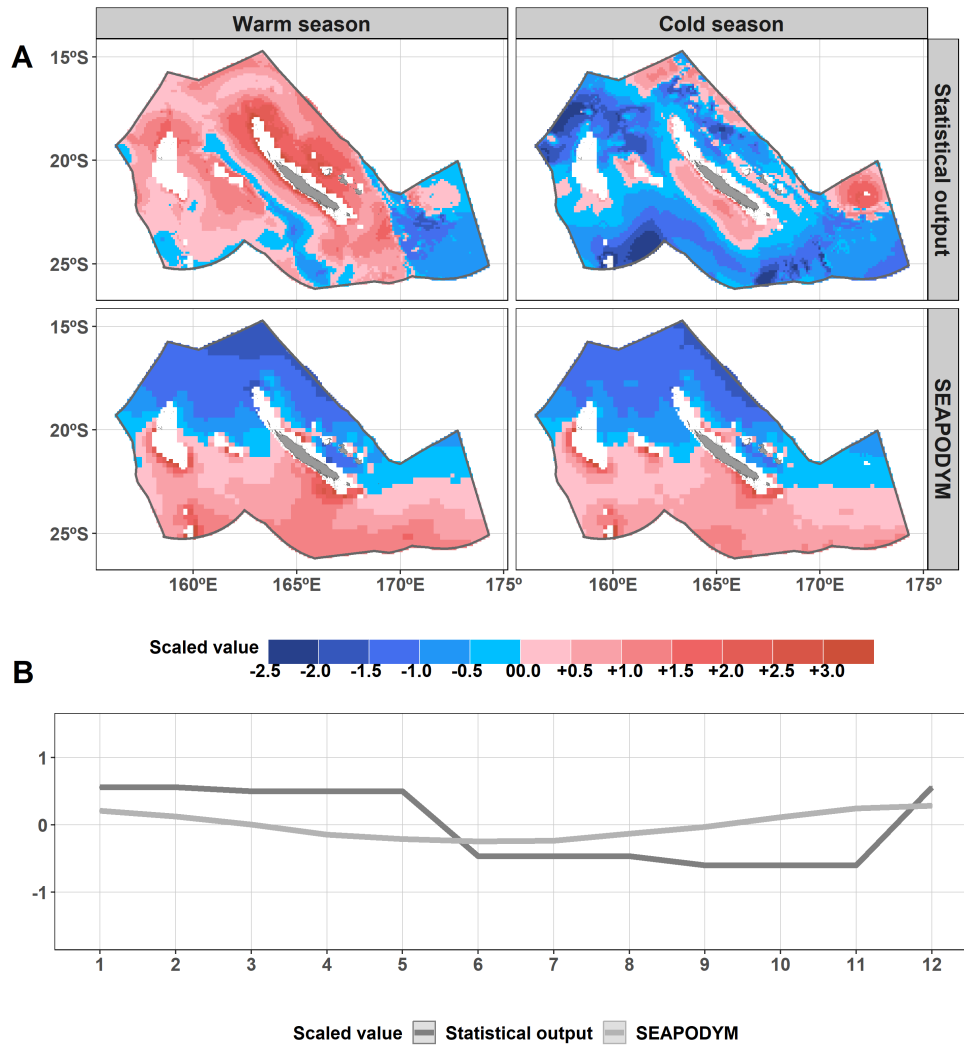


FIGURE 2.9 – Corrected backscatter values predicted on average for the hybrid GAMM2/SVM model with a variation coefficient inferior to 6% (Statistical output, Panel A, top row), and SEAPODYM-MTL model (panel A, bottom) averaged by season. Only cells predicted by SEAPODYM-MTL are shown in both rows of panel A. Same data averaged by month (panel B). Values on the three panels are scaled and centered for comparison.

## 2.4 Discussion

Backscatter values from 54 ADCP surveys at 75 kHz and 150 kHz over 19 years (1999-2017) were used to examine micronekton dynamics in the upper 120m of the ocean in the New Caledonian EEZ (south-west Pacific), assuming that micronekton density was proportional to the backscatter values. A strong diel signal was found as well as a clear seasonal cycle, an effect of El Nino and a longer-term temporal trend. The link to environmental variables such as SSTs, surface chlorophyll, depth of 20°C isotherm, bathymetry, and distance to coast were studied. A hybrid model constructed with two statistical models (GAMM2 and SVM) was used for predictive statistical modelling of backscatter values. A large variability in spatial distribution was found over seasons. Those spatial distributions were quite different from separate SEAPODYM-MTL model simulations.

### 2.4.1 ADCP-EK60 comparison

The lag between mean ADCP levels was relatively large, about 20dB. Due to the absence of similar offset among EK60 Nectalis data (Figure 2.3), this lag was linked to the reported ADCP device change and not to a biological effect. High positive correlations between the 70 kHz  $S_{v\_EK60}$  and the 150 kHz and 75 kHz  $S_{v\_ADCP}$  have been previously observed in other regions [Brierley *et al.*, 1998; Griffiths, 1996]. Based on the positive correlations, data from both ADCP devices could be combined and analyzed as one dataset when adjusted to a common EK60 reference. With this methodology, we studied data from ADCP at different frequencies to obtain a long time series for the present region (19 years by aggregating the data from the two devices including 12 years for the 150 kHz and 7 years for the 75 kHz).

Although the relationships with the EK60 reference signal allowed combining data from the two ADCP devices, uncertainty remained among cruises using the same ADCP device. By analyzing the 54 cruises together, the methodology assumed that cruises performed with each ADCP device (38 cruises for the 150 kHz and 16 cruises for the 75 kHz) were comparable, *i.e.* that relationships found between  $S_v$  and environmental variables or across time were due to biological change and were not linked to a device temperature dependence for example. We based this hypothesis on previous studies where several ADCP cruises are aggregated to analyze them together [*e.g.* Ashjian *et al.* 2002, Bianchi & Mislan 2016, Blanc *et al.* 2008, Chereskin & Tarling 2007, Kaneda *et al.* 2002, Liljebladh & Thomasson 2001, Radenac *et al.* 2010, Tarling *et al.* 2001]). Moreover, regression curves for EK60 signal for one cruise (one color on Figure 2.3) were linear whereas the cruises covered areas including large variations of temperature, particularly between the north and the south of the EEZ (Figure 2.1). This analysis indicated a constant survey dependent shift rather than an environmental effect such as a device dependence to temperature. Finally, we had no other choice than using a unique set of estimated regression parameters for all the cruises as only 6 cruises with EK60 data were available. For future studies using S-ADCPs, we would recommend recording EK60 reference transects at least once a year for calibration.

While the size-range of organisms detected by ADCP was not defined precisely, both ADCP devices were thought to detect a broad range of organisms from macro-zooplankton to micronekton in the 20-120m layer. Smeti *et al.* [2015] using data from zooplankton nets and TAPS (Tracor Acoustic Profiling System) concluded 150 kHz ADCP is appropriate to detect organisms such as macro-zooplankton. The

very high correlations of the ADCP signal with EK60 at various frequencies as presented in [Menkes \*et al.\* \[2015\]](#) and in the present study confirm the contribution of the micronekton to the 70 and 75 kHz ADCP backscatter.

## 2.4.2 Environmental predictors

All relationships between ADCP backscatter and environmental variables had relatively simple and smooth shapes.

The relationship between SST and Sv was increasing and non-linear, reaching a first maximum at 23.5°C and then a second above 26°C after a significant rising slope. There were fewer SST values sampled above 28°C, and so the relationship had to be taken with caution above 28°C. This type of relationship with two temperature optimums could express contrasted situations either spatially, *e.g.* as in [Boersch-Supan \*et al.\* \[2017\]](#) or by season as observed in the Gulf of Maine [[Hazen \*et al.\*, 2009](#)]. In the present study, it seemed due to a clear difference between warm and cold seasons but also between north and south regions.

The relationship between backscatter and chlorophyll-a (proxy of primary production) showed an increase with a plateau in higher values. [Escobar-Flores \*et al.\* \[2013\]](#) found a strong correlation to chlorophyll-a (used as a proxy for the primary productivity) and the acoustic backscatter at the scale of the entire south Pacific. However, they obtained a bell-shaped relationship instead of the plateau predicted in our study. Their maximum backscatter was obtained for about 0.5 mg.mm<sup>-3</sup> chlorophyll-a concentration, very similar to the found asymptotic chlorophyll-a concentration value. At the global scale, a similar strong positive link was found between the 38kHz acoustic backscatter (EK60 echosounder) in the mesopelagic layer and satellite derived primary production [[Irigoiien \*et al.\*, 2014](#)]. However, [Boersch-Supan \*et al.\* \[2017\]](#) in the Indian Ocean and [Hazen & Johnston \[2010\]](#) in the central equatorial Pacific did not find such significant relationships suggesting that they may be ecosystem or region dependent. In any case, understanding the mechanisms that link chlorophyll or primary productivity and micronekton requires the understanding of the intermediate zooplankton compartment; hence measuring at the same time phytoplankton, zooplankton and micronekton is required to better understand the interaction processes in the lower trophic compartments.

We found that the backscatter decreased gradually with increasing distance to the coast. Especially, the backscatter values increased close to the reef during the warm season (DJF and MAM). This pattern was seen both for the main island and for the Chesterfield Reefs. It could be linked to an intensification of primary productivity close to the coast, and conversely more oceanic patchiness offshore [[Escobar-Flores \*et al.\*, 2013](#)]. Shallow waters offer a reduced habitat for mesopelagic organisms and induce a densification of the different functional groups that they constitute [[Escobar-Flores \*et al.\*, 2018](#); [Lehodey \*et al.\*, 2010](#)]. Low backscatter values far to the reef can also be linked to change in species composition, with species responding differently to acoustic frequencies. For example, in the Southern Ocean, a clear change in species composition was observed between the neritic zone and the oceanic zone [[Duhamel \*et al.\*, 2000](#); [Koubbi \*et al.\*, 2011](#)]. In the Southern California Bight, [Davison \*et al.\* \[2015b\]](#) observed what they called a “seasonal basin effect” that they found to be consistent with blooms of the siphonophore *Nanomia bijuga*. In the Southern Ocean between New Zealand and the Ross Sea, [Escobar-Flores \*et al.\*](#)

[2018] found that while the backscatter (38 kHz) consistently and significantly decreased from north to south, higher biomass of mesopelagic fish were estimated from net sampling in the central region. Clearly, in absence of *in situ* sampling the acoustic data alone could be misleading and this was discussed further in the modelling section below.

Bathymetry and distance to the coast were not correlated because of the New Caledonian EEZ complex topography. Relationship between the backscatter and bottom depth showed an optimum around 2000m depth. The areas with a bottom depth between 1500m and 2500m were located between the main island and the Loyalty islands and south the main islands as well as around Chesterfield, Bellona, Fairway and Lansdowne and they did include seamounts. Seamounts can have an aggregation effect for micronekton as demonstrated by other studies, but it highly depends on the type of seamount (*e.g.* seamount shape, seamount depth, upwelling presence) and the type of organisms as not all species are aggregating around seamounts [Drazen *et al.*, 2011; Morato *et al.*, 2008, 2010]. From our study, we could not conclude of any direct seamount aggregation effect. A better characterization of these seamounts would be necessary, including variables such as distance to the seamount and typology, *e.g.* depth of the summit, shallow or deep and sharp or flat morphology.

Higher backscatter values were found when the 20°C isotherm was closer to the surface, but with a larger confidence interval before 150m depth and after 250m where sampled values were more scattered. The depth of the 20°C isotherm was a proxy for the thermocline location. A deep 20°C isotherm (and thus thermocline) likely limits possible nutrients inputs in the euphotic surface layer [Kessler & Cravatte, 2013]. On the contrary, the closer it is to the surface, the higher the vertical mixing is in the surface layers bringing more nutrients to the photic layer, and the more productive the surface layer is. This productivity increase propagated through the food web as potentially detected here and in other studies [Benoit-Bird & McManus, 2012; Lebourges-Dhaussy *et al.*, 2014]. Therefore, together with biogeochemical variables and sea surface temperature, the 20°C isotherm appeared an interesting proxy of the thermocline in the context of climate change to understand and monitor the impacts of increased temperature and vertical stratification of the water column on prey availability for top predators [Ceccarelli *et al.*, 2013; Choy *et al.*, 2016]. The 20°C isotherm is also used to characterize mesoscale activity with deeper closed-contours of 20°C isotherm characterizing anticyclonic “downwelling-type” eddies and shallower 20°C closed-contours isotherms characterizing cyclonic “upwelling-type” eddies. Eddy activity is relatively important around New Caledonia as mentioned in introduction. Previous studies have demonstrated a positive impact of eddies on the primary production [Chelton *et al.*, 2011; Gaube & McGillicuddy, 2017; McGillicuddy *et al.*, 2007] and some impacts on zooplankton [Goldthwait & Steinberg, 2008; Hauss *et al.*, 2016; Lebourges-Dhaussy *et al.*, 2014]. The relationship with micronekton was less clear and sometimes contradictory or specifically related to observed eddies [Behagle *et al.*, 2014; Brandt, 1983; Griffiths & Wadley, 1986; Sabarros *et al.*, 2009]. Further studies to determine how eddies could affect the backscatter and the micronekton should include specific metrics to eventually propose a typology.

Finally, we did not test a possible effect associated to the dissolved oxygen concentration because oxygen is not limiting in this sub-tropical zone. Furthermore, oxygen is especially important for the maximum depth of migration [Bertrand *et al.*, 2010; Bianchi *et al.*, 2013b; Maas *et al.*, 2014] which is not a parameter that we consider in this study limited to the nighttime abundance in the 20-120m layer.

### 2.4.3 Variability of acoustic backscatters in the New Caledonian EEZ

#### Mean spatial distribution

Without independent dataset to validate our predicted distributions, the use of two different modeling approaches offered an alternative to assess the prediction robustness. GAMMs have been largely used to explain backscatter value variability with environmental data [Bertrand *et al.*, 2004; Boersch-Supan *et al.*, 2017; Escobar-Flores *et al.*, 2018; Hazen & Johnston, 2010]. Machine learning algorithms like SVM have been used for species distribution modeling [Drake *et al.*, 2006] but not yet applied to acoustic data. One major difference between models was how they dealt with interaction terms : GAMM relationships between  $S_v$  and environmental variables had the same shape for the two ADCP devices, whereas SVM relationships had different shapes. The underlying assumption was that depending on the ADCP frequency, organisms could respond differently and thus could show different responses to oceanographic variables. As we did not know what the reality was and as quadratic errors for the two models were very close, assuming common patterns seemed to be a reasonable way : the use of the two methods concurrently increased the confidence that we had in predictions. Moreover, predicted spatial patterns were also coherent with the one based on GAMM1 that included latitude and longitude instead of environmental predictive variables (Appendix 2.4.5). However, acoustic data remained relatively complicated to analyze due to the high collinearity level that was difficult to include in statistical models and to understand due to a persistent uncertainty about which organisms were measured.

The two approaches, GAM and SVM, generally agreed with some exceptions. Both models predicted higher backscatter close to the reefs during the warm season and in the southern part of the EEZ during the cold season. These areas were characterized by high chlorophyll-a concentration, warm waters, close to the coast and an optimum bathymetry. The main island western coast seemed to be a favorable habitat all year long. On the contrary, low predicted backscatter values in the south of the EEZ during the austral winter (Figure 2.8A) were in the highest chlorophyll-a concentration waters. The SST may be too low, despite the high chlorophyll-a concentration, to be favorable to backscatter values. The combination of all those intertwined environmental parameters determined the value of the backscatter at a specific location and time and defined the micronekton habitat.

The areas where the two models diverged the most were the northern part of the southeast corner of the EEZ, the Fairway-Landsdowne Banks, and the northern part of the EEZ. Those areas had been all sampled several times (Figure 1.1). The variability predicted by the models could be linked to the variability in oceanographic variables used as predictors or in observed scattering values.

#### Temporal variability

Not surprisingly, the largest variability in abundance of micronekton in the observed layer (20-120 m) was associated to the DVM, which is a well-known ubiquitous phenomenon [Bianchi & Mislán, 2016]. Sun elevation was found to explain the largest part of  $S_{v\_ADCP}$  variability with higher values during the night than during the day.  $S_{v\_ADCP}$  became constant across a 24 hours cycle when sun elevation was lower than  $-20^\circ$  for the night and higher than  $10^\circ$  for the day. The sun elevation thresholds values were close to the values used in SEAPODYM-MTL to define a 'night period' and a 'day period' [Lehodey *et al.*, 2015].

The difference in the mean backscatter value between Night and Day was coherent with previous results [Domokos, 2009].

Backscatter echo intensity was globally higher during the warm season (February-March) and lower during the cold season (July-August) with a clear seasonal cycle both by the GAMM1 results (Figure 2.5) and the second hybrid GAMM2/SVM, thus providing a robust result. The secondary peaks in the seasonal cycle could be linked to different rates of recruitment and mortality according to the species and so different optima inducing different peaks in species abundance over the year. This hypothesis was reinforced by the fact that areas predicted as favorable habitat changed across years (Figure 2.8A), and may be due to favorable habitat for different species. Such variability could be expected given the high diversity of micronekton observed in the region, with more than 480 species of fishes, crustaceans, squids and gelatinous organism [Payri, 2018].

A significant influence of ENSO on the acoustic densities was detected in the EEZ, with higher values during El Niño compared to La Niña or neutral years. We showed that micronekton density increased with both increasing surface chlorophyll-a and SST (Figure 2.7). El Niño is characterized by colder SSTs [Delcroix & Lenormand, 1997] but more productive waters in New Caledonian EEZ [Dandonneau & Gohin, 1984; Radenac *et al.*, 2012]. Therefore, we suggested that the chlorophyll effect (positive anomaly) associated to El Niño was stronger than the temperature (negative anomaly) effect to explain higher backscatter during El Niño. Additionally, we knew that ENSO may impact micronekton species, especially on their recruitment [Hewitt *et al.*, 2003; Quetin & Ross, 2003]. Such mechanisms also likely occurred in New Caledonian waters.

An interesting long-term temporal trend was also observed over the 1999-2017 time period, with 8 years of acoustic density decrease from 1999 to 2007, followed by 8 years of increase from 2007 to 2015 (Figure 2.6). This trend was possibly link to IPO/PDO cycle (Interdecadal Pacific Oscillation/Pacific Decadal Oscillation). The PDO fluctuations have basin wide effects on sea surface temperature and thermocline slope that are similar to El Niño (warm phase) and La Niña (cold phase) but on an approximately 10 years cycle [Mantua & Hare, 2002]. A PDO warm period started in 2008 that coincided with the increasing trend of backscatter values. However, we did not identify any related long-term anomaly in the oceanographic variables used as predictors in this study, and the shift in backscatter after 2007 remained unexplained.

#### 2.4.4 Interest for ecosystem modeling

The predicted backscatter had been compared to the micronekton biomass outputs predicted by the ecosystem model SEAPODYM for the functional groups inhabiting the epipelagic layer during nighttime. If we assumed that backscatter was directly proportional to the biomass of all micronekton organisms included in these functional groups, a good match between the two products would provide confidence in the results of both the ecosystem model and the statistical approach used to inter-calibrate and merge a large volume of acoustic data collected with ADCP. This was not the case. There was some consistency between predicted backscatter and biomass during the cold season, but overall common spatial patterns were weak and the seasonality predicted from the ecosystem model was also weaker and shifted in time in comparison to the statistical predictions. The micronekton SEAPODYM biomass distribution in the

epipelagic layer at night was close to the average distribution of chlorophyll-a with higher productivity in the southern region (Figure 2.9), but a delayed seasonal peak (Nov-Dec) of five months relatively to the peak of chlorophyll-a that occurs around July-August [Condie & Dunn, 2006; Smeti, 2015]. The predicted average backscatter had a seasonal peak in the warmest months (Feb-Mar) and higher values in average in the northern warmer region.

For a better understanding of these results, it seemed essential to characterize the community of mesozooplankton and micronekton species in these regions and seasons, the target strengths of dominant species at different frequencies and their cycles of abundances. It was possible for instance that the observed discrepancy between these model outputs was due to seasonal blooms of gas-bearing siphonophores [Davison *et al.*, 2015a; Proud *et al.*, 2018b] or similar organisms that have strong acoustic resonance but low energy (carbon) content. Conversely large biomass of mesopelagic fish without gas-filled swimbladders can be present but transparent to the acoustic signal [Foote, 1980]. Trawl data would be needed to validate or invalidate such hypothesis. Continue to validate ecosystem model is another essential task. SEAPODYM-MTL advection model may appear too simple to take into account the spatial variation of observed micronekton distribution across seasons, based on our acoustic estimates. Implementing a zooplankton compartment in SEAPODYM-MTL may improve that model by giving more flexibility to the model to better fit observed backscatter values.

Compare ecosystem model outputs with equivalent observations such as acoustic is challenging. The biomass of taxonomic groups defined in ecosystem models need to be converted into measures suitable for comparison, in that case target strength, by making simple approximations of target shape and assumptions regarding density and sound speed contrasts [Lavery *et al.*, 2007; Scoulding *et al.*, 2015]. This approach still requires collecting *in situ* data to attribute which part of the ecosystem model biomass is observable or not with a given acoustic frequency. A multi-platform of observation combining nets, acoustic and imagery techniques and eDNA appears necessary to achieve this goal [Handegard *et al.*, 2013; Lehodey *et al.*, 2015].

#### 2.4.5 Conclusions and perspectives

Our results brought additional evidence that ADCP echosounders were valuable data source for studying micronekton variability through time and space. The access to a large historical ADCP acoustic database was of primary interest, especially in the context of the climate change, to explore past variability of macro-zooplankton and micronekton. We provided an approach to merge two un-calibrated acoustic datasets using a recent reference calibrated dataset. Key environmental predictors such as SST, chlorophyll-a, thermocline depth, bathymetry and distance to coast seemed sufficient to statistically predict the backscattering intensity recorded from ADCP in the New Caledonian EEZ. The temporal and spatial variability of the signal had been analyzed and provided interesting result at seasonal, inter-annual (ENSO) and long-term scales. Finally, we showed that a state-of-the-art model (SEAPODYM-MTL) did not always reproduce our acoustic estimates. To be fully comparable with ecosystem model outputs, a research effort on the development of acoustic observation models must be promoted. Acoustic data need to be complemented with multiple observation platforms to reduce overall bias in estimates of micronekton biomass and use those estimates to assess, initiate and assimilate into ecosystem models.



Continuous and long-term monitoring at various spatial and temporal scales has multiple applications in the domains of ecosystem-based fishery management, marine spatial planning, conservation and monitoring of the climate change [Kloser *et al.*, 2009].

The case of New Caledonia and the implementation of the Coral Sea Natural Park (<https://mer-de-coraill.gouv.nc/>) provide a good example of close link between science and management. Observed and predicted distributions of micronekton along with knowledge of top predators distributions are central to refining management and conservation measures in such a vast oceanic region. Cooperation and coordination at a larger international scale is also highly desirable, *e.g.* through the Global Ocean Observing System (GOOS), to model and forecast the impact of the climate change on the functioning of the ecosystems and to propose eventually long term mitigation and conservation measures [Bax *et al.*, 2018; Muller-Karger *et al.*, 2018].

## Appendix

### Appendix A

TABLEAU 2.5 – Details on the cruise used in the paper, with the cruise name, the index number used in the main text, the date of start and end, the number of 5 minutes bins, the quarter, the total distance of the cruise, the ADCP device and the DOI for each cruise. Warm season : DJF (December, January, February) and MAM (March, April, May) and cold season : JJA (June, July, August) and SON (September, October, November).

| Cruise name   | Index number | Start      | End        | Number of 5 min bins | Quarter | Total distance (km) | ADCP device | DOI               |
|---------------|--------------|------------|------------|----------------------|---------|---------------------|-------------|-------------------|
| wespalis1     | 1            | 14/10/1999 | 09/11/1999 | 1051                 | SON     | 2365                | BB150       | 10.17600/99100110 |
| wespalis2     | 2            | 13/04/2000 | 10/05/2000 | 785                  | MAM     | 2355                | BB150       | 10.17600/100040   |
| frontalis1    | 3            | 29/03/2001 | 25/04/2001 | 1065                 | MAM     | 1387                | BB150       | 10.17600/1100030  |
| diapalis1     | 4            | 25/10/2001 | 30/10/2001 | 1347                 | SON     | 509                 | BB150       | 10.17600/1100100  |
| diapalis2     | 5            | 10/12/2001 | 21/12/2001 | 1710                 | DJF     | 518                 | BB150       | 10.17600/1100140  |
| diapalis3     | 6            | 18/01/2002 | 21/01/2002 | 368                  | DJF     | 111                 | BB150       | 10.17600/2100010  |
| diapalis4     | 7            | 04/04/2002 | 08/04/2002 | 862                  | MAM     | 336                 | BB150       | 10.17600/2100120  |
| diapalis5     | 8            | 21/05/2002 | 26/05/2002 | 1362                 | MAM     | 531                 | BB150       | 10.17600/2100130  |
| diapalis7     | 9            | 03/02/2003 | 12/02/2003 | 1824                 | DJF     | 1401                | BB150       | 10.17600/3100020  |
| diapalis8     | 10           | 10/06/2003 | 13/06/2003 | 575                  | JJA     | 438                 | BB150       | 10.17600/3100080  |
| secalis1      | 11           | 04/07/2003 | 17/07/2003 | 1527                 | JJA     | 1952                | BB150       | 10.17600/3100090  |
| pil2          | 12           | 28/07/2003 | 31/07/2003 | 515                  | JJA     | 653                 | BB150       | none              |
| bula4a        | 136          | 25/08/2003 | 27/08/2003 | 568                  | JJA     | 655                 | BB150       | none              |
| diapalis9     | 14           | 08/10/2003 | 15/10/2003 | 1370                 | SON     | 1197                | BB150       | 10.17600/3100120  |
| nor1          | 15           | 20/10/2003 | 06/11/2003 | 4396                 | SON     | 3528                | BB150       | 10.17600/3100030  |
| teralis1      | 16           | 08/12/2003 | 21/12/2003 | 474                  | DJF     | 623                 | BB150       | none              |
| pil3          | 17           | 28/01/2004 | 01/02/2004 | 155                  | DJF     | 383                 | BB150       | 10.17600/4100010  |
| pvs1          | 18           | 11/02/2004 | 19/02/2004 | 1895                 | DJF     | 2498                | BB150       | 10.17600/4100080  |
| frontalis2    | 19           | 02/04/2004 | 29/04/2004 | 887                  | MAM     | 1515                | BB150       | 10.17600/4100040  |
| bula5a        | 20           | 31/05/2004 | 02/06/2004 | 578                  | MAM     | 691                 | BB150       | 10.17600/4100060  |
| bula5r        | 21           | 16/06/2004 | 18/06/2004 | 536                  | JJA     | 721                 | BB150       | 10.17600/4100060  |
| salomon       | 22           | 14/10/2004 | 22/11/2004 | 734                  | SON     | 2107                | BB150       | 10.17600/4100090  |
| pvs3          | 23           | 26/11/2004 | 02/12/2004 | 1017                 | SON     | 1369                | BB150       | 10.17600/4100120  |
| secalis2      | 24           | 08/12/2004 | 21/12/2004 | 2157                 | DJF     | 2726                | BB150       | 10.17600/4100110  |
| mareva1       | 25           | 28/02/2005 | 06/03/2005 | 713                  | DJF     | 1380                | BB150       | 10.17600/5100020  |
| secalis4      | 26           | 08/11/2006 | 21/11/2006 | 752                  | SON     | 1781                | BB150       | 10.17600/6100120  |
| bsmf          | 27           | 03/05/2007 | 31/05/2007 | 938                  | MAM     | 1417                | BB150       | 10.17600/7100030  |
| flusec        | 28           | 12/08/2007 | 28/08/2007 | 1736                 | JJA     | 2599                | BB150       | 10.17600/7100060  |
| zonalis       | 29           | 01/03/2008 | 14/03/2008 | 3287                 | MAM     | 2900                | BB150       | 10.17600/8100060  |
| concalis      | 30           | 27/04/2008 | 11/05/2008 | 3059                 | MAM     | 2709                | BB150       | 10.17600/8100010  |
| gyrafort      | 31           | 01/06/2008 | 22/06/2008 | 1586                 | JJA     | 2056                | BB150       | 10.17600/8100040  |
| secargo       | 32           | 07/05/2010 | 18/05/2010 | 2583                 | MAM     | 2480                | BB150       | 10.17600/10100020 |
| nectalis1     | 33           | 30/07/2011 | 15/08/2011 | 3756                 | JJA     | 3683                | BB150       | 10.17600/11100050 |
| sprayalis2    | 34           | 17/10/2011 | 20/10/2011 | 745                  | SON     | 741                 | BB150       | 10.17600/11100110 |
| nectalis2     | 35           | 26/11/2011 | 14/12/2011 | 4649                 | SON     | 4052                | BB150       | 10.17600/11100070 |
| essaiglider   | 36           | 06/05/2012 | 08/05/2012 | 284                  | MAM     | 198                 | BB150       | 10.17600/12100040 |
| geodeva5      | 37           | 10/05/2012 | 19/05/2012 | 475                  | MAM     | 852                 | BB150       | none              |
| momalis1      | 38           | 23/05/2012 | 07/06/2012 | 1418                 | MAM     | 2202                | BB150       | none              |
| ipod          | 39           | 05/08/2012 | 11/08/2012 | 1770                 | JJA     | 1051                | OS75        | 10.17600/12100080 |
| bifurcation   | 40           | 01/09/2012 | 14/09/2012 | 1818                 | SON     | 2250                | OS75        | 10.17600/10100020 |
| sprayalis3    | 41           | 01/10/2012 | 03/10/2012 | 261                  | SON     | 664                 | OS75        | 10.17600/12100110 |
| spot1         | 42           | 07/10/2012 | 10/10/2012 | 787                  | SON     | 554                 | OS75        | 10.17600/12100120 |
| polynesie2013 | 43           | 17/02/2013 | 20/07/2013 | 1019                 | DJF     | 1236                | OS75        | none              |
| loss          | 44           | 29/10/2013 | 04/11/2013 | 1680                 | SON     | 1528                | OS75        | 10.17600/13100090 |
| nectalis3     | 45           | 21/11/2014 | 08/12/2014 | 4454                 | SON     | 3824                | OS75        | 10.17600/14004900 |
| nectalis4     | 46           | 19/10/2015 | 25/10/2015 | 1810                 | SON     | 1505                | OS75        | 10.17600/15004000 |

|           |    |            |            |      |     |      |      |                   |
|-----------|----|------------|------------|------|-----|------|------|-------------------|
| chest1    | 47 | 05/11/2015 | 24/11/2015 | 1352 | SON | 2148 | OS75 | 10.17600/15004500 |
| comeval   | 48 | 25/03/2016 | 08/04/2016 | 1433 | MAM | 2371 | OS75 | 10.17600/16003500 |
| kanacono  | 49 | 23/08/2016 | 29/08/2016 | 725  | JJA | 845  | OS75 | 10.17600/16003900 |
| carioca   | 50 | 03/09/2016 | 01/10/2016 | 698  | SON | 2184 | OS75 | 10.17600/16004000 |
| nectalis5 | 51 | 23/11/2016 | 06/12/2016 | 1750 | SON | 2604 | OS75 | 10.17600/16004200 |
| puffalis  | 52 | 18/03/2017 | 31/03/2017 | 1669 | MAM | 1854 | OS75 | 10.17600/17003300 |
| maracas3  | 53 | 07/08/2017 | 09/08/2017 | 261  | JJA | 769  | OS75 | 10.17600/17003700 |
| kanadeep  | 54 | 31/08/2017 | 26/09/2017 | 1278 | JJA | 4526 | OS75 | 10.17600/17003800 |

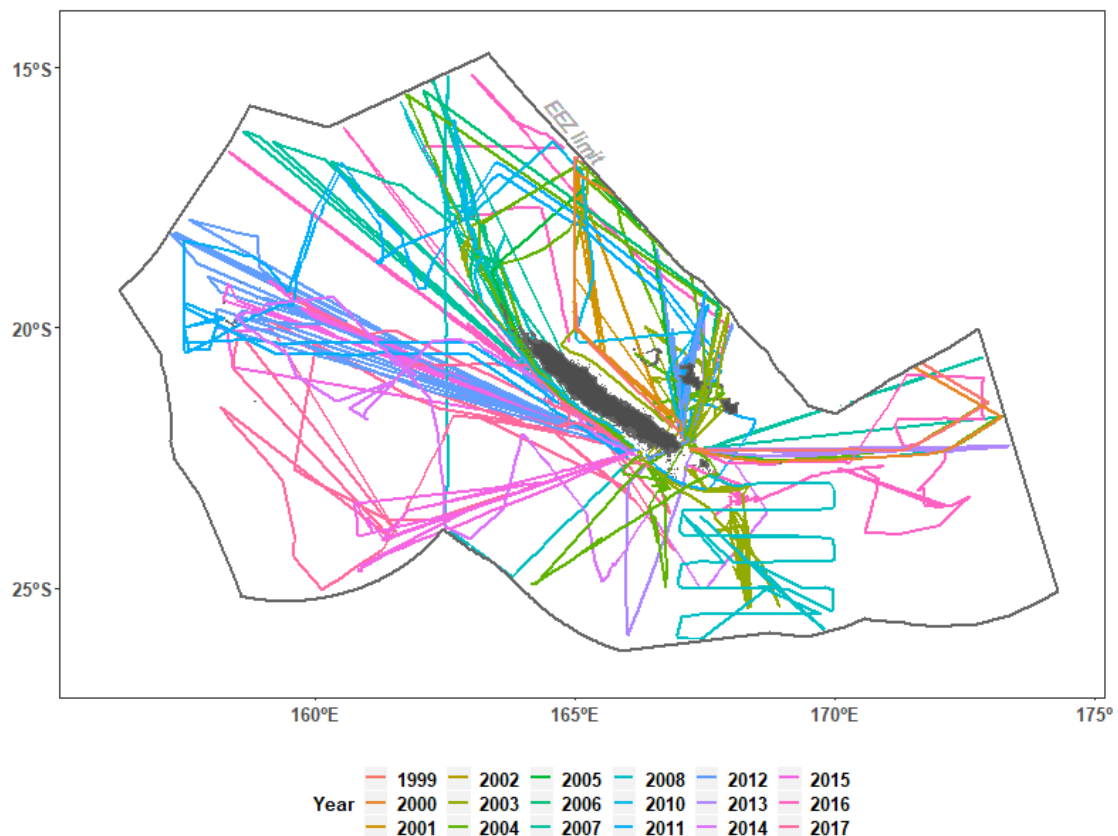


FIGURE 2.10 – All cruises tracks colored by the year of sampling.

## Appendix B

We determined the vertical profiles of scattering volume ( $S_v$ ) from shipboard ADCP using two separate equations depending on the ADCP data mode acquisition.

For 150 kHz Broadband ADCP measurements between 1999 and 2012, the echo intensity was converted into Scattering Volume ( $S_v$ , in dB) using the equation (2.1) from Deines [1999] modified by Gostiaux & van Haren [2010] as :

$$S_v = C + \log_{10}[(T_x + 283.16)R^2 - L_{DBM} - P_{DBW} + 2\alpha R + 10 \log_{10}[10^{(K_c E_a)/10} - 10^{(K_c E_{noise})/10}]] \quad (2.1)$$

where  $E_a$  is the ADCP raw echo intensity (counts) and  $E_{noise}$  is the noise (counts),  $T_x$  is the temperature of the transducer ( $^{\circ}C$ ),  $LDBM$  is  $10\log_{10}$ (transmit pulse in meter),  $PDBW$  is  $10\log_{10}$ (transmit power, in Watts)  $R$  is depth along the beam (m),  $\alpha$  is sound absorption coefficient (dB/m) in water calculated using the World Ocean Atlas 2005 density climatology [Antonov *et al.*, 2006; Locarnini *et al.*, 2006]. These parameters are recorded during acquisition.  $K_x = 127.3/T_e$  with  $T_e$  (in  $^{\circ}K$ ) is the temperature of the electronic system [RDI, 1998] taken here as  $T_x$ .  $K_c$  is a conversion factor for echo intensity (in dB/counts). For the constants  $C$  and  $PDBW$ , we used the default parameters given in Deines (1999)'s table 1 ( $C=-153.3$  and  $PDBW=23.8$  in dB). To evaluate  $E_{noise}$ , we estimated the minimum of the echo intensities  $E_a$  at each vertical profile when the ship was on station. Indeed, Heywood *et al.* [1991] discussed a bias between on station signal versus underway signal during which that noise level increased and they finally only used on-station signal to estimate  $E_{noise}$  (we also found a similar bias in our dataset). We then averaged these minima over each entire cruise to obtain  $E_{noise}$ .

For Ocean Surveyor 75 kHz Narrowband ADCP measurements between 2012 and 2017, the echo intensity was converted into Scattering Volume ( $S_v$ , in dB) using the standard sonar equation given by RDI [1998] :

$$S_v = \log_{10} \left[ \frac{4.47 * 10^{-20} K_2 K_s (T_x + 273.16) (10^{(K_c E_{noise})/10} - 1) R^2}{c P K_1 * 10^{-2\alpha R/10}} \right] \quad (2.2)$$

with the same notation as Equation 2.1.  $K_2$  is a system noise factor ( $K_2 = 2.5$ , dimensionless) and  $K_s$  is the ratio of system bandwidth to the square of transducer diameter ( $K_s = 1.09 * 10^5$  at 75 kHz);  $K_2$  and  $K_s$  are taken from RDI [1998]. We must emphasize that  $K_1$  in equation 2.2 is unavailable for our instrument and our contacts with RDI could not help us to determine its value. RDI [1998] provides a way to calculate that coefficient which depends on the power voltage supply of the instrument used. In the absence of further information on that voltage supply from RDI, we took 220V, which is the power supply onboard the R/V Alis. Choosing a different voltage will offset the backscatter similarly for all cruises using NB 75 kHz.

Figure 2.4.5 (top) shows the 20-120m depth-averaged backscatter for 150 kHz BB ADCP by cruise ordered chronologically. Surprisingly, one can note two abrupt changes in backscatters delineating 3 groups of cruises. Group1 includes cruises from Westpalis1 (1999) to Mareva1 (2005). Group 2 includes Secalis4 (2006) to Secargo (2010) and group 3, Nectalis1 (2011) to Momalis1 (2012) (Figure 2.4.5). Each shift corresponded to a specific intervention on the instrument (e.g, changes in the deck unit and beam repairs, D. Varillon, pers. communication). These shifts, if kept, prevents to merge all the cruises to conduct a global analysis of the dataset. For each group, we calculated mean backscatter by averaging all cruises of a given group for the 20-120m layer. Then, offsets for groups 2 and 3 were calculated separately, relative to group 1 as :  $\alpha_2 = \overline{S_v}^{-1} - \overline{S_v}^{-2}$  and  $\alpha_3 = \overline{S_v}^{-1} - \overline{S_v}^{-3}$ , considering group 1 as the reference. We added the offset of each cruise according to their group ( $\alpha_2$  for group 2 and  $\alpha_3$  for group 3). This choice of group 1 as the reference is arbitrary, as we do not have means to calibrate the instruments. However, it is a mean to make data of all cruises coherent and the choice of the reference group does not have any impact on the analysis. A qualitative validation of our method is shown on Figure 2.4.5. Using offsets present two advantages : it does not change the variability into the dataset, nor the function of distribution.

Once corrected, the distribution of the mean  $S_v$  values of the cruises do not present any obvious

“group biases” (Figure 2.11, bottom) thus giving us reasonable confidence in considering all the cruises in our dataset for our analysis.

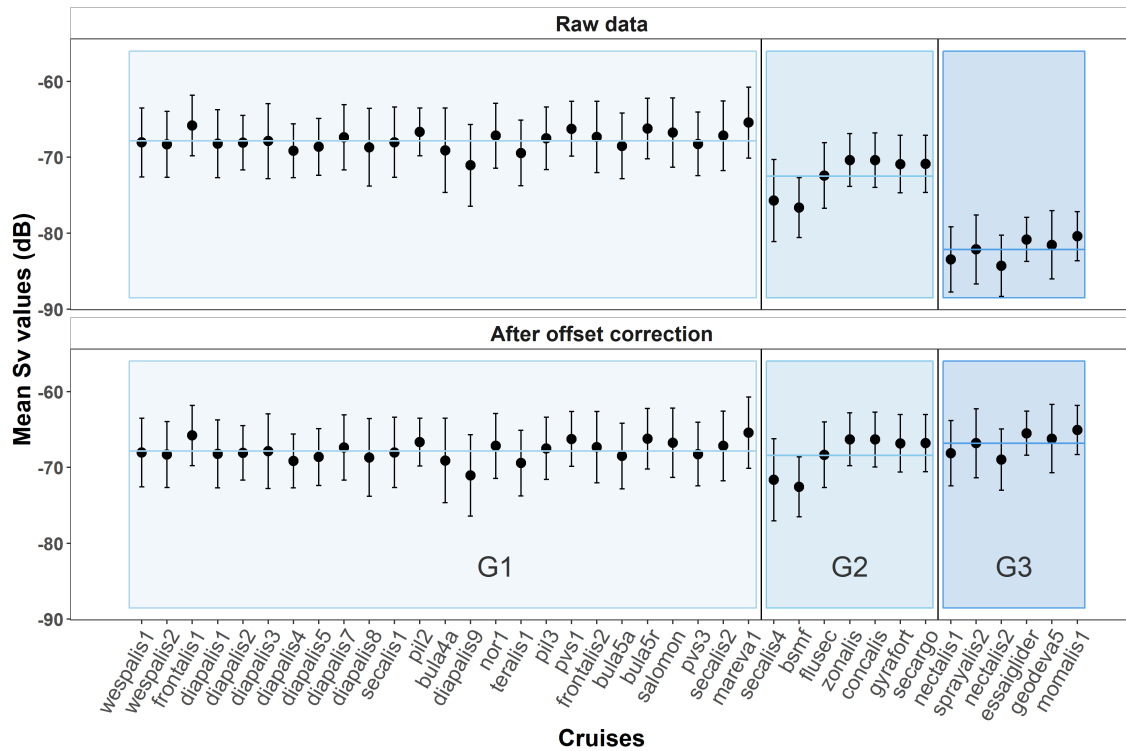


FIGURE 2.11 – Backscatter values averaged between 20m and 120m for each cruise using the 150 kHz SADC, in chronological order. G1, G2 and G3 indicate the 3 groups with abrupt changes (see text). Top : before correction, bottom : after correction. Dashed lines are for the mean backscatter value by ADCP devices.

### Appendix C

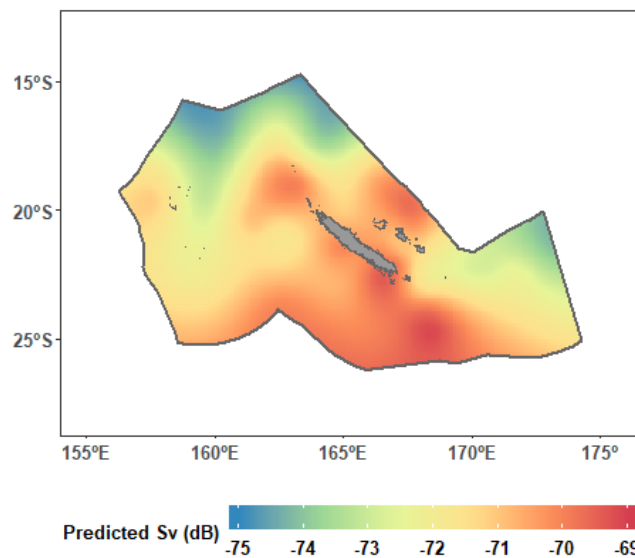


FIGURE 2.12 – Backscatter predicted by the GAMM1 by the spatial term (i.e.  $s(\text{lon}, \text{lat})$ ).

# Inter-chapter

Chapter 2 evaluated seasonal, interannual and spatial variability of micronekton relative abundance in the 20-120m layer. For that, we used ADCP data acquired through 54 cruises over 19 years. We detected a decrease in the relative abundance of micronekton in the New Caledonian EEZ from 1999 to 2007 followed by an increase. We also highlighted the influence of ENSO with an increase in abundance during the El Niño phases. Finally, we showed poor spatial cohesion between SEAPODYM predictions, an ecosystem model, and our echo intensity predictions. The ADCP comparison to EK60 data increased spatial and temporal coverage by combining two ADCP frequencies. However, this method did not allow us to inter-calibrate cruises inside each frequency. Moreover, the limited vertical range constrained analysis to the top 120meters of the water column. As such, we could not explore potential variability in the vertical distribution of micronekton. The third chapter tackled these two last limitations of non-calibration and restricted vertical range by using EK60 data. EK60 records need a calibration step to be able to analyze the data and therefore cruises recording EK60 are less frequent. However, the calibration step allows robust comparisons between cruises. While the second chapter focused on long-term variability, the third chapter focused on seasonal variability. In addition, the third chapter studied the micronekton vertical distribution between 0 and 600meters and its spatial and seasonal variability.





## Chapitre 3

# Seasonal and spatial variability in the vertical distribution of pelagic forage fauna in the southwest Pacific

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## Abstract

Acoustic data are an invaluable source of information for characterizing the distribution and abundance of mid-trophic level organisms (MTLOs) in the ocean. These organisms play a key role in the ecosystem as prey of top predators and as predators of lower trophic level organisms, as well as in carbon export towards deeper layers. This study used 38 kHz-EK60 acoustic echosounder data from six cruises spanning 2011-2017 to explore the seasonal and spatial variability of MTLOs' 10-600m vertical distribution in the New Caledonian (South Pacific) Exclusive Economic Zone. A total of 16715 acoustic vertical profiles were clustered into homogeneous groups. Two small shallow scattering layers (SSLs) between 0 and 100m, and one large deep scattering layer (DSL) at around 550m depth characterized the mean MTLOs' vertical distribution. A machine-learning model (eXtreme Gradient tree Boosting algorithm, XGBoost) was fitted to explain the acoustic profiles clusters with environmental variables as predictors. Sun inclination was the most important factor in structuring the vertical profile shapes due to the diel vertical migration signal, followed by the mean oxygen value of the top 600m. Bathymetry, 20°C isotherm depth, 0-600m mean temperature and euphotic depth were the next most significant variables. Wind, surface chlorophyll-a, SST, and mean salinity had a lower influence on the shape of the vertical profiles. The model was then used to construct vertical echograms at the scale of the New Caledonian EEZ, showing an accuracy up to 87% in cross validation. Across the EEZ, the shape of vertical acoustic profiles were comparable, though layer echo intensities varied spatially with a marked north-south gradient that remained relatively constant seasonally. The vertically-averaged acoustic values were characterized by a maximum to the south of the EEZ in summer, mainly driven by high oxygen values as well as shallow euphotic depth. We also estimated a migrant proportion between day DSL and night SSL of about 75%. Our methodology offers a promising approach for analyzing the vertical control of the environment on MTLOs for other oceanic provinces, while also providing a framework to investigate the corresponding trophic interactions between MTLOs and their predators feeding at different depths and times. Moreover, our findings stress the need to consolidate knowledge on species composition in order to optimize acoustic data interpretation.

**Keywords :** *Micronekton, echosounder, Pacific Ocean, mesopelagic zone, sound scattering layer, environment*

## 3.1 Introduction

In pelagic ecosystems, mid-trophic level organisms (MTLOs), also referred to as micronekton, are composed of crustaceans, molluscs, gelatinous organisms and fish with size ranging from 1 to 20cm long [Bertrand *et al.*, 2002a; Young *et al.*, 2015]. MTLOs play an important role as intermediate components between lower trophic levels (phytoplankton and zooplankton) and predators including commercially targeted fish species [Bertrand *et al.*, 2002a; Duffy *et al.*, 2017; Olson *et al.*, 2014] as well as emblematic endangered marine species [Lambert *et al.*, 2014; Miller *et al.*, 2018]. The feeding habitats and vertical behaviors of predators through the water column are very diverse [e.g. Benoit-Bird & McManus, 2012; Choy *et al.*, 2017]. Moreover, the habitat depth range of a specific predator may change spatially, as a function of prey distribution or due to physiological tolerance to environmental parameters [Houssard

*et al.*, 2017; Schaefer & Fuller, 2010; Schaefer *et al.*, 2007]. Ecosystem Based Fishery Management (EBFM) aims to develop relevant knowledge on ecological mechanisms and processes that shape such predator-prey interactions [Christensen *et al.*, 1996; Koslow, 2009]. To date, most of the studies assessing the influence of prey distribution on predator distribution at a regional scale used ecosystem models outputs [e.g. Lambert *et al.*, 2014; Miller *et al.*, 2018]. Observations and data on the vertical distribution of prey are still lacking, although they could greatly contribute to calibrate state-of-the-art ecosystem models that inform EBFM [Fulton *et al.*, 2005; Lehodey *et al.*, 2010; Maury, 2010; Pauly *et al.*, 2000; Shin & Cury, 2001].

MTLOs are usually aggregated into layers and these layers are present everywhere from the surface down to 2000m depth [Opdal *et al.*, 2008]. The thickness of a single layer ranges from a few meters to tens of meters, and the layer can horizontally spread over hundreds of kilometers [Benoit-Bird *et al.*, 2017]. MTLOs layers residing in the epipelagic zone (0-200m) refer to Shallow Scattering Layers (SSL) and the ones residing in the mesopelagic zone (200-1000m) refer to Deep Scattering Layers (DSL). The layer aggregation of pelagic organisms is a highly organized process of many individuals reacting to predation pressure as well as to environmental resources such as food availability or oxygen concentration [Benoit-Bird *et al.*, 2017; Ritz *et al.*, 2011]. The MTLOs layer characteristics (depth, echo intensity, composition and number of layers) vary geographically and seasonally [e.g. Escobar-Flores *et al.*, 2018]. The DSL depth has been linked to various environmental variables such as seawater density [Godo *et al.*, 2012] or oxygen concentration [Bianchi *et al.*, 2013a; Klevjer *et al.*, 2016]. Primary production and sea temperature also affect the DSL and SSL echo intensity [Escobar-Flores *et al.*, 2013; Irigoien *et al.*, 2014] and DSL is sometimes split into more than one layer composed with different species [Ariza *et al.*, 2016; Benoit-Bird & Au, 2004].

Day DSL and night SSL are connected through diel vertical migration (DVM), a well-known phenomenon observed at the global scale [Bianchi & Mislán, 2016; Klevjer *et al.*, 2016]. DVM is recognized today as the world's largest animal movement [Hays, 2003]. DVM patterns relate to population-wide movements in the water column, with ascents and descents of a large proportion of the MTLOs from the mesopelagic zone, where they remain during day time, toward the more productive 0-200m layer where they feed during the night [Pearre, 2003]. By daily migrating between surface and deep waters, MTLOs actively contribute to the downward flux of nutrients and particulate organic matter via their respiration and excretion processes [Ariza *et al.*, 2015; Drazen & Sutton, 2017]. Quantifying the proportion of MTLOs performing DVM and identifying the environmental drivers can thus contribute to a better understanding of the overall role of DVM in the carbon cycle [Aumont *et al.*, 2018; Belcher *et al.*, 2019].

Data from scientific calibrated echosounders can provide us a proxy of the vertical distribution of SSL and DSL [Kloser *et al.*, 2002]. Single-frequency acoustic data from echosounders at 38 kHz and lower frequencies can typically describe both SSL and DSL down to 1000m, encompassing the entire DVM. Because they vary widely in two dimensions (depth and time/distance), echograms are complex to analyze in relation to a varying multi variate environment. Most studies simplify information contained in the depth profile of an echogram through few metrics and analyze them through time together with environmental variables. For instance, acoustic backscatter has been studied using invariant depth-averaged vertical layers (e.g. 0-200m and 200-1000m) [e.g. Bedford *et al.*, 2015; Behagle *et al.*, 2014; Doray *et al.*, 2009]. Other studies extracted schools or layers and studied these layers' depth, thickness and echo intensity [Burgos & Horne, 2008; Proud *et al.*, 2018a]. These methods provide information on the layer echo

intensity variability but not on the vertical structure variability. [Behagle \*et al.\* \[2016\]](#) and [Boersch-Supan \*et al.\* \[2017\]](#) classified vertical acoustic profiles but they did not actually test the influence of environmental parameters on their classification results.

To our knowledge, there is not actually any robust method that statistically links the whole MTLOs' vertical distribution to environmental variables. We attempted to fill part of this gap in the present study, by designing a method to link the acoustic MTLOs' vertical distribution to oceanographic conditions; and using this method to predict MTLOs vertical echograms in un-sampled areas with similar environmental conditions. We used acoustic vertical profiles as sampling units from six cruises, and classified them into clusters to first describe the main vertical profile modes. We then modeled, with a machine learning algorithm, clusters as a function of environmental variables to understand the main links between oceanographic factors and vertical distribution. We finally predicted vertical echograms and migrant proportion between SSL and DSL at the scale of the New Caledonian EEZ in un-sampled regions where oceanographic data were available.

## 3.2 Material and Methods

Our study area fell within the New Caledonian Exclusive Economic Zone (EEZ), a region of more than 1.4 million km<sup>2</sup>. Recent studies have provided an overview of the physical and biological oceanographic context in the New Caledonian EEZ [[Ceccarelli \*et al.\*, 2013](#); [Menkes \*et al.\*, 2015](#)]. Studies specifically focusing on micronekton have explored species richness and diversity in the region, identifying more than 480 MTLOs species [*e.g.* [Grandperrin, 1975](#); [Payri \*et al.\*, 2019](#)], as well as the spatial-temporal MTLOs distribution averaged in the 20-120m layer [[Receveur \*et al.\*, n.d.](#)]. We focused on the MTLOs vertical distribution aspect on the present study.

### 3.2.1 Acoustic data

We gathered data from 6 cruises on board the R/V Alis in the New-Caledonia EEZ between 156°E–175°E and 14°S–27°S from 2011 to 2017 (Figure 3.1, Table 3.1). During the cruises, *in situ* acoustic data were recorded continuously using an EK60 echosounder (SIMRAD Kongsberg Maritime AS, Horten, Norway) connected to 4 split-beam transducers at 38, 70, 120 and 200 kHz. EK60 calibration was performed according to [Foote \*et al.\* \[1987\]](#) for each cruise. In the present study, we used the 38 kHz only. The hull-mounted transducer was 4m below the surface and a layer of 6m below the transducer face was deleted from the records (data collection started at 10m below the surface). The maximum detection range was 800m for all the surveys except for N1 cruise, where the records were limited to 600m depth. For consistency, the analyses were thus limited to 600m.

All raw acoustic data were processed with the open-source Matecho software [[Perrot \*et al.\*, 2018](#)]. A first cleaning step removed ghost bottom echoes. Then, four semi-automatic cleaning filters were applied to : (i) remove acoustic device interference ('un-parasite' Matecho filter), (ii) remove attenuated signals ('white pings' filter), (iii) remove elevated signals ('deep spike' filter) and (iv) reduce background noise [[De Robertis & Higginbottom, 2007](#)]. Details of filter parameters could be found in [Behagle \*et al.\* \[2016\]](#) and [Perrot \*et al.\* \[2018\]](#). After data cleaning, the echo-integration was done on cells of 1m-deep and

0.1nm-long, providing for each integrated cell the volume backscattering strength  $S_v$  data (dB.re.1.m<sup>-1</sup>) (hereafter referred to as echo intensity), the linear measure of the volume backscattering strength  $s_v$  (m<sup>-1</sup>) ( $s_v = 10^{\frac{S_v}{10}}$ ) and the area backscattering strength  $S_a$  (dB.re.1.m<sup>2</sup>.m<sup>-2</sup>) a proxy for the MTLOs biomass [Iri-goien *et al.*, 2014] [Maclennan *et al.*, 2002]. We used the linear form  $s_v$  when arithmetic operations were necessary.

Vertical profiles were smoothed using a locally polynomial quantile regression [Koenker, 2004] to remove high-frequency peaks (*e.g.* interferences or very small schools that create peaks in an acoustic profile) that were considered non-interpretable in the present study. Each vertical profile ranging from 10 to 600 m was averaged in 4-m vertical bins keeping the 0.1-nm horizontal resolution. Correlations between consecutive vertical profiles were high for distances ranging from 0.1 to 0.4 nm and decreased after. We then selected one profile out of four to limit autocorrelation effects. The final dataset was composed of 16715 vertical profiles.

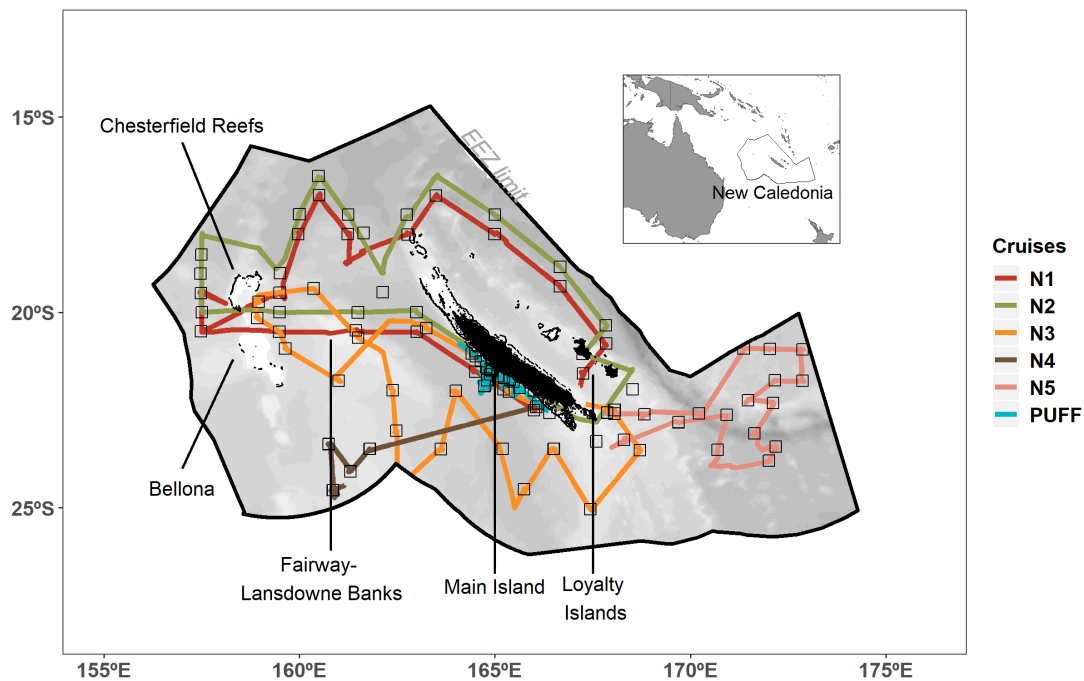


FIGURE 3.1 – Cruise tracks of the R/V Alis with EK60 echosounder (colored lines) in the New Caledonian Exclusive Economic Zone. Black boxes show CTD stations. The background grey colors represent the seabed depth (where lighter colors are shallower). Note that N1 and N2 tracks overlap but N2 track has been slightly shifted to the north for visualization purposes.

TABLEAU 3.1 – Details on the cruises used in the paper, with the cruise name, the date of start and end, the number of 0.1nm bins, and the DOI of each cruise.

| Cruise name     | Start      | End        | Number of 0.1nm bins | DOI               |
|-----------------|------------|------------|----------------------|-------------------|
| Nectalis 1 (N1) | 30/07/2011 | 15/08/2011 | 3681                 | 10.17600/11100050 |
| Nectalis 2 (N2) | 26/11/2011 | 14/12/2011 | 2896                 | 10.17600/11100070 |
| Nectalis 3 (N3) | 21/11/2014 | 08/12/2014 | 3617                 | 10.17600/14004900 |
| Nectalis 4 (N4) | 19/10/2015 | 25/10/2015 | 1034                 | 10.17600/15004000 |
| Nectalis 5 (N5) | 23/11/2016 | 06/12/2016 | 3989                 | 10.17600/16004200 |
| Puffalis (PUFF) | 18/03/2017 | 31/03/2017 | 1498                 | 10.17600/17003300 |

### 3.2.2 Environmental data

Table 3.2 displays the environmental variables (and their spatial resolution) selected to explore the physical drivers of the MTLOs' vertical distribution. For each vertical profile, environmental data were extracted at the dates and positions of the acoustic samples.

Bathymetry data were extracted from the ZoNéCo database at a 500m spatial resolution [ZoNéCo, 2013]. Sun inclination was calculated as a function of spatial position and date, with negative values for nights and positive values for days [Blanc & Wald, 2012; Michalsky, 1988]. Twilight periods were arbitrarily determined when sun inclination was in the range  $-10^{\circ}$  and  $10^{\circ}$ . These were removed from the final dataset. During these periods, as organisms actively swim up or down, organisms' orientation changes in the water column, creating strong variability in backscatter [McGehee *et al.*, 1998; Zedel *et al.*, 2005]. Hence, migration vertical profiles are highly changeable.

TABLEAU 3.2 – Environmental variable summary with unit, source and resolutions. Variables with an asterisk (\*) were downloaded via the Copernicus portal, CMEMS (Copernicus Marine Environment Monitoring Service) (<http://copernicus.eu/main/marine-monitoring>). Variables with a temporal resolution 'clim' are climatologic. Details on the variables and on the sources are provided in the main text. Water masses names are for TSW : Tropical Surface Water; SPTWS : South Pacific Tropical Water South; SPTWN : South Pacific Tropical Water North; WSPCW : Western South Pacific Central Water; AAIW : Antarctic Intermediate Water.

| Variable name                              | Unit               | Source  | Temporal resolution | Spatial resolution    |
|--|--------------------|---|---------------------|-----------------------|
| Bathymetry                                 | km                 | ZoNéCo, 2013  | -                   | 500 m                 |
| Sun elevation                              | $^{\circ}$         | Calculated from position and date                                   | -                   | -                     |
| Sea Surface Temperature (SST) (*)          | $^{\circ}\text{C}$ | Advanced Very High Resolution Radiometer (AVHRR) infrared satellite | Day                 | $\frac{1}{4}^{\circ}$ |
| Depth of the 20 degrees isotherm (D20) (*) | m                  | ARMOR3D   | Week                | $\frac{1}{4}^{\circ}$ |
| Depth of euphotic depth                    | m                  | MERCATOR GLORYS2V4  | Week                | $\frac{1}{4}^{\circ}$ |
| Norm of winds (*)                          | m/s                | Cross-Calibrated Multi-Platform (CCMP-v2)                           | Week                | $\frac{1}{4}^{\circ}$ |
| Norm of geostrophic currents (*)           | m/s                | ARMOR3D   | Week                | $\frac{1}{4}^{\circ}$ |
| Chlorophyll-a (*)                          | mg/m <sup>3</sup>  | GlobColour-Processors versions : MODIS 2014.0.1/VIIRS 2014.0.2      | Day                 | $\frac{1}{4}^{\circ}$ |
| Proportion of TSW water mass               | %                  | CARS and ARMOR3D  | Clim                | $\frac{1}{2}^{\circ}$ |
| Proportion of SPTWN water mass             | %                  | CARS and ARMOR3D  | Clim                | $\frac{1}{2}^{\circ}$ |
| Proportion of SPTWS water mass             | %                  | CARS and ARMOR3D  | Clim                | $\frac{1}{2}^{\circ}$ |
| Proportion of WSPCW water mass             | %                  | CARS and ARMOR3D  | Clim                | $\frac{1}{2}^{\circ}$ |
| Proportion of AAIW water mass              | %                  | CARS and ARMOR3D  | Clim                | $\frac{1}{2}^{\circ}$ |
| Water column oxygen                        | $\mu\text{mol/kg}$ | CARS  | Clim                | $\frac{1}{2}^{\circ}$ |
| Water column temperature                   | $^{\circ}\text{C}$ | ARMOR3D   | Clim                | $\frac{1}{2}^{\circ}$ |
| Water column salinity                      | m <sup>3</sup> /kg | ARMOR3D   | Clim                | $\frac{1}{2}^{\circ}$ |

### Inter-annual surface variables

Sea Surface Temperature (SST) was taken from the NOAA OI SST High Resolution Dataset at a daily resolution [Reynolds *et al.*, 2007]. The depth of the 20°C isotherm and the surface geostrophic ocean velocity amplitude were extracted from the Armor3D dataset [Guinehut *et al.*, 2012] available at a weekly time scale. The depth of the euphotic zone was extracted from the MERCATOR GLORYS2V4 reanalysis [Garric *et al.*, 2017] at a weekly resolution. Surface wind amplitudes were obtained from Cross-Calibrated Multi-Platform [CCMP-v2, Wentz *et al.*, 2015] datasets at a weekly resolution. Surface chlorophyll-a was extracted from GLOBCOLOUR [Saulquin *et al.*, 2009] at a daily resolution. All section 3.2.2 variables were extracted on a ¼° spatial grid. We used these variables as environmental covariates for modeling acoustic profiles (see section 3.2.3).

### 3D ocean datasets

In addition to surface values, Armor3D provided an ocean reanalysis of observed vertical profiles of ocean temperature (T) and salinity (S) [Guinehut *et al.*, 2012]. Armor3D was used rather than CTD field data, because CTD casts were only taken at a limited number of sampling stations (156 stations, Figure 1). However we systematically checked the matching between CTDs and Armor3D data (correlation of 0.99 for temperature values and 0.96 for salinity values). We extracted the oxygen (O<sub>2</sub>) vertical distribution from the climatological dataset CARS [Ridgway *et al.*, 2002] as inter-annual data are not available. We also checked the matching between CTDs and CARS data and we found a correlation of 0.74. We used the 6-606m monthly averages of seasonal temperature, salinity and oxygen (30m vertical resolution) at a 1/2° spatial resolution as environmental variables for modeling acoustic profiles (see section 3.2.3).

### Water masses

Water masses describe bodies of water with homogenous physical properties, and constitute a synthetic way of understanding the physical oceanography. Water masses can be defined in terms of temperature, salinity (hence density) and oxygen values and have been described in the south west Pacific [Gasparin *et al.*, 2014; Germaineaud *et al.*, 2016]. We pooled temperature, salinity and oxygen values for all depths in the top 606m (with a 30m vertical resolution) as derived from Armor3D and CARS (Appendix 3.13). We then classified data with a k-means algorithm [Hartigan & Wong, 1979] and identified five distinct water masses corresponding to those identified by Gasparin *et al.* [2014] and Germaineaud *et al.* [2016] (Appendix 3.13). The cluster results were transformed into water mass covariates by calculating, for each acoustic profile, the proportion in depth occupied by the corresponding water mass in the water column.

### 3.2.3 Statistical methods

Figure 3.2 displayed the schematic framework of the analyses, considering one acoustic vertical profile as the sampling unit (one ‘observation’ hereafter). We first reduced the vertical dimension by principal component analysis and then classified the acoustic profiles in homogenous groups using their

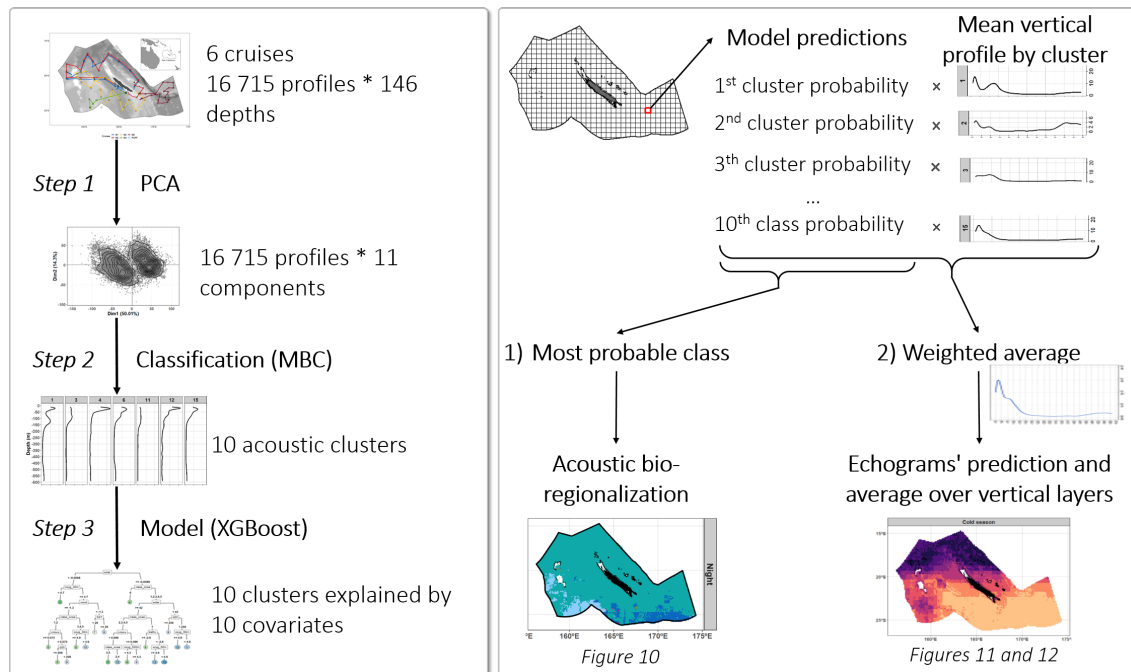


FIGURE 3.2 – Diagram explaining the different steps of the analysis. Details of the approach are provided in the text.

principal coordinates as variables. In the last step, we fitted a machine-learning type model to link vertical profile clusters to environmental variables.

### Noise reduction and classification

A Principal Component Analysis [PCA, Jolliffe, 2011] allowed to reduce the dimensions of observations (from 146 depths per profile to a smaller number per profile) (Figure 3.2, left panel, step 1). Vertical acoustic profiles were then grouped using a model-based clustering (MBC) (Figure 3.2, left panel, step 2). As PCA brings similar observations closer in new space, we performed clustering based on the density of points. Each cluster was centered around points (*i.e.* the clusters' center) where the point density was the highest in the PCA space [Fraley & Raftery, 2002]. We maximized the Bayesian Information Criteria (BIC) [Raftery, 1995] to select the appropriate number of clusters. BIC values as a function of the number of classes were plotted, and we added the BIC values derivative to better identify discontinuities.

### Metrics on vertical profiles

Acoustic metrics were calculated using  $s_v$  (linearized backscatter) according to Urmy *et al.* [2012]. We calculated the mean backscatter value over the entire vertical profile (called 'density') and a mean depth location calculated by the average sampled depths weighted by their  $s_v$  values (called 'center of mass'). We calculated a proxy of the acoustic aggregation rate over the water column : a high value corresponds to high backscatter concentrated over short depth ranges in the vertical profiles (called 'aggregation'). These metrics are detailed in Table 3.3 (see also Urmy *et al.* 2012).

TABLEAU 3.3 – Details of parameters and formulas used for metric calculations.  $s_v$  is the linear measure of the volume backscattering strength ( $m^{-1}$ ),  $z$  is the depth (m) and all integrals are calculated between the first depth level (10m) and the deepest depth (600m).

| Name           | Metric                              | Formula  | Parameters | Unit             |
|----------------|-------------------------------------|--|------------|------------------|
| Density        | Mean volume backscattering strength | $10 * \log_{10} \left( \frac{\int s_v(z) dz}{H} \right)$ | H=146      | dB re 1 $m^{-1}$ |
| Center of mass | Mean vertical localization          | $\frac{\int Z.s_v(z) dz}{\int s_v(z) dz}$                | -          | m                |
| Aggregation    | Index of aggregation                | $\frac{\int s_v(z)^2 dz}{(\int s_v(z) dz)^2}$            | -          | $m^{-1}$         |

### Environmental factors driving the acoustic clusters

A machine-learning model was fitted to link the acoustic clusters to environmental covariates (Figure 3.2, left panel, step 3). We used the XGBoost algorithm (eXtreme Gradient tree Boosting), which is an optimized distributed gradient boosting designed to be highly efficient, flexible and portable [Chen & Guestrin, 2016]. XGBoost uses machine-learning algorithms under the Gradient Boosting framework. The basic idea is to incrementally create new sub-models that improve the residuals or errors of prior sub-models, and then merge sub-models together to make the final prediction. Gradient boosting uses a gradient descent algorithm to minimize the loss when adding new models. We used cross-validation (CV) to tune parameters [Browne & Cudeck, 1989], with the proportion of well-classified observations in the validation dataset as the criterion. The model was first fitted on a training dataset (75% of randomly selected profiles) and then tested on a validation dataset (the remaining 25% of data). To prevent overfitting, XGBoost parameters were set equal to 0.3 for the learning rate and to six maximum tree depths. Environmental variables listed in section 3.2.2 were included as covariates.

To rank the importance of covariates, SHapley Additive exPlanation (SHAP) values were computed [Lundberg *et al.*, 2018] for the overall model and for each cluster. SHAP values indicated how much a given covariate value could change the predicted value compared to the prediction done without this covariate [Lundberg & Lee, 2017]. For instance, a high SHAP value for a given covariate value indicates a strong significance in the prediction. For a given prediction, the difference between the value predicted by the model (*i.e.* the set of probabilities to be in each acoustic cluster) and the predicted value without one covariate was calculated. To take into account the integration order of the remaining covariates, all possible orders of covariate inputs were tested for predictions. Then, all differences were added to calculate SHAP values. Following the same process, SHAP values were calculated for other covariates. By averaging SHAP values by covariate across all observations, the explanatory variables in the final model were ranked.

In the same way, SHAP values were averaged by covariates across groups of observations (for example acoustic clusters) to determine the importance of each explanatory variable for those groups. To visualize the importance of variables by cluster in the predicted observations, we first normalized and centered the covariates. Then we plotted, by acoustic cluster and for each covariate, SHAP values for each predicted value associated with that covariate, with color coding for the normalized covariate value (green to yellow, see Figure 3.8 and section 3.3.2 for a complete interpretation).



## Model predictions

We next used the model as a predictive tool (Figure 3.2, right panel) based on the climatology of all explanatory variables computed on a given spatial cell (latitude and longitude resolution of  $\frac{1}{4}^\circ$ ). The distribution of prediction dataset values were similar to observation dataset values (Appendix 3.15). For each spatial cell, the model predicted the probability to belong to each acoustic cluster. Two alternative approaches were considered to finally allocate one acoustic profile per cell : 1) we selected the acoustic cluster with the highest probability; and 2) we calculated each mean vertical profile by cluster, and then we averaged the mean vertical profiles of clusters weighted by their predicted probability (Figure 3.2, right).

The second option allowed us to predict acoustic values for all EEZ cells by month, during day and night, and at each depth. We then estimated echograms for the whole EEZ and produced maps of the integrated 10-600m acoustic value by season. Finally, we quantified the proportion of migrant MTLOs (%) with :

$$M_p = \frac{s_v^N - s_v^d}{s_v^n}$$

with  $M_p$  representing the proportion of migrants,  $s_v^n$  the mean  $s_v$  for a given vertical layer (e.g. 10-200m) during the night in  $m^{-1}$  and  $s_v^d$  the mean  $s_v$  for the same layer during the day.

Statistical analyses were performed using [R Core Team, 2018] version 3.5.0. Classification was carried out using the library *mclust* [Scrucca et al., 2016] with the "VVV" option. Extreme gradient boosting tree was carried out with the *xgboost* package [Chen et al., 2018].

## 3.3 Results

The six cruises provided a dataset covering the two mains seasons as well as most of the New Caledonian EEZ. Cruises N2, N2 and N5 were carried out during the warm season (December-May), and N1 and N4 during the cold season (June-November) (Table 3.1). The New Caledonian EEZ was reasonably well sampled, with cruise tracks for N1 and N2 covering the northern region, N3 the west, N4 the south-west, N5 the south-east, and Puffalis close to the coast (Figure 3.1). The full dataset encompassed more than 17500km (*i.e.* about 9500nm), including 16715 vertical profiles of 146 depth points in the 10-600m depth range.

### 3.3.1 Main patterns of MTLOs vertical distribution

The first two axes of the PCA accounted for 64.3% of the variability and revealed two high density regions of acoustic profiles well separated on the first axis. Within these regions a secondary maximum appeared, separated on the second axis (Figure 3.3A). The first axis split night from day profiles (50%), and the second axis split the vertical profiles geographically : those located in the north from those located in the south of the EEZ (14.3%). The cumulative variance explained by the axes increased relatively

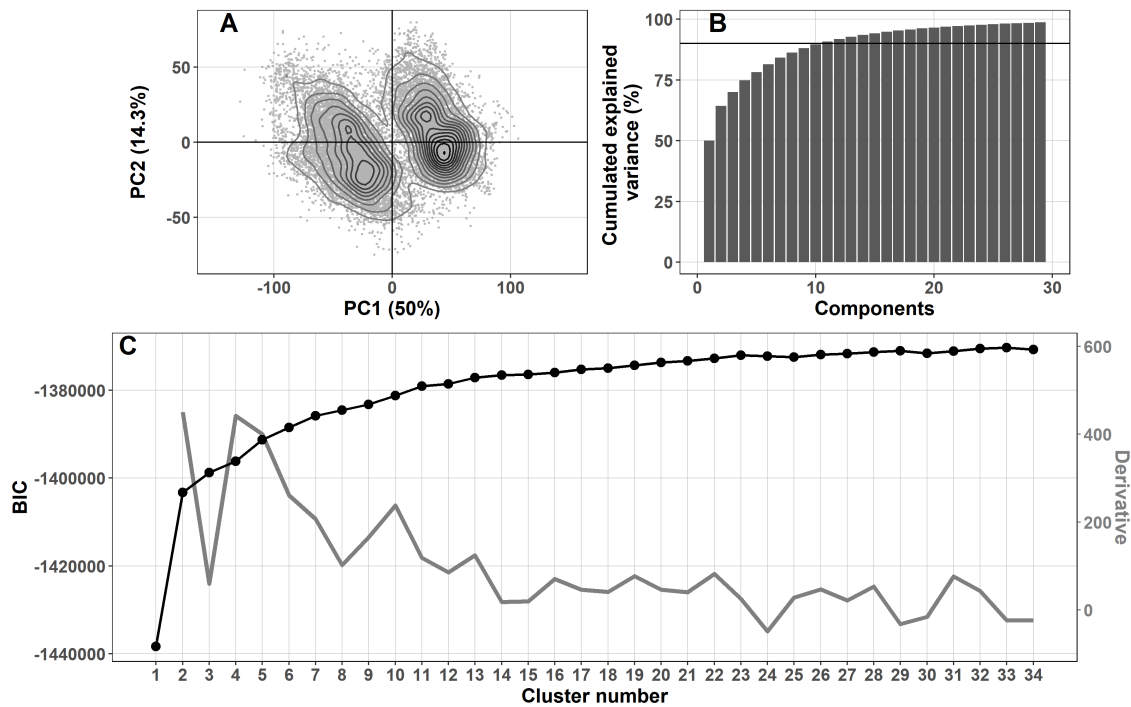


FIGURE 3.3 – PCA results with the two first axes (panel A) and the cumulative variance explained by the PCA dimensions (panel B). MBC classification results : the BIC (Bayesian Information Criterion) is represented as a function of the potential number of classes in black, with its derivative curve in grey (panel C).

quickly (Figure 3.3B). We thus kept the first 11 PCA components for the MBC classification step, as these 11 dimensions (instead of the initial 146 depths) contributed to 90% of the vertical profile shapes. Based on the BIC curve and its derivative function, 10 clusters were chosen rather than two or four which are the three first peaks highlighted by the derivative curve. Two or four clusters appeared too low to represent correctly the high diversity in acoustic vertical profile shape observed among the 16715 observations (Figure 3.3C). Moreover, the BIC increased quickly between one and 10 clusters, after which the rate of decrease was smaller. Finally, 10 clusters allowed us to keep the number of cluster interpretable.

Day and night profiles were almost perfectly separated into different acoustic clusters. Six clusters were mainly composed of day profiles (light grey bar on Figure 3.4A, referred as ‘day group’ hereafter) and four clusters were composed mainly of night profiles (dark grey bar on Figure 3.4A, referred as ‘night group’ hereafter). The number of acoustic profiles per cluster ranged from 277 to 2065, with one cluster indicative of very insignificant specific features : cluster 10 contained less than 300 vertical profiles, while the other clusters described frequent features with more than 1000 profiles per cluster. The spatial distribution of the acoustic clusters indicated a north-south separation for both day and night groups (Figure 3.4B) with day clusters 1 and 6 and night cluster 5 in the north, and clusters 7 (day), 4 and 8 (night) in the south of the EEZ.

Among the six day clusters (Figure 3.5), we observed persistent detections at 20-80m, which were composed of non-migrant MTLOs staying within the 0-150m zone during the day. DSLs were located between 450 and 600m depth. Cluster 10 displayed an intermediate layer in the 350-400m range. Cluster 9 had the highest density and cluster 6 the lowest, showing a very flat profile indicative of a near empty water column (Table 3.4). The center of mass of the clusters varied according to the echo intensity of the SSL and DSL : the shallowest center of mass (338.2m) of cluster 2 was due to a strong SSL, while cluster 10

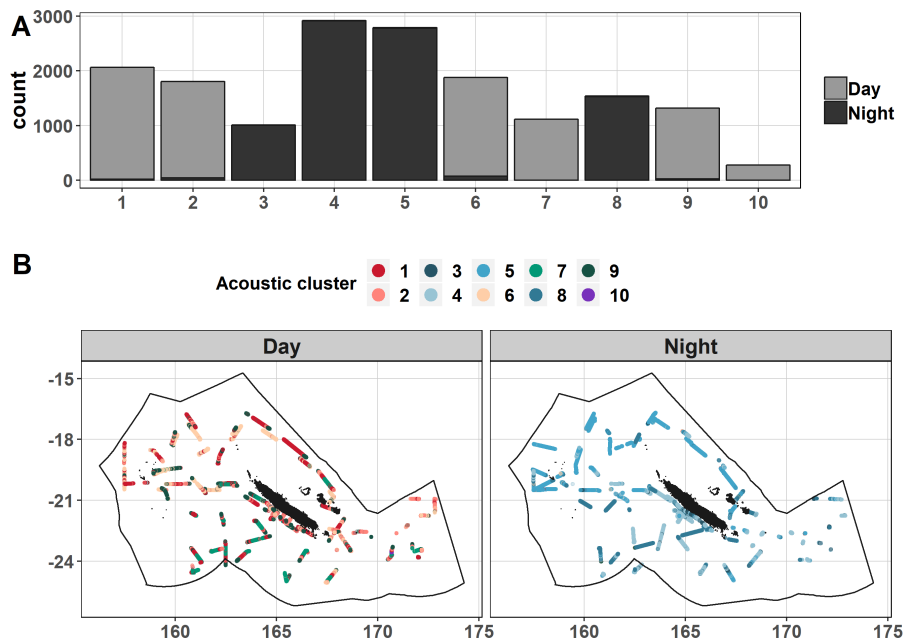


FIGURE 3.4 – Classification results with the number of day and night vertical profiles in each acoustic cluster (panel A) and the spatial position of all vertical profiles colored by the acoustic cluster they belong to by day (left) and by night (right) (panel B).

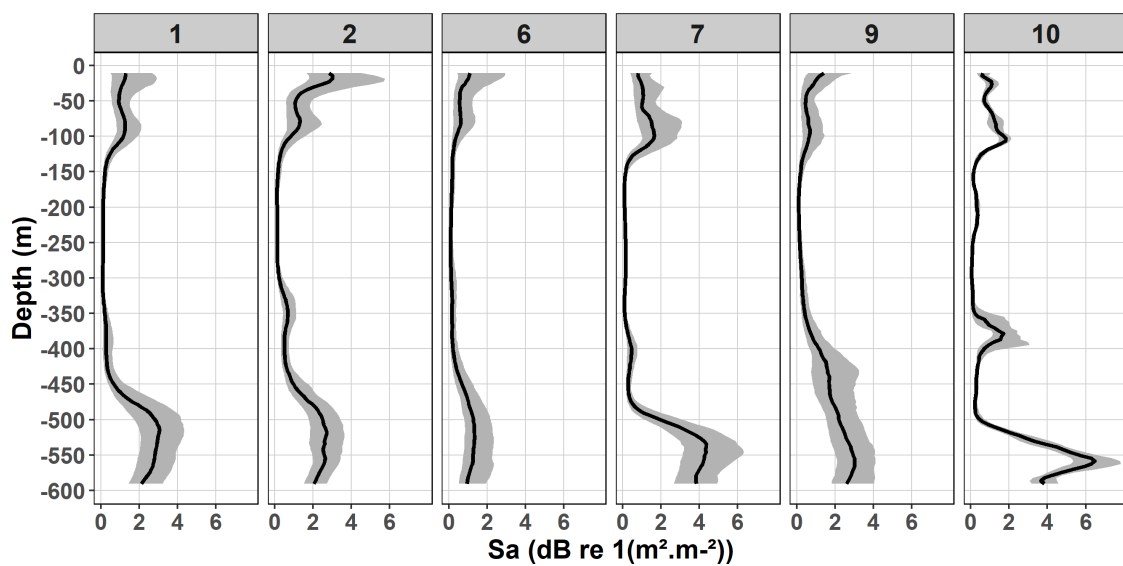


FIGURE 3.5 – Vertical profile medians for each day acoustic class. The grey ribbon is the interquartile range.

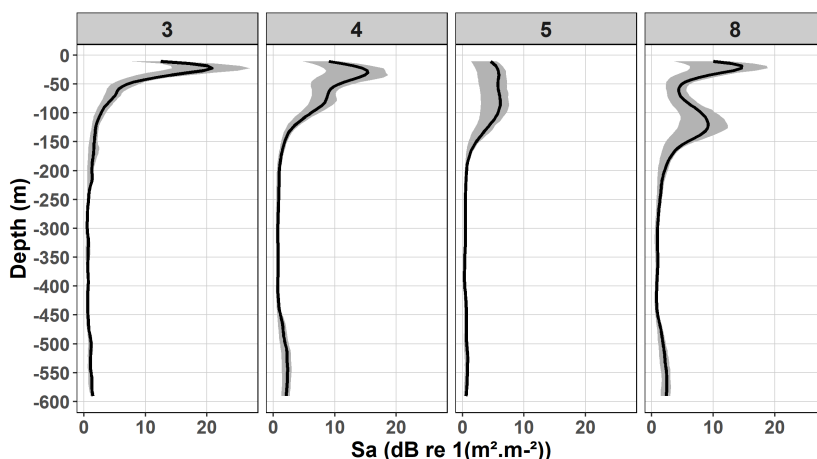


FIGURE 3.6 – Vertical profile means for each night acoustic class. The grey ribbon is the interquartile range.

TABLEAU 3.4 – Parameters for profiles. Details of calculations are given in Table 3.

|                    | Day<br>1 | Day<br>2 | Night<br>3 | Night<br>4 | Night<br>5 | Day<br>6 | Day<br>7 | Night<br>8 | Day<br>9 | Day<br>10 |
|--------------------|----------|----------|------------|------------|------------|----------|----------|------------|----------|-----------|
| N observations     | 2065     | 1805     | 1010       | 2919       | 2787       | 1878     | 1116     | 1538       | 1320     | 277       |
| Density (dB)       | -75.6    | -75.2    | -72.7      | -71.7      | -74.0      | -76.8    | -75.3    | -71.4      | -75.0    | -75.7     |
| Center of mass (m) | 369.3    | 338.2    | 144.3      | 174.7      | 152.7      | 339.6    | 375.0    | 187.0      | 385.2    | 408.5     |
| Aggregation (m-1)  | 1.28     | 1.18     | 2.55       | 1.72       | 1.63       | 1.02     | 1.63     | 1.36       | 0.96     | 1.84      |

had the deepest mass center (408.5m) due to an intense DSL. For other clusters, the center of mass varied between 340 and 385m depth, indicating an almost equivalent ratio between DSL and SSL intensities. Clusters 7 and 10 were the most aggregated clusters (aggregation index greater than 1.5). Indeed, these two clusters showed a narrower DSL than the other clusters. Cluster 9 showed a more gradual change in DSL intensity than other clusters (Figure 3.5) and a very small aggregation index (Table 4), indicating a diffuse vertical distribution through the water column. In addition, profiles of cluster 9 were mainly located at the beginning or at the end of transects (Figure 3.4B).

The shape variability among clusters of the night vertical profiles (Figure 3.6) was concentrated on the epipelagic zone (0-200m). Two clusters had two well-marked SSL (clusters 4 and 8) and other clusters had one high peak only (cluster 3). Clusters 4 and 8 had the highest densities (Table 3.4) and were found in the south (Figure 3.4B). By contrast, cluster 5 had the smallest densities and was mainly found in the north. The deepest mass center was 187m for cluster 8 and the shallowest was 144m for cluster 3, which had a very intense SSL. Clusters 4 and 8 in the south of the EEZ had, on average, a deeper mass center than other clusters. Cluster 8 was the most aggregated, and cluster 5 ranked second. Clusters 3 and 4 were less aggregated.

### 3.3.2 Environmental influence on the vertical distribution

The relationships between acoustic clusters and environmental covariates were examined using XG-Boost modelling (Figure 3.2, left panel, step 3). Among the 16 explanatory variables, the least important covariates were the proportion of the five water masses and ocean currents. They were removed from the final model as all five together increased the success rate of the model (*i.e.* the rate of the well-classified

profiles from the validation dataset) by 1% only. The success rate of the most parsimonious model reached 87%.

The most influential variable on the profile shape was sun inclination (Figure 3.7). This major effect was due to the DVM signal. The second most influencing variable was oxygen followed by bathymetry, 20°C isotherm depth, mean temperature over 6-606m and euphotic depth. Wind, chlorophyll-a, and SST ranked then. Mean salinity was the last one.

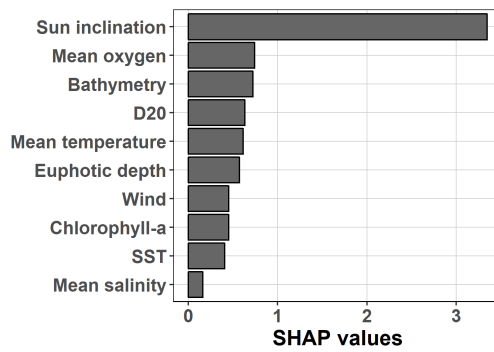


FIGURE 3.7 – Mean SHAP values for the predictions by each environmental covariate (y-axis).

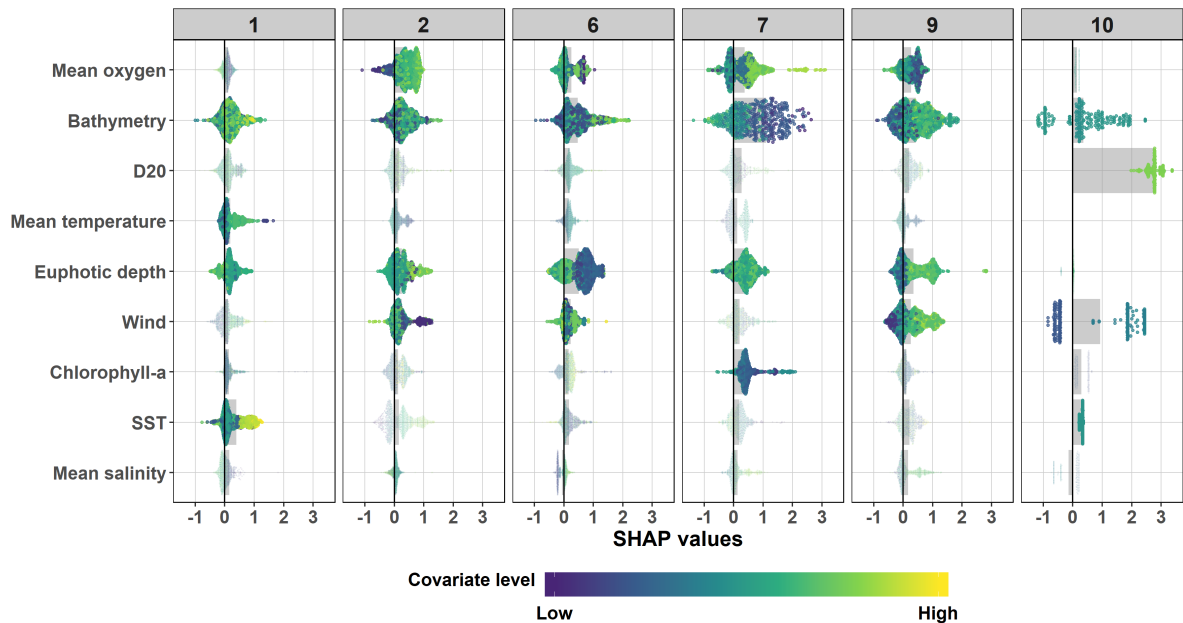


FIGURE 3.8 – SHAP (SHapley Additive exPlanation) values (*x-axis*) by covariate (*y-axis*) for each day cluster (*columns*). Every observation is one dot on each row. The SHAP value (*x-axis*) represents the influence of a given covariate on the prediction. The dot color represents the covariate normalized value/level : yellow for high value (high normalized SST for example) and dark blue for low value (low normalized SST for example). The height of one patch (the violin shape) gives an indication of the dot density. Grey rectangles by row and by column show the mean SHAP value by cluster and by covariate. Based on these grey rectangles, dots of the four most important covariates by cluster are plotted in brighter colors.

As the sun inclination influence is obvious by comparing day and night clusters, we removed it from Figures 3.8 and 3.9 to clarify and simplify them. The SHAP values of sun inclination were presented in Appendix 3.14.

For the acoustic cluster 1, significant covariates were bathymetry, mean temperature, euphotic depth and SST (Figure 3.8). The high values of mean temperature and SST had a strong influence on this clus-

ter (green and yellow colors indicating high temperature values together with high SHAP value), as well as values of deep bathymetry. High oxygen, bathymetry, deep euphotic depth and weak wind contributed significantly to the profiles of cluster 2. For cluster 6, low oxygen and shallow euphotic depth were important, as well as mixed bathymetry values. The shallowest values of bathymetry, relatively deep values of euphotic depth, low chlorophyll-a and high oxygen shaped vertical profiles of cluster 7. Profiles of cluster 9 were mainly influenced by intermediate values of sun inclination (Appendix 3.14) as well as low mean oxygen, bathymetry, deep euphotic depth, and strong wind. Finally, profiles of cluster 10 were mostly influenced by deep 20°C isotherm depth.

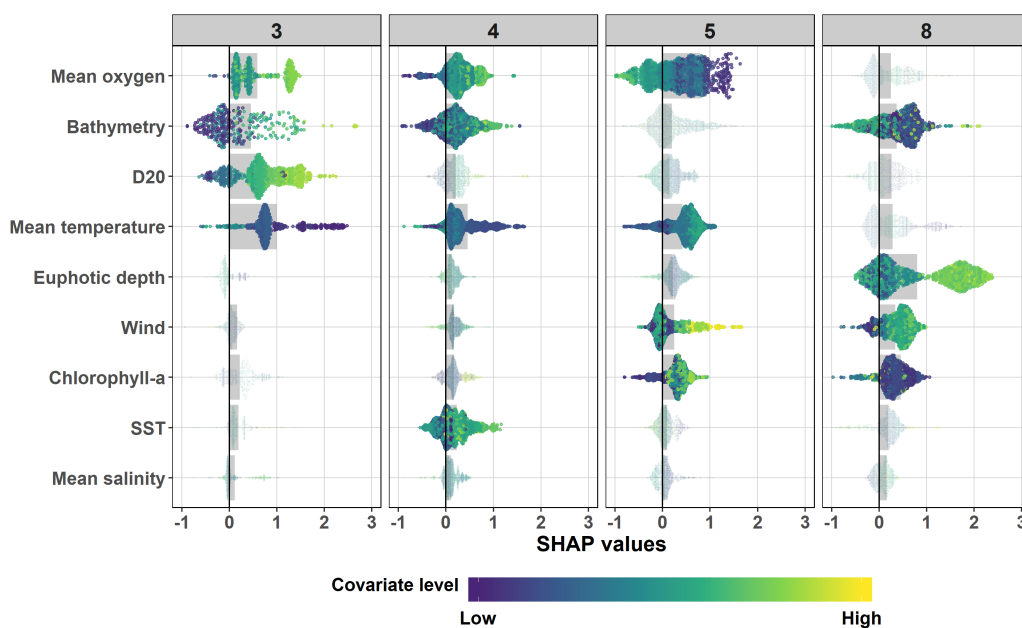


FIGURE 3.9 – Same as Figure 3.8 but for the night classes.

For the night group, the oxygen level influenced all clusters except cluster 8, with low oxygen values for cluster 5, and high oxygen values for clusters 3 and 4 (Figure 3.9). The bathymetry shaped all clusters except cluster 9 with a large diversity of values. Deep 20°C isotherm depth acted on cluster 3. Quite warm temperatures were important for cluster 5 and extremely cold temperatures for clusters 3 and 4. The deep euphotic depth impacted cluster 8 and strong winds clusters 5 and 8. Very low chlorophyll-a concentration had a strong influence on cluster 8 and relatively high chlorophyll-a concentration on cluster 5. Quite warm SST drove cluster 4. Finally, mean salinity did not influence any cluster.

Generally, the low oxygen values influenced clusters in the north of the EEZ (clusters 1, 5, 6), and high oxygen and low chlorophyll-a were significant for clusters in the south (clusters 2, 4, 7 and 8). Bathymetry and oxygen influenced almost all clusters, while the impact of other covariates was more variable among clusters.

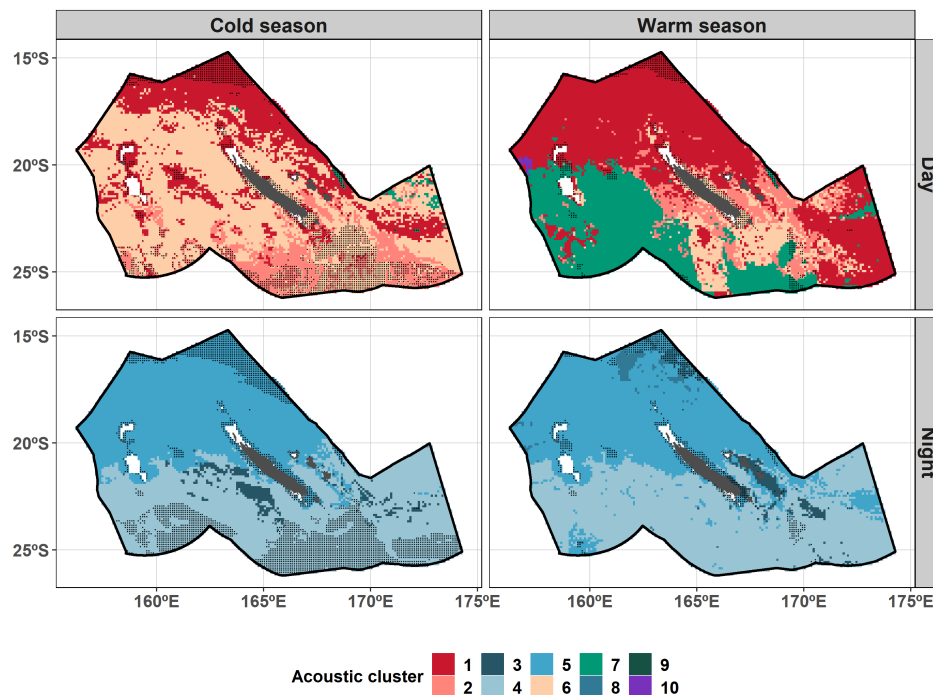


FIGURE 3.10 – Main cluster predicted for day (1<sup>st</sup> row) and night (2<sup>nd</sup> row) during the cold season (left column) and the warm season (right column). Small black dots identify extrapolated points (*i.e.* where predictions were made with at least one covariate value falling outside of the sampled range). White areas represents non-predicted regions.

### 3.3.3 Prediction at a larger spatial scale

#### Acoustic regionalization

Figure 3.10 displayed the spatial distribution of the most probable acoustic clusters by season and by day and night. Day distribution was patchier than night distribution. During the day, cluster 1 dominated in the north during the warm season with a southward extension of its spatial range during the cold season. Cluster 2 occurred in the south during the two seasons. The southwest corner was partially invaded by cluster 7 during the warm season. Cluster 10 was present during the warm season scattered in isolated patches east of Chesterfield reefs (refer to Figures 3.1 for feature names). At night, cluster 5 dominated in the north of the EEZ, and cluster 4 in the south. The cluster distribution patterns were very similar during both seasons; however, a small southward extension of cluster 5 was predicted during the warm season. Cluster 3 patches was present in the west of Main Island during the east season but in the east of Main Island during the warm season. Cluster 8 was mainly in the north during the warm season.

#### Vertical predictions of MTLOs distribution

Following section 3.2.3, for each spatial cell, we calculated an average vertical acoustic profile by weighting each mean clusters' vertical profile by the probability of cluster occurrence predicted by the model. After estimating the quality of predictions for a given transect, we predicted acoustic vertical profiles at the scale of the New Caledonian EEZ, and integrated values for the 10-600m vertical layer as well as the 10-200m vertical layer to calculate a migrant's proportion.

For illustration, we selected N4 track that encompassed 1034 observations. A visual comparison of the predicted reconstructed echogram versus the observed echogram indicated that the method reproduced the main patterns of the observed echogram (Figures 3.11A and 3.11B). Dynamics of some small layers were replicated, as in box (2) where the shallowest SSL became more intense, or in box (3) where the shallowest SSL connected with the deepest SSL. However, some other features were not well reproduced, as for boxes (1) or (5) where predicted values did not replicate observed changes. Finally in box (4), there was an observed intensification of the deepest SSL whereas the model predicted an intensification of the shallowest SSL. The high correlation between observed and predicted  $S_v$  values pooled for all depths for the N4 cruise (Figure 3.11C, correlation = 0.88, p-value < 0.0001) indicated again that the methodology could be used to predict echograms in non-sampled areas if the range of environmental variables was similar to sampled data.

By averaging predicted acoustic values in the whole water column (10-600m), we proposed an integrated view of the spatial and seasonal variations of the MTLOs' distribution (Figure 3.12). The mean backscatter maximum always occurred in the south of the EEZ, extending toward the north during the warm season.

The proportion of MTLOs migrating within the epipelagic (10-200m) during the night showed a larger part of migrant population below 20°S, especially in the southeast (Figure 3.12B). Migrant proportion varied spatially spanning a range from 75% in the north to 85% in the south with mean values around 78%.

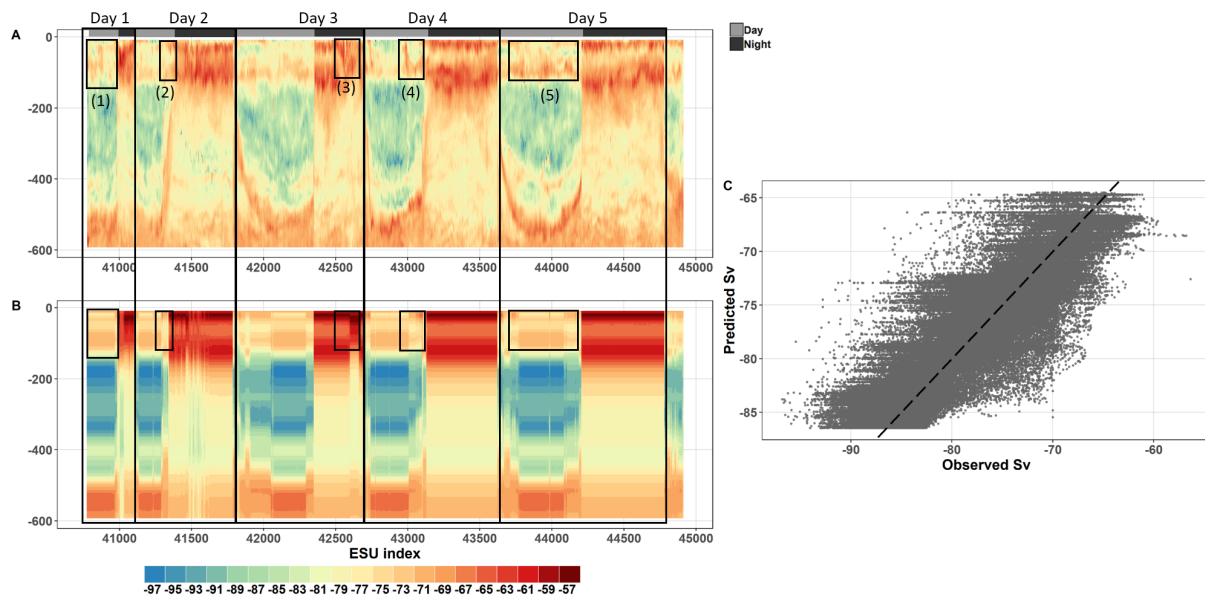


FIGURE 3.11 – N4 echogram observed (panel A) and predicted (panel B). The scatter plot of predicted values as a function of observed values with the  $y = x$  dashed line over all data of N4 (panel C). Boxes drawn on the plots are discussed in the main text as box (1), (2), etc.



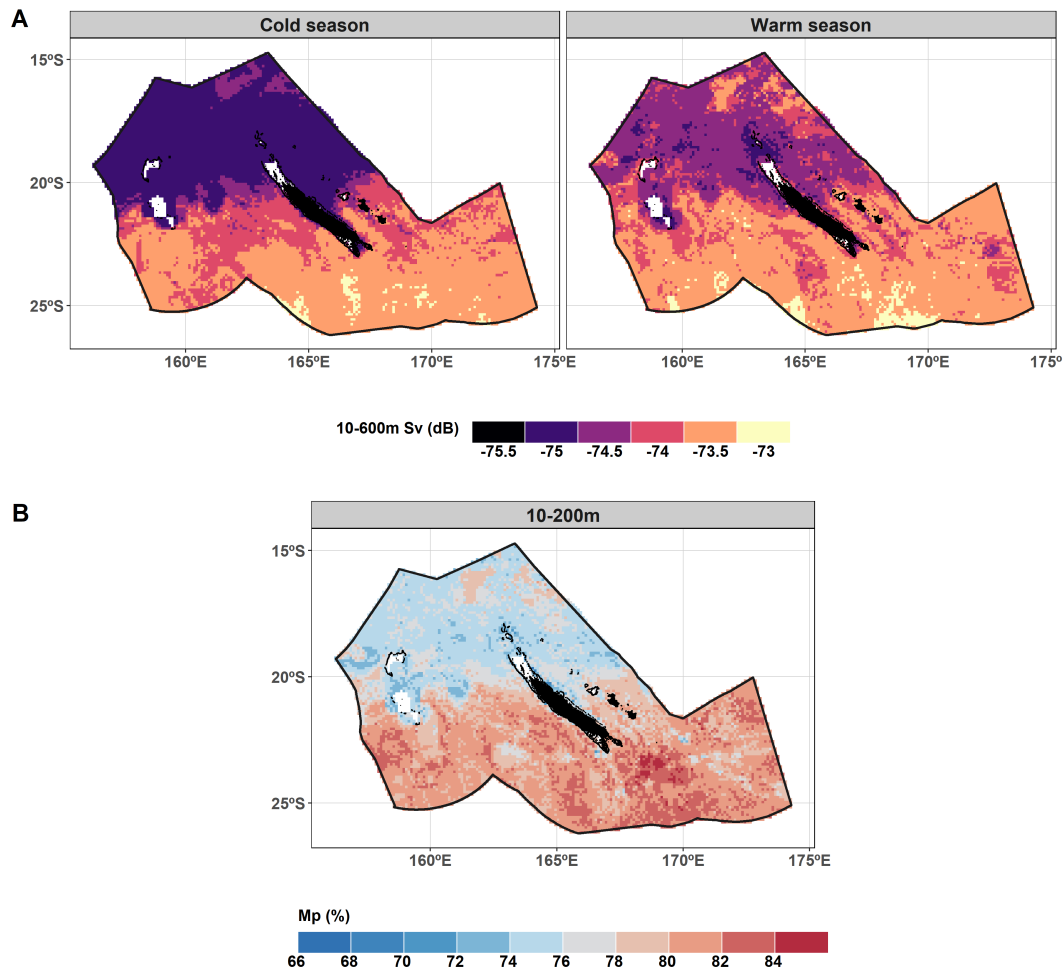


FIGURE 3.12 – Predictions of the Sv averaged over the day and the night and through the entire water column (10-600m) for the cold season (*left*) and the warm season (*right*) (panel A). The ratio of migrants (%) between the night and the day for the epipelagic layer (10-200m) (panel B).

### 3.4 Discussion

By analyzing six cruises of EK60 vertical profiles, we provided new insights into the spatiotemporal MTLOs' vertical distribution in the New Caledonian EEZ. We proposed a statistical framework to link MTLOs' vertical distribution to oceanographic conditions. This framework allowed us to predict acoustic vertical distribution with some success in un-sampled areas. Sun inclination and the mean oxygen concentration were the main factors driving the acoustic vertical profile shape. Three homogeneous acoustic based regions were identified in the New Caledonian EEZ : the north with weak DSL and SSL during the cold season and stronger DSL during the warm season ; the southwest corner with strong DSL and SSL and a center of gravity deeper than in the west ; and the southeast corner with strong SSL and the shallowest center of gravity. Northern vertical distribution was mainly influenced by low mean oxygen values, and southwest distributions were mainly influenced by waters with deep chlorophyll maxima and high oxygen concentration. Due to this spatial pattern of vertical distributions, there were generally more MTLOs in the south of the New Caledonian EEZ than in the north and the migrant's proportion was about 78%.

### 3.4.1 Methodological framework

Behagle *et al.* [2016] performed classification of acoustic vertical profiles but they did not statistically link clusters to environmental covariates. Proud *et al.* [2018a] developed an innovative approach and classified acoustic layers below 200m to investigate the MTLOs' vertical distribution variability. Using a 38 kHz global dataset, they identified six spatially-coherent regional clusters using estimated probability distributions of local SSL depth and of echo intensity. They mapped the clusters at a global scale and matched them with Longhurst's provinces [Longhurst, 1995, 2007]. In our work, we fitted relationships between mean MTLOs' vertical distribution and environmental covariates and were able to predict vertical acoustic profiles in un-sampled areas and so at a larger spatial scale than cruise tracks.

Our proposed methodological framework treated the vertical acoustic profiles as the sampling unit. We thus kept all the shape information contained by the profiles; echo intensity and location of intermediate layers or moderate peaks were taken into account in the analyses. The PCA allowed us to represent the profile data in a lower-dimensional space, reducing the degrees of freedom while keeping 90% of the variability of the raw dataset. This lower-dimensional space was then grouped into 10 clusters that captured the large variabilities of vertical shapes and identify three large homogeneous regions. Clusters were then used in a machine learning algorithm, an approach still underused in analyses of marine data despite their efficiency [De'ath, 2007; Elith *et al.*, 2008]. These approaches are often seen as 'black boxes' and the interpretation of the results remains challenging. Here, we obtained a high performance level (87% in cross validation) for the XGBoost modelling. At the same time, the importance of each covariate was ranked, and we evaluated how they influenced each acoustic cluster through SHAP values that have been shown to be reliable indicators of covariate influence (compare to Gain, split count or Saabas) [Lundberg & Lee, 2017]. However, the use of SHAP values did not allow us to explore the degree of the interactions among covariates.

The XGBoost model predicted the probability of belonging to a given acoustic cluster based on a vector of covariate values. We could do that when the range of covariate values used for the model prediction were similar to the range covered by the initial data used to build the model. Expected for extremely low values of temperature, oxygen and salinity and for shallow waters, covariates ranges used for prediction were well sampled (Appendix 3.15). Regions where predictions were done out of the covariate range sampled were relatively small, mainly around the Main Island, and extreme northern and southern parts of the EEZ in the cold season (Figure 3.10, black points). The narrow range of un-sampled covariate values even for the two widely different seasons suggests that observational sampling was sufficient for the current purpose of the paper.

Using the predicted probabilities at a given point, we reconstructed an acoustic profile by weighting the mean cluster profiles by these probabilities for each point, leading to a complete 3-D reconstruction of acoustic profiles in the EEZ. Despite that correlation between pooled observed and reconstructed backscatter values was high, the variability inside the scatter plot remained relatively high (Figure 3.11C). Predicted values could vary from +/- 10dB for an observed value, pointing out to the limits of the model in terms of reproducing the exact variability. Yet, the main strength of the model was to reproduce the MTLOs' vertical distribution patterns in space and time rather than predict echo-intensities per se. A change of a few dB in the backscatter values may result in large biomass changes [Proud *et al.*, 2018b]. Indeed, for layers dominated by Myctophids, a 10dB change with a 38 kHz frequency could translate into

a three-fold increase in animal density [Benoit-Bird, 2009].

In addition, the use of the 38kHz frequency could help in detecting organisms with a swimbladder (mostly fish) while excluding other organisms without gas-filled swimbladders [Davison *et al.*, 2015a]. Foote [1980] even showed that more than 95% of the organisms' backscatter at 38 kHz was produced by gas-filled swimbladders of fish and gas-filled pneumatophores of siphonophores. One major limitation of our study was the inability to determine if changes in layer intensity and depth position were due to changes in MTLOs' quantity or in MTLOs' compositions. Developing a similar method including organisms' composition would be of great interest. Some efficient algorithms already exist [*e.g.* Ariza *et al.*, 2016; Behagle *et al.*, 2017; Kloser *et al.*, 2016; Korneliussen *et al.*, 2008] based on two or three frequencies that allow for distinguishing among different types of organisms in echograms. Going further into such analysis would require an extensive program of *in situ* sampling with appropriate trawls to identify the species composition of the different layers. So far, with the *in situ* samplers available and given the species diversity already observed [Ceccarelli *et al.*, 2013][Payri *et al.*, 2019], it is unlikely that such a goal can be met in the near future in the New Caledonian region or in the Coral Sea in general.

### 3.4.2 Acoustically based regionalization

Studies of biogeography require methods that partition large areas into distinct regions with homogeneous biological and/or physical oceanographic conditions [*e.g.* Longhurst, 1995, 2007]. Our findings provide evidence that statistical new tools used on acoustic recordings are valuable for conducting regionalization that take into account the MTLOs' distribution in the water column. Several studies already include information on mesopelagic organisms [Sutton *et al.*, 2017], even SSL depth and echo intensity [Proud *et al.*, 2017, 2018a]. Our methodological framework is reproducible at a global scale, and contributes to the general effort for partitioning the mesopelagic domain using acoustic information on the MTLOs' vertical distribution. Such an expansion would require the acquisition of acoustic data on a large scale and on a 'routine' basis, as is done for other variables on ship of opportunity.

### 3.4.3 Environmental drivers of the MTLOs vertical distribution

Physiological tolerance varies by species [Duffy *et al.*, 2017]. Hence, direct relationships between acoustics echo-intensities and environmental covariates are complex to understand due to the high species diversity including MTLOs. In this section, we made some hypothesis based on the literature about environmental effects on MTLO dynamics without analyzing them by species.

#### Role of the most significant covariates

Sun inclination was by far the most important covariate influencing acoustic vertical profiles. Indeed, the DVM pattern impacts drastically the shape of the vertical profiles at night and during the day. MTLOs ascents and descents depend strongly on light intensity, with migrating organisms generally going up to the surface at night to feed, and returning back to deep layers during the day to avoid visual predation [Benoit-Bird & Au, 2004; Hays, 2003].

The oxygen concentration averaged over the 6-606m water column was the second most important covariate influencing the vertical profiles. We found that vertical profiles with higher mean density were influenced by high oxygen values, therefore we added the oxygen influence on the mean echo intensity in addition to the influence on MTLOs' residing depth previously demonstrated. Indeed, in the South Pacific, the lower vertical expansion of the MTLOs' daytime and nighttime SSL is limited by the depth of the oxygen minimum [Bertrand *et al.*, 2010], and Bianchi *et al.* [2013a] demonstrated at a global scale that the higher the oxygen concentration, the deeper the DSL daytime depth.

Our results are in contrast with the widespread hypothesis that low oxygen concentrations provide a refuge from large visual predators and so enhance acoustic values [Bianchi *et al.*, 2013b; Steinberg *et al.*, 2008]. As there is no oxygen minimum zone in the region, MTLOs may go deeper in the water column during the day to minimize predatory pressure and so search for the oxygenated zone during the night to replenish any oxygen depletion developed during their diurnal stay. Therefore, oxygenated water would attract more MTLOs and so would enhance the acoustic values as we shown here. The fact that mean oxygen was more important among night clusters reinforced this hypothesis. As oxygen minimum zones are predicted to expand both spatially and vertically in the future (Keeling *et al.*, 2010), the direct impacts on predator distribution [Stramma *et al.*, 2012] are likely to be heightened by changes in prey distribution.

Bathymetry was the third important variable that influenced vertical profiles (Figure 3.7). The topography of the deep ocean floor is complex around New Caledonia [Gardes *et al.*, 2014], with the presence of three ridges, numerous seamounts with a high shape diversity, one trench and some sedimentary basins. The presence of seamounts, distance to the coast, differences in the topography of the ocean floor between the north and south New Caledonian EEZ did affect MTLOs vertical distribution. The highest 10-600m mean predicted acoustic values occurred in the southeast corner, which was characterized by a variable topography with both shallow and deep bottom depths (Figure 3.12). Shallow waters offer lower-quality habitat for mesopelagic organisms and may induce a densification of MTLOs in the upper layers of the water column [Escobar-Flores *et al.*, 2018]. In addition, the southeast corner of the EEZ has a high density of seamounts that can enhance the mean backscatter values. Seamount impacts on MTLOs dynamics are a function of the type of seamount (*e.g.* isolated or not, shape, depth, upwelling, currents) and of the organisms that aggregate around seamounts [*e.g.* Drazen *et al.*, 2011; Morato *et al.*, 2008, 2010; Rogers, 2018].

### **Other environmental drivers of MTLOs vertical distribution**

The deep euphotic zone had a strong influence on clusters with a deeper mass center (clusters 7, 8 and 9). A deep euphotic zone indicates a deep chlorophyll maximum characterizing oligotrophic areas and dominated by vertical processes with nutrients coming from deep waters. Given that three clusters showed more intense deep SSL compare to other clusters, we assume that a deep euphotic zone allowed ecosystem organization around the chlorophyll maximum with deep zooplankton maxima and, in turn, deep SSL.

Mean temperature and SST also impacted acoustic clusters. Spatial patterns of the mean temperature showed a strong north-south gradient, with one front well delimited around 20°S [Menkes *et al.*,

2015]. This north-south separation coincides with the spatial distribution of the predicted acoustic clusters (Figure 3.10). We hypothesized that mean temperature was simply a measure of hydrographic features that likely reflected different oceanographic conditions. Therefore, mean temperature appeared to delimit large homogeneous regions (the north from the south of the EEZ) rather than having a direct impact on organisms.

A deep 20°C isotherm strongly impacted profiles of clusters in the south during the warm season. The depth of the 20°C isotherm is a proxy of thermocline location : a deeper 20°C isotherm is associated with higher stratification and limits nutrient inputs in the euphotic surface layer [Kessler & Cravatte, 2013; Le Borgne *et al.*, 2011]. Conversely, a 20°C isotherm close to the surface boosts vertical transport of nutrients to the euphotic layer, and could potentially stimulate the trophic web through enhancing phytoplankton, zooplankton and micronekton production [Benoit-Bird & McManus, 2012; Lebourges-Dhaussy *et al.*, 2014]. We emphasized that the link to the isotherm depth was not causal (isotherm depths do not act on animals) but instead reflected different oceanographic conditions. Isotherm depth is a proxy for the presence of eddies. Keppler *et al.* [2018] identified two areas relative to eddies : a smaller number of eddies with a longer lifetime in the southern portion of the EEZ part compared to the northern part, with a clear limit at 20°S that corresponds with the spatial delimitation of Figure 3.10.

High values of surface chlorophyll-a concentration had a strong influence on profiles, with the highest echo intensities at the surface layer. We suggested that the enhancement of primary production at the surface during the day could be associated with enhanced zooplankton production, leading to an increase in MTLOs' density in that part of the water column. The trophic link of a positive relationship between primary production and mesopelagic organisms had been found previously [Escobar-Flores *et al.*, 2013; Irigoien *et al.*, 2014], but at a much wider scale.

Finally, we did not find any effect of the water mass proportions in the New Caledonian EEZ while previous studies [Behagle *et al.*, 2016; Jungblut *et al.*, 2017; Sutton *et al.*, 2017] documented this factor as significant. Water masses are often linked to biogeographical provinces [Briggs & Bowen, 2012] at a wide spatial scale. We hypothesized that the size of New Caledonian EEZ and the lack of contrasting water masses precluded the detection of a significant effect in our case.

#### 3.4.4 Conclusion and perspectives

While acoustics provides a useful avenue for routine measurement of crucial trophic compartments, it remains that analyses of such datasets depend on knowledge of the species giving rise to the analyzed signal. Indeed, it is crucial to increase our understanding of the actual relationships between acoustic output and true species composition and density. So far, in our region, the lack of adequate *in situ* sampling is a major limitation to our understanding of the ecological processes based on acoustic data.

Our findings highlighted the importance of environmental variables characterizing the structure of the water column, such as the mean oxygen, the euphotic depth (as a proxy for the vertical structure of primary production) and the 20°C isotherm depth (as a proxy for the functioning of ocean dynamics such as upwelling or down welling). Investigating the links between the 3-D oceanographic conditions and the MTLOs' dynamics requires information on the physics, biogeochemistry and biology of the upper (< 1000m) water column. Accessing 3-D high-resolution oceanographic data or models to understand

complex interactions at the acoustic data acquisition scale is not yet possible. For instance, we did not find a satisfying 3-D biogeochemical model estimating the values of primary production that matched with our *in situ* data. Consolidating and validating coupled dynamical-biogeochemical 3-D models will strongly contribute to a better comprehension of the pelagic ecosystem.

Variability in MTLOs' layer depths during day and night impacts predator-prey interactions, including the predators' energy budget allocated to feeding. For active vertically migrating predators, the possibility to feed in shallow, warm, and rich water brings energetic savings [Hazen *et al.*, 2015]. Acoustic data are extremely helpful for analyzing predator-prey interactions on a wide scale [Bertrand *et al.*, 2003; Koslow, 2009]. Indeed, acoustics recorded continuously along vessels' tracks allow building datasets with a better coverage than trawl data or predators' stomach content, for example. However, the surface sampled along the tracks remains small compared to the surface of predators feeding. Our model gave the possibility to fill gaps around acoustic cruise tracks while keeping all the information contained on acoustic profiles. Then, by averaging vertical predictions on a specific vertical layer (*e.g.* 0-30m to link to seabirds foraging compartment), we offer an innovative method to predict a proxy of prey biomass (through echo intensity) that could be used in predator niche modeling on large spatial and temporal scales [Briand *et al.*, 2011; Lambert *et al.*, 2014; Miller *et al.*, 2018].

Further, our method may provide a valuable contribution to assess the climate change impact on MTLOs, and consequently on the whole pelagic ecosystem. The increase in ocean temperature, the extension of low-oxygen zones [Bindoff *et al.*, 2007; Doney *et al.*, 2012] as well as the possible decrease of the primary production [Bopp *et al.*, 2013] predicted under future scenarios of environmental change will have dramatic effects on MTLOs distribution (*i.e.* layer position, abundance and biomass). Our model, including predictive oceanographic variables could help to predict changes in MTLOs vertical distribution for the next 100 years using climate change scenarios as Proud *et al.* [2017] did.

## Appendix

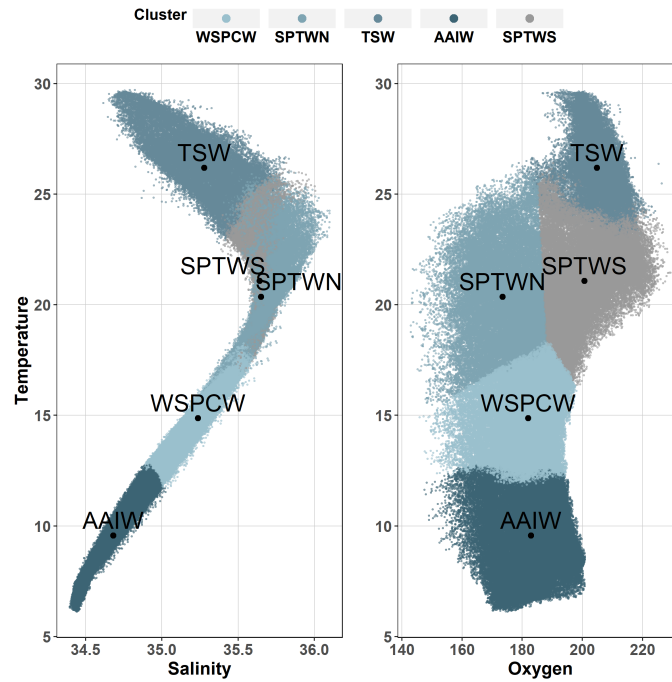


FIGURE 3.13 – Salinity values pooled for all depths over the 12 months (*x-axis*, left) and oxygen values pooled for all depths over the 12 months (*x-axis*, right) as a function of temperatures values pooled for all depths over the 12 months (*y-axis*). Colors represent results from k-means clustering (*i.e.* water masses identified. TSW : Tropical Surface Water ; SPTWS : South Pacific Tropical Water South ; SPTWN : South Pacific Tropical Water North ; WSPCW : Western South Pacific Central Water ; AAIW : Antarctic Intermediate Water.

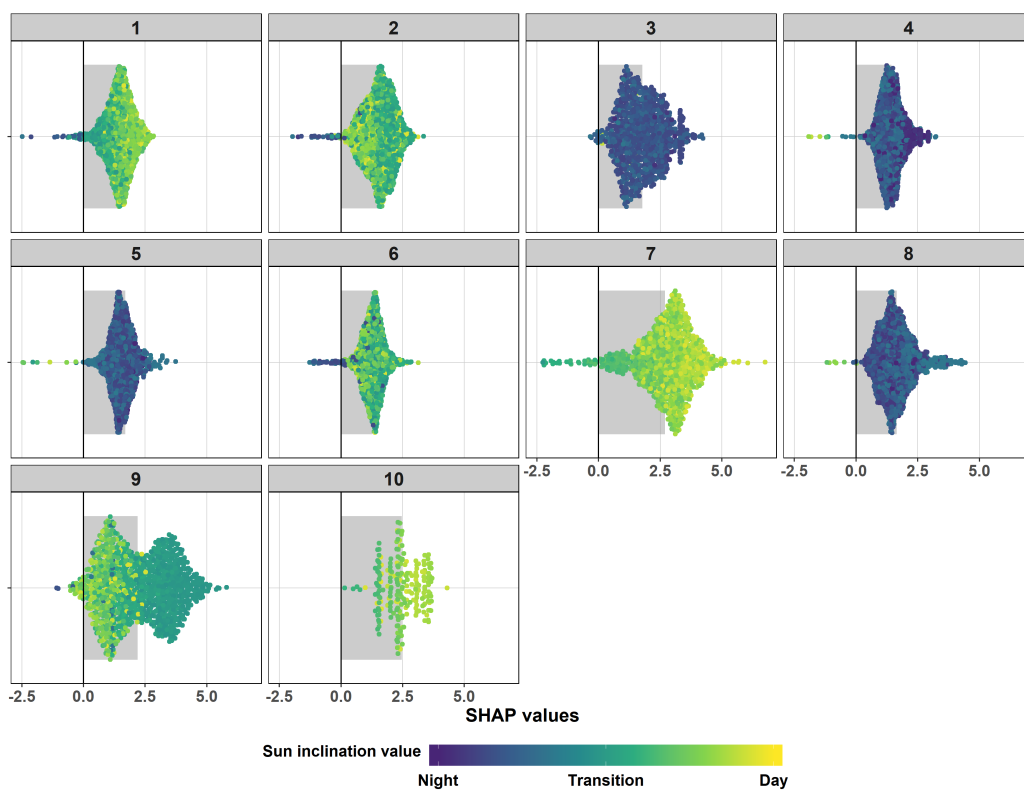


FIGURE 3.14 – SHAP (SHapley Additive explanation) values ( $x$ -axis) of the sun inclination covariate by cluster : blue colors represent a strong influence of negative sun inclination values, *i.e.* high probability to be in this cluster during the night, and yellow colors reflect a high probability to be in this cluster during the day.



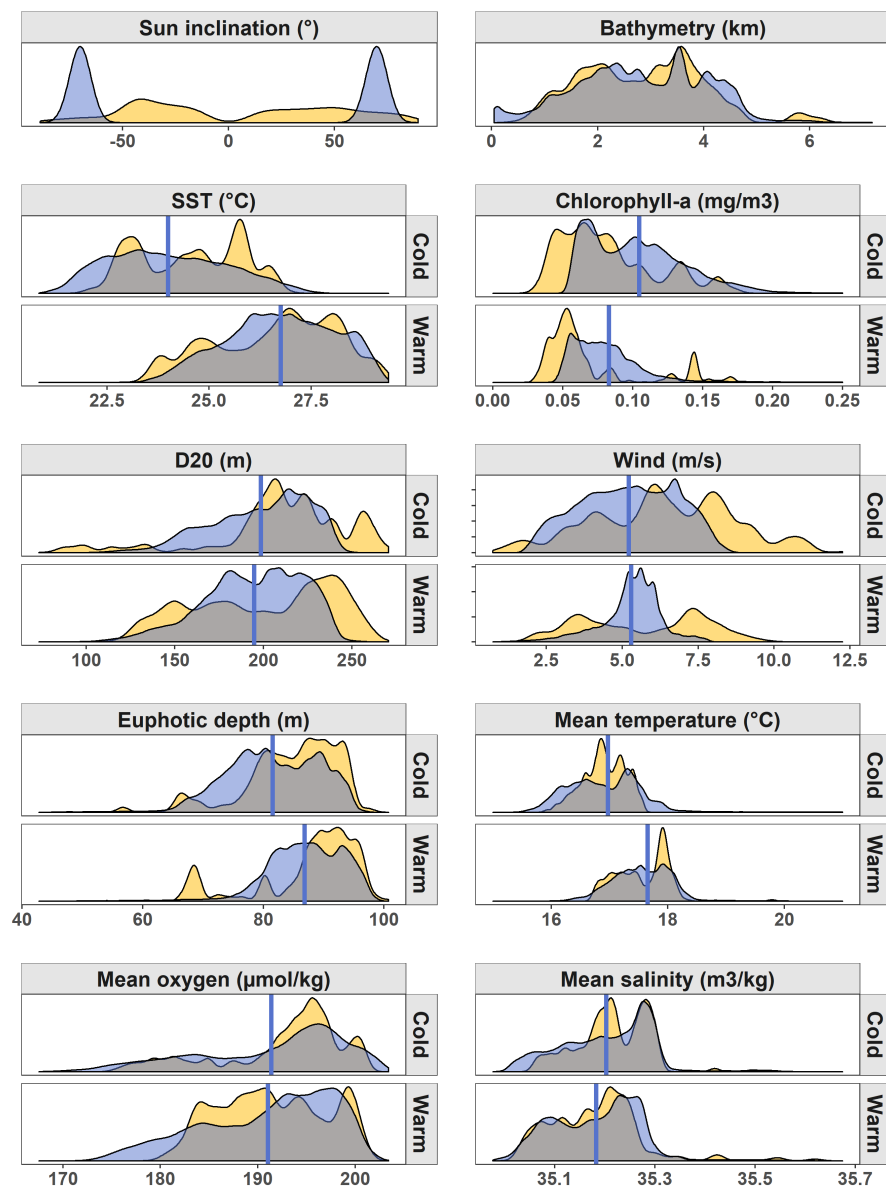
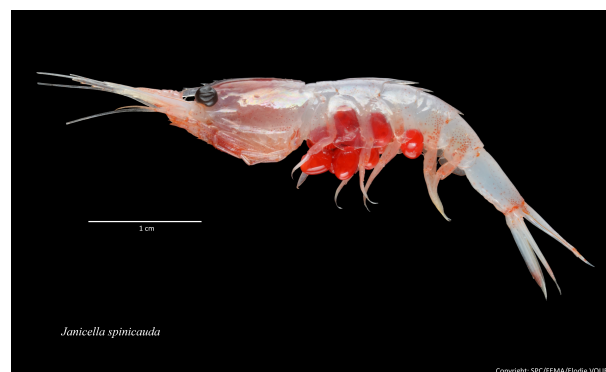


FIGURE 3.15 – Distribution of values observed (yellow) and used for the prediction (blue) by variable and by season in the XGBoost model. Blue vertical bars show the mean value of each variable by season in the prediction dataset.

# Inter-chapter

Chapter 3 evaluated the seasonal and spatial variability of micronekton vertical distribution. For that, we used EK60 data acquired through six cruises. Sun inclination was the most structuring variable for vertical distribution. Mean oxygen and bathymetry were the next most important drivers of micronekton vertical distribution. We identified three acoustically homogenous regions : north of 21°S with low Deep Scattering Layer (DSL) and low Shallow Scattering Layer (SSL) ; the southwest corner (high SSL at 80m and very high SSL at 30m) ; and, the southeast corner (high SSLs and very high DSL at 550m). These regions stayed relatively stable across seasons. Due to variable vertical distributions, mean echo intensity of the southern EEZ region was always higher than in the north. We also approximated the migrant proportion of the region, about 75%. However, due to the absence of information about species composition, we cannot conclude if echo intensity changes were linked to real micronekton abundance change or species composition changes modifying the acoustic signal. To answer this question, the next chapter focuses on characterizing micronekton species assemblages. For that, we analyzed trawl data collected during the six cruises used for the analysis of the EK60 data.





# Chapitre 4

## Micronekton richness and assemblages in the Natural Park of the Coral Sea

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## Abstract

Mesopelagic resources are central to the ecosystem but remain poorly studied mainly due to the lack of data. This paper investigated the richness and assemblages of micronekton organisms and their habitat in the Natural Park of the Coral Sea around New Caledonia (southwest Pacific) using data from 141 pelagic trawls. A total of 67 130 micronekton individuals (fish, crustaceans, and molluscs) were collected, with 421 species identified, among 237 genus and 161 families. In the analyses we focused on 22 species, each were present in more than 33 trawls (*i.e.* in more than 25% of the total number of trawls) and studied their spatial distribution and vertical dynamic behaviour. Community structure was investigated through Region of Common Profile (RCP), an innovative statistical multivariate method allowing to study both species assemblages and environmental conditions influence on species occurrence probability. Seven major assemblages were identified, mainly driven by time of the day and depth. Environmental variables such as mean oxygen concentration, mean temperature and bathymetry, also influenced micronekton assemblages, inducing a north/south distribution pattern. Two major day-assemblages were identified, both distributed over the whole EEZ but segregated by depth, one in waters shallower than 250m and the other one in deeper waters. The four night-assemblages were also mostly segregated by depths, with two community changes at approximately 80m and 250m, as well as spatially. The predominant 0-80m northern assemblage was dominated by crustacean whereas the southern assemblage was dominated by one crustacean species, three cephalopod species and four fish species. The 80-250m assemblages were characterized by more cephalopod and fish species in the south than in the north. Generally, the northwest part of the EEZ was more diverse than the southwest part. Based on our results, we identified three important areas to be considered for special management measures as part of the Natural Park of the Coral Sea.

**Keywords :** *Micronekton, richness, assemblages, Southwest Pacific Ocean, mesopelagic zone*

## 4.1 Introduction

Marine biodiversity is predicted to decrease in the coming years at the global scale [Garcia Molinos *et al.*, 2016; Worm & Lotze, 2016] with human activities such as fishing, pollution and habitat perturbation, identified as key drivers of this decrease [Diaz *et al.*, 2019; Lotze *et al.*, 2006]. Climate change, another main threat to marine diversity is causing large modifications in species spatial distribution [Cheung *et al.*, 2009; Hillebrand *et al.*, 2018; Lotze *et al.*, 2019; Pecl *et al.*, 2017] and therefore induces local changes in assemblages composition [Dornelas *et al.*, 2014].

This global loss of biodiversity is threatening the ecosystem functioning as well as the services they provide, essential for human well-being [Beaumont *et al.*, 2007; Cardinale *et al.*, 2012; Hannah *et al.*, 2013; Worm *et al.*, 2006]. Marine Protected Areas (MPAs) and Large-scale Marine Protected Areas (LSMPAs) have been identified as key species conservation tools [Christie *et al.*, 2017; Davidson & Dulvy, 2017; Ehler & Douvère, 2009], as well as to mitigate the effects of climate change [Roberts *et al.*, 2017]. In the vast pelagic domain, MPAs have been offered as tool to protect migratory species [Davis *et al.*, 2012]. However, it has been emphasized that at the global scale the current level of protection of marine ecosystems spatially mismatched the important regions in terms of diversity, for instance main diversity

hotspots are mostly outside protected areas [Lindegren *et al.*, 2018]. This relatively inefficient global management could be explained by the knowledge gap in marine species ecology (especially environmental drivers of their spatial distribution) and species interactions (trophic or others) [Dornelas *et al.*, 2014]. Therefore, climate change impacts could be mitigated by improving the understanding of species optimal environmental conditions and by including it in global strategic frameworks for management and conservation [Glover *et al.*, 2018; Pecl *et al.*, 2017]. However, this should not be limited to a small number of species, as it is often the case, but it should target to encompass the whole species assemblages [Fisher *et al.*, 2011].

In pelagic ecosystems, mid-trophic level organisms (MTLOs), also referred to as micronekton, include crustaceans, molluscs, gelatinous organisms and fish with size ranging from 1 to 20cm long [e.g. Young *et al.*, 2015]. Micronekton species play a central role in the pelagic ecosystem as food of predators including commercially targeted species such as tuna [Bertrand *et al.*, 2002a; Duffy *et al.*, 2017; Olson *et al.*, 2014] and emblematic marine species such as seabirds, cetaceans and sharks [Lambert *et al.*, 2014; Miller *et al.*, 2018]. Hence, micronekton diversity directly impacts predators diet [Duffy *et al.*, 2017; Portner *et al.*, 2017]. Micronekton performs daily migrations between the surface layer (0-200m), where they stay during the night, and the mesopelagic layer (200-1000m), where they stay during the day to avoid visual predation. This largely participates to the downward flux of nutrients and particulate organic matter via respiration and excretion processes [Ariza *et al.*, 2015; Drazen & Sutton, 2017; Hidaka *et al.*, 2001]. This Diel Vertical Migration pattern (DVM) is observed in the world ocean [Bianchi & Mislán, 2016; Klevjer *et al.*, 2016] and is performed by a large majority of species (75% of organisms in the southwest Pacific according to Receveur *et al.* 2019). Despite their important role, the dynamic of micronektonic species in their environment is still poorly understood [Hidalgo & Browman, 2019; St. John *et al.*, 2016]. In particular, species vertical behaviour (e.g. percentage of individuals performing DVM) is one knowledge gap to solve in order to include micronekton into biogeochemical models of carbon cycle [Aumont *et al.*, 2018]. The large intrinsic micronekton diversity [Olivar *et al.*, 2017], and the poor observation level complicate a complete understanding of the mesopelagic species ecology. Indeed, each micronektonic species has a specific habitat that is challenging to identify [Duffy *et al.*, 2017].

In the New Caledonian Exclusive Economic Zone (EEZ), located in the Coral Sea at the south-western edge of the Pacific Ocean, top predator diet studies [Allain *et al.*, 2012; Olson *et al.*, 2014; Williams *et al.*, 2014; Young *et al.*, 2010] and trawl data analyses [Grandperrin *et al.*, 1999; Menkes *et al.*, 2015; Young *et al.*, 2011] revealed a high diversity of micronekton organisms [Payri *et al.*, 2019]. This high diversity also supports high richness of top predators species [Ceccarelli *et al.*, 2013; Laran *et al.*, 2016b], with the presence of several species of cetaceans [Garrigue *et al.*, 2015; Mannocci *et al.*, 2014b], sharks [Bakker *et al.*, 2017; Boussarie *et al.*, 2018] and seabirds [Borsa *et al.*, 2014, 2015; Weimerskirch *et al.*, 2017]). Moreover, the seabed topography is complex around New Caledonia [Gardes *et al.*, 2014], with the presence of three ridges, numerous seamounts with a high shape diversity, one trench and some sedimentary basins. Such bathymetry offers large habitats diversity that could enhance micronekton diversity and biomass as demonstrated for seamounts [Drazen *et al.*, 2011; Morato *et al.*, 2010] and ridges [Hudson *et al.*, 2014; Laptikhovskiy *et al.*, 2017].

The Natural Park of the Coral Sea was recently created in oceanic waters of New Caledonia (Decree 2014-1063/GNC). However, robust scientific information on the productivity and functioning of this pelagic ecosystem, including micronekton dynamics and role in food webs, are still lacking [Ceccarelli *et al.*,

2013; Gardes *et al.*, 2014]. Hence, additional information on micronekton assemblages and diversity will contribute to designing the Natural Park management plan, accounting for the conservation of the food stock of all top predators. In this context, the large diversity of predators and micronekton makes the New Caledonian EEZ the perfect case study to understand the pelagic ecosystem functioning and to implement efficient management tool. Using data from 141 mesopelagic trawls conducted in New Caledonian EEZ in 2011–2016, we applied Region of Common Profile (RCP) methodology to quantitatively characterize the micronektonic assemblages, to identify the environmental conditions influencing those assemblages and to determine their spatial distribution. RCP also allowed the description of the vertical distribution of the most abundant species as well as their spatial distribution.

## 4.2 Methods

### 4.2.1 Sample collection

We gathered data from five cruises (Nectalis 1 to 5, DOIs : 10.17600/11100050, 10.17600/11100070, 10.17600/14004900, 10.17600/15004000, 10.17600/16004200) on board the R/V Alis in the New Caledonian Exclusive Economic Zone, covering the area between 156°E–175°E and 14°S–27°S over the period 2011 to 2016 (Figure 4.1A). The sampling strategy of the five cruises aimed at covering both spatially and temporally the whole New Caledonian EEZ (Appendix 4.8). Nectalis 2, Nectalis 3 and Nectalis 5 were carried out during the warm season (December-May), and Nectalis 1 and Nectalis 4 during the cold season (June-November). Moreover, Nectalis 1 and Nectalis 2 covered the northern region, Nectalis 3 the west, Nectalis 4 the south-west and Nectalis 5 the south-east. Acoustic data were recorded continuously during cruises using an EK60 echosounder (SIMRAD Kongsberg Maritime AS, Horten, Norway) connected to four split-beam transducers at 38, 70, 120 and 200 kHz.

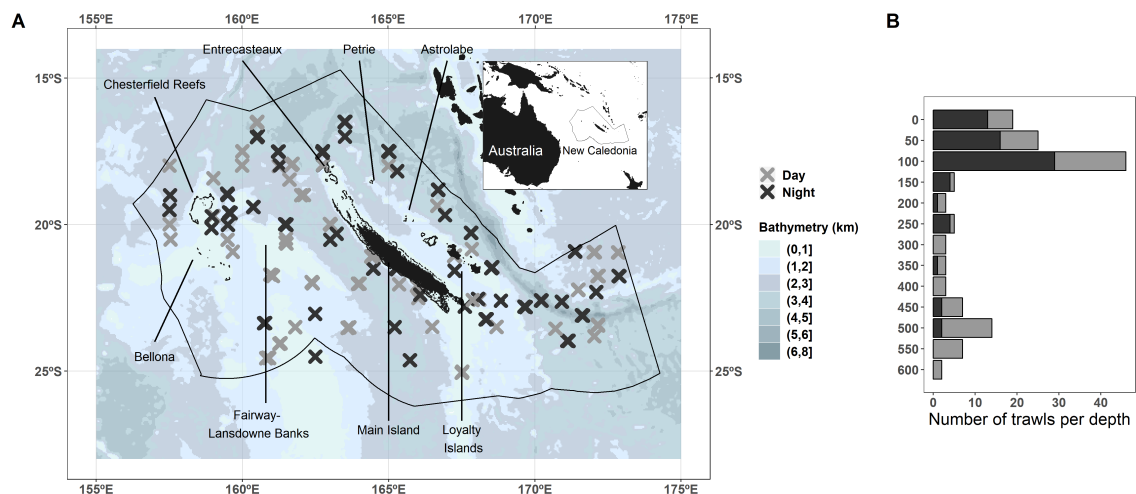


FIGURE 4.1 – Trawls spatial position coloured by the moment of the day (grey and dark crosses) in the New Caledonian Exclusive Economic Zone. The background blue colours represent the seabed depth (where lighter colours are shallower). Note that trawls from two cruises partially overlap and for visualization purposes some trawls in the north have been slightly shifted to the north.

Micronekton organisms were sampled at each station with a mid-water trawl with a 10 mm mesh.

Vertical and horizontal mouth opening of about 10 m were monitored with trawl opening sensors (Scanmar, Asgardstrand, Norway). Horizontal tows were conducted to target aggregations visually detected with the EK60 echosounder, both during day and night periods (Figure 4.1B). Once the net was stabilized at the echo depth, based on Scanmar depth positioning information, it was towed for about 30min with a vessel speed around 3-4 knots. One or two trawls were conducted at each station, at depth varying between 10 and 590m during the day and between 10 and 520m during the night. Organisms collected were quickly sorted by broad taxon (*e.g.* Crustacea, Actinopterygii, Cephalopoda) onboard the vessel and immediately frozen at -20°C.

In the laboratory, specimens were defrosted and identified to the lowest possible taxon based on morphologic criteria and using identification keys. Identified specimens were counted and weighted. Gelatinous organisms were removed from analysis as accurate counts and weights cannot be recorded due to the fragility of those organisms and their high percentage of water. Indeed, they are easily damaged during trawling and freezing, limiting the accuracy of the identification. Individuals from colonies were separated, making the counting of organisms imprecise and thawing make them loose their water content such that weighting was non representative of the fresh wet weight.

The volume filtered by the net was calculated as  $V = SD$ , with  $S = hv$  and  $D = Rc$ ,

$$c = 2 \tan^{-1} \left( \sqrt{\frac{a}{1a}} \right) \text{ and}$$

$$a = \left[ \sin \left( \frac{lat_2 - lat_1}{2} \right) \right]^2 + \cos(lat_1) \cos(lat_2) \left[ \sin \left( \frac{lon_2 - lon_1}{2} \right) \right]^2$$

Where  $V$  is the volume filtered ( $m^3$ ),  $S$  is the net mouth opening ( $m^2$ ),  $h$  and  $v$  are the net horizontal and vertical mouth opening (m),  $D$  is the distance covered by the trawl (m),  $R = 6371e^3$  is the earth radius,  $lat_1$ ,  $lat_2$ ,  $lon_1$ ,  $lon_2$  are the latitude and longitude of the start and the end of the set at the chosen depth (radian). More details about Nectalis 1 and Nectalis 2 are given in [Menkes \*et al.\* \[2015\]](#).

#### 4.2.2 Environmental variables

Environmental variables were selected to explore the sampling conditions of micronekton assemblages (Table 4.1). For each trawl, environmental data were extracted at the date and position of the sample.



TABLEAU 4.1 – Summary of environmental variables with unit, source, and resolutions. Variables with a temporal resolution ‘Clim’ are climatological data (2000-2018). Details on the variables and on the sources are provided in the main text.

| Variable name       | Unit              | Source  | Temporal resolution | Spatial resolution |
|---------------------|-------------------|---|---------------------|--------------------|
| Moment              | -                 | Sun inclination calculated  | -                   | -                  |
| Trawl depth         | m                 | Measured with Scanmar sensors                                     | -                   | -                  |
| Bathymetry          | km                | ZoNéCo 2013   | -                   | 500 m              |
| Bathymetry slope    | °                 | ZoNéCo 2013   | -                   | 500 m              |
| 20°C isotherm depth | m                 | ARMOR3D   | Week                | ¼°                 |
| Chlorophyll-a       | mg/m <sup>3</sup> | GlobColour-Processors versions :<br>MODIS 2014.0.1/VIIRS 2014.0.2 | Day                 | ¼°                 |
| Mean temperature    | °C                | ARMOR3D   | Clim                | ½°                 |
| Mean oxygen         | µmol/kg           | CARS  | Clim                | ½°                 |

Sun inclination was calculated as a function of spatial position and date [Blanc & Wald, 2012; Michalsky, 1988] and trawl were categorized into ‘Day’ and ‘Night’ periods (negative values corresponding to Night and positive values to Day). Bathymetry data was extracted from the ZoNéCo database at a 500m spatial resolution [ZoNéCo, 2013]. Slope of bottom was calculated as the spatial derivate of the bathymetry.

The depth of the 20°C isotherm (referred as ‘isotherm depth’ hereafter) were extracted from the Armor3D dataset [Guinehut *et al.*, 2012] available at a weekly time scale. Chlorophyll-a surface concentration was extracted from GLOBCOLOUR [Saulquin *et al.*, 2009] at a daily resolution. All variables were extracted on a ¼° spatial grid.

Armor3D provided an ocean reanalysis of observed vertical profiles of ocean temperature (T) [Guinehut *et al.*, 2012] and CARS vertical distribution of oxygen concentration (O<sub>2</sub>) [Ridgway *et al.*, 2002]. As inter-annual data were not available for CARS, we used the climatology calculated between 2000 and 2018 for these two data. Armord3D and CARS were used rather than *in situ* field data, because CTD casts were only taken at a limited number of sampling stations. However we systematically checked the matching between CTDs and Armor3D temperature (correlation of 0.99) and between CTDs and CARS oxygen (correlation of 0.74). We used the 0-600m (the trawl depth range) averages of climatologic temperature and oxygen concentration (30m vertical resolution) at a 1/2° spatial resolution.

We checked the absence of collinearity between variables by ensuring that Spearman correlations were below 0.5.

### 4.2.3 Statistical analysis

#### Methodological background

Commonly used methods to study species assemblages or to do regionalization are mostly based on dissimilarity metrics between sites [Gotelli & Ellison, 2012] allowing to group sites with similar species composition. The link between the groups and the environmental parameters is done in a second step, often by fitting a model between groups and environmental variables or by averaging variables by group

[e.g. Ariza *et al.*, 2016; Olivar *et al.*, 2012; Williams & Koslow, 1997]. However, firstly such approaches do not allow understanding the links between species composition and the environmental conditions [Hill *et al.*, 2017]. Secondly, methods based on dissimilarity metrics implicitly assume a mean-variance relationships (e.g. linear) that is not true [Warton & Hui, 2017; Warton *et al.*, 2012]. To oppose these two large limits, the use of model-based approach allows to explore species assemblages and the response of species abundance to environmental variables in only one step [Warton *et al.*, 2015b]. This method also allows to check the quality of the model and predictions by looking at residuals [Warton *et al.*, 2015a]. Therefore, in the present study, assemblages and environment influence was tested using the RCP (Region of Common Profiles) method, a model-based approach [Foster *et al.*, 2013]. RCP method is based on multivariate generalized linear models (GLMs) and aims at simultaneously group trawls of similar species composition and describes assemblages' variability using environmental variables [Hill *et al.*, 2017].

One RCP was defined as a group of trawls where the probability to observe one species assemblage was approximately constant among trawls and distinct from other groups of trawls [Foster *et al.*, 2013]. To link with other more commonly used methods, RCPs could be viewed as clusters of trawls, but in a probabilistic world. The probability for one trawl to belong to one RCP varied according to environmental variables. The method had the great advantage to allow predictions of RCP's where trawls are absent.

### **Model parametrization**

One assemblage, also called 'RCP', is defined as a group of trawls where the probability to observe one species assemblage was approximately constant among trawls and distinct from other groups of trawls [Foster *et al.*, 2013]. To link with other more commonly used methods, RCPs could be viewed as clusters of trawls, but in a probabilistic world. The method offered the advantage to do predictions of RCP's where trawls are absent.

The model predicts two outputs : (1) the probability of observing each RCP based on a set of environmental values and (2) each RCP composition, i.e. probabilities of observing each species by RCP and.

For one species, the probability to belong to one RCP is called species prevalence. The sum of species prevalence by RCP was considered to be a proxy of species richness. This prevalence sum ranged from zero (if no species were predicted to be present) to  $n$ , the total number of species (if all species were predicted to be present with a probability of one). The higher this sum is, the higher the probability of species occurrence is and, therefore, hereafter, we used 'species richness' to speak about this sum of prevalence values.

Only specimens identified at the species level were considered to fit the model. The response variable was the number of individuals by species and by trawl, that we modelled using RCP methodology with a Negative Binomial sampling distribution and a log link function. The model was estimated with maximum penalized likelihood. The number of individuals by species and by trawl was explained as a function of the time of the day (categorical variable with two levels, day and night), and seven quantitative variables (trawl depth, bathymetry, slope, chlorophyll-a concentration, isotherm depth, mean oxygen concentration and mean temperature) (Table 4.1).

Trawls were different in terms of duration (from 16min to 56min). Moreover, the total number of sampled individuals strongly varied among trawls (from 1 to 1544), mostly due to acoustic detection targeted or not. To take into account these two factors showing a variability of sampling effort among trawls, we added by trawl the total number of individuals divided by the volume filtered as a sampling factor [Foster, 2017].

We used the Bayesian Information Criteria (BIC) [Hui *et al.*, 2015; Raftery, 1995] and our personal knowledge of the region based on acoustics data analyses [Receveur *et al.*, 2019, n.d.] to select the appropriate number of RCPs.

### Model predictions

To visually explore environmental drivers on the occurrence probability by RCP, partial dependence plots were produced. Hence, we fixed all environmental variables to their mean values expect one, and we then predicted RCPs probabilities for the remaining variable increasing from its minimal value to its maximal [Friedman, 2001].

We then spatially predicted RCPs probabilities for the whole New Caledonian EEZ. It required the calculation of the climatology of the two inter-annual variables (*e.g.* chlorophyll-a concentration and isotherm depth) and coupled with the four other variables (mean oxygen concentration, mean temperature, moment of the day, trawl depth, bathymetry and slope) we predicted at a 1/4° spatial resolution the probability of each cell of the grid to belong to each RCP. We only predicted RCPs probabilities within the range of values of each environmental variable. For example mean temperature associated to trawls ranged between 15.6°C and 24.3°C, so predictions were only performed within this range to avoid extrapolation. We then extracted the most probable RCP by grid cell. We also calculated mean richness for each spatial cell by averaging RCP species richness weighted by RCP presence probability.

To improve our understanding of species ecology, we calculated occurrence probability of each species by grid cell by : multiplying RCP presence probability by species prevalence inside this RCP, and summed across all RCPs. With this technic, we were able to predict occurrence probability of one species function of varying environmental conditions [Foster *et al.*, 2013; Hill *et al.*, 2017].

### Model validation

As described in the previous paragraph, we calculated species occurrence probability based on a set of environmental variables. To validate these predicted probabilities, we did 4-fold cross validation [Browne & Cudeck, 1989]. The model was first fitted on a training dataset (75% of randomly selected trawls) and then tested on a validation dataset (the remaining 25% of trawls) four times. The Area Under the Curve (AUC) was then calculated by species (a species was 'present' with a predicted probability higher than 0.5). AUC indicates the probability that the model predicts a presence when a presence was observed (called a true positive). It gives a measure of the model robustness to predict the presence of the considered species : the higher the AUC, the better the model prediction.

Following Hill *et al.* 2017, we performed 500 bootstrap optimization with random first values to avoid

drawing broad conclusions based on a local likelihood maximum and to measure the method's accuracy. The species profile of each RCP was then averaged between the 500 simulations.

Statistical analyses were performed using R [R Core Team, 2018] version 3.5.0. RCP models were carried out using the *RCPmod* package [Foster, 2017; Foster *et al.*, 2013].

## 4.3 Results

### 4.3.1 Trawl dataset

After removing gelatinous organisms, the total number of specimens was 35,180 weighting about 50kg and ordered in 624 taxa (*i.e.* a mix of specimens identified at different taxonomic levels as family, genus, species). A total of 252 species among 152 genus and 77 families were identified. Myctophidae, Euphausiidae, Sternoptychidae, Pyroteuthidae, Oplophoridae and Gonostomatidae were the most abundant families, with more than 500 specimens among all trawls (Appendix 4.4).

The full dataset encompassed 141 trawls in the 10-600m depth range. Three trawls were removed because of technical problems during trawling, and three more because no specimen were identified at the species level. We kept 22 species that occurred in more than 25% of the trawls (*i.e.* in more than 33 trawls out of 135). The cumulative abundance of these 22 species corresponded to 64% of the total abundance sampled (22 473 individuals out of 35 180) and 55% of the total weight sampled (27.1kg over 49.6kg). We removed nine additional trawls for which none of the 22 most frequent species were sampled, and three additional trawls because environmental variables were not available at the sampling location. Therefore, the final dataset analysed was composed of 123 trawls with the abundance of 22 species. Most of the night trawls were conducted between 0 and 250m depth whereas day trawls usually ranged between 0 and 600m (Figure 4.1B). The 22 species retained for the assemblage analyses belong to the Myctophidae, Euphausiidae, Sternoptychidae, Oplophoridae, Gonostomatidae, Cranchiidae, Phrosinidae, Hydromyidae, Phronimidae and Pyroteuthidae families (Appendix 4.9).

### 4.3.2 Assemblage description

Doing 7, 12, 14 or 15 RCPs had smaller BIC values compared to surrounding RCPs numbers (Appendix 4.10). Moreover, in the New Caledonian EEZ, Receveur *et al.* 2019 highlighted three large homogenous regions at the New Caledonian EEZ scale. Based on BIC curve and to be able to compare to acoustics region, we chose to separate the trawls dataset in seven RCPs. The RCP model diagnostic plots indicated that the model was adequate to describe variation in data (*e.g.* independence of observed data, good residuals distribution, and residuals' independence to fitted values) (Appendix 4.11). There was no evidence of residual spatial auto-correlation by species (Appendix 4.12).

Assemblages were split into two groups : i) RCP1 and RCP5, which demonstrated the lowest species richness (3.1 and 4.1 respectively) with few species dominating and ii) RCP2, RCP3, RCP4, RCP6 and RCP7, which were richer (species richness above 6) (Figure 4.2). RCP1 was mainly composed by *Phrosina semilunata* (crustacean) and *Cranchia Scabra* (mollusc) and RCP5 by the crustacean *Janicella spinicauda*

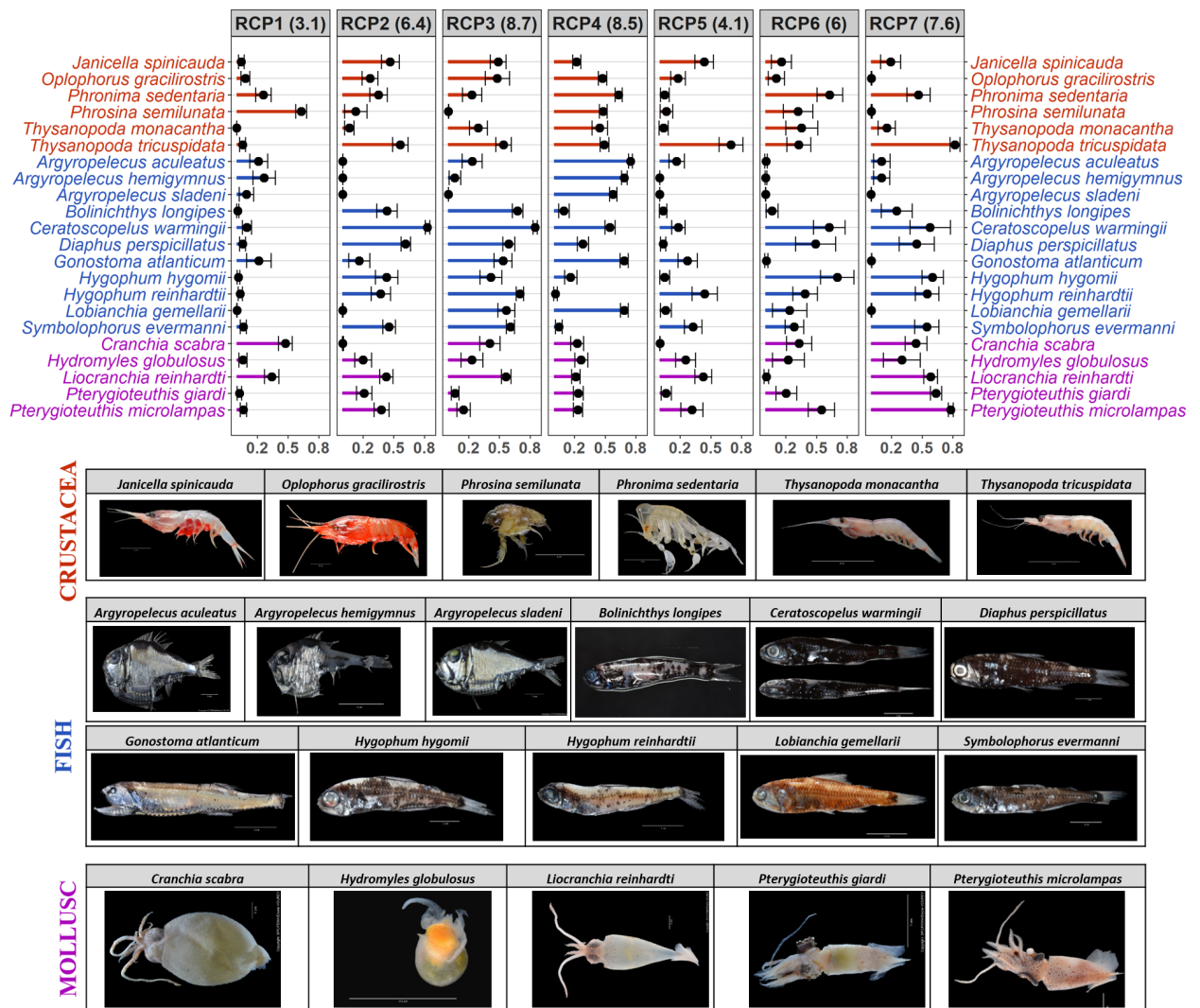


FIGURE 4.2 – The species prevalence for each RCP (Region of Common Profile or trawls groups with shared species' composition) (1–7) showing the average and standard deviation of occurrence probability for each species. Standard deviations and means are calculated by taking 500 bootstrap samples of model parameters, generating expected probability of occurrences for each species in each RCP. The number given in parenthesis after RCP names is the sum of all species' prevalence, used as proxy of species richness. All pictures are ©SPC/FEMA/Elodie Vourey.

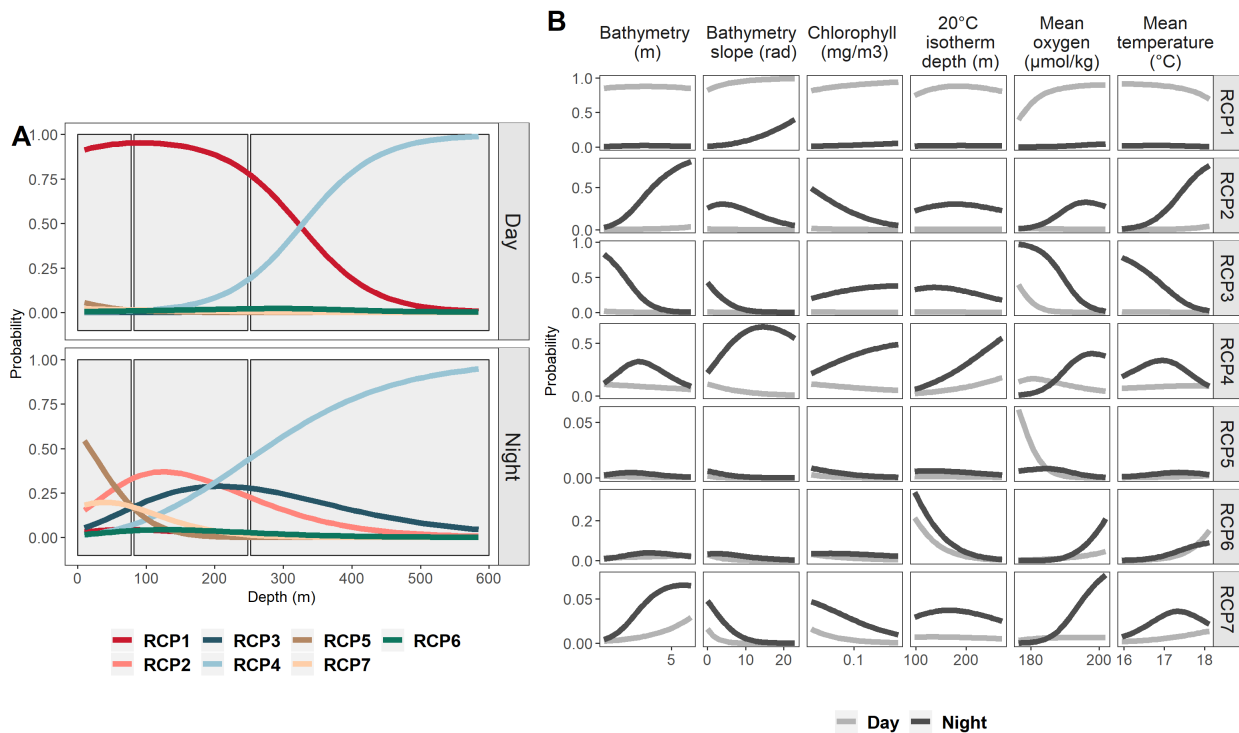


FIGURE 4.3 – Response of each RCP (Region of Common Profile) to depth during day and night periods (rows) (panel A), and to bathymetry, bathymetry slope, chlorophyll-a concentration, 20°C isotherm depth, mean oxygen concentration and mean temperature during the day (grey line) and during the night (black line) (panel B). Panel A's black boxes show vertical layers used for predictions in Figure 4.4.

and *Thysanopoda tricuspидata* as well as few fish species (*Hygophum reinhardtii* and *Symbolophorus evermanni*) and one mollusc (*Liocranchia reinhardtii*).

Almost all species were dominant for RCP3, except the three *Argyropelecus* sp. and *Pterygioteuthis* sp.. RCP2 looked like RCP3 but with a smaller total richness, with especially less fish. RCP4 had high probabilities for almost all crustacean species, and for the three *Argyropelecus* sp.. RCP6 had three crustacean species with large prevalence, three fish and one mollusc. Two *Pterygioteuthis* sp., *Liocranchia reinhardtii*, *Thysanopoda tricuspидata*, were especially dominant in RCP7.

### 4.3.3 Environmental variables influencing assemblages

Probability of RCPs' presence was especially driven by the depth and the moment of the day (Figure 4.3A). During the day, mainly 2 RCP were observed : RCP1 was found in the top 300m of the water column and RCP4 was found in waters deeper than 300m. At night, layers deeper than 200m were mainly occupied by RCP4 too. For RCP1, probability of presence in relation to environmental variables were mostly constant, supporting the large effect of depth. Mean oxygen concentration above 190μmol/kg favoured RCP1 presence. Variables influencing RCP4 were shaped and different between day and night. During the night, RCP4 optimal values were for intermediate bathymetry, slope and mean temperature and for high chlorophyll-a concentration, high mean oxygen concentration and deep 20°C isotherm depth. In this RCP4, optimal values were opposite during the day for slope, chlorophyll-a concentration and mean oxygen concentration values.

Among the RCPs found in the top 200m during the night, RCP7 was found mainly in waters with deep bathymetry, and high oxygen concentration whereas RCP5 was found in waters with low oxygen concentration during day (Figure 4.3B). RCP2 and RCP3 were found between 80 and 400m during the night. Deep bathymetry and warm mean temperature were important for RCP2 whereas cold temperature, low oxygen values and shallow bathymetry were the factors influencing RCP3. Finally, RCP6 was found at a very low probability in the whole water column during both day and night, and was driven by very shallow 20°C isotherm depth, and high mean oxygen and warm mean temperature.

#### 4.3.4 Spatial and temporal distribution of predicted assemblages

Based on RCPs depth distribution (Figure 4.3A), we selected three vertical layers to predict RCPs probabilities on a 1/4° spatial grid, and to examine spatial extend of species assemblages. The maximum probability of presence for RCP5 and RCP7 was for depth between 0 and 80m, while for RCP2 and it was between 80 and 250m, and for RCP4 below 250m. Therefore we averaged predictions over these three vertical layers. By averaging RCP predicted probabilities for the entire New Caledonian EEZ by month, we assessed the seasonal cycle of each RCP probability.

During the day, RCP1 dominated almost the whole EEZ between 0 and 250m, except for the extreme north (RCP5), and the region around Chesterfield/Bellona reef for the whole water column (RCP6) (Figure 4.4A). RCP4 occupied the entire EEZ below 250m, except for the Chesterfield/Bellona area (RCP6). Night predictions were more partitioned and there were differences among the three vertical layers with a general north/south splitting. Over 0-80m, RCP5 dominated the area north of 21°S and RCP7 dominated the southern east area during two seasons. The southwest corner was dominated by RCP5 during the warm season (*e.g.* from December to May) and RCP3 during the cold season (*e.g.* from June to November). Between 80 and 250m, RCP2 prevailed during the warm season whereas RCP3 prevailed during the cold season. The 250-600m spatial distribution at night was very close to the day for the same layer with a domination of RCP4. RCP2 was the most probable assemblage at night, and RCP6 at day around Chesterfield/Bellona reef.

The predicted seasonal cycle of RCPs also showed the dominance of RCP1 between 0 and 250m and RCP4 below during almost all the year during the day. RCP4 dominated all year long at night below 250m too. However, at night, there was switch between RCP5 and RCP3 in the surface layer and between RCP2 and RCP3 in the 80-250m layer (Figure 4.4B).

Between 0 and 80m, the species richness was higher in the area south of 21°S and was especially high in the Chesterfield/Bellona reefs region and in Entrecasteaux reefs, located at the north of the main island. The 80-250m spatial distribution of richness showed larger values in the northwest compared to the southeast and was also higher around Chesterfield/Bellona reefs. In the 250-600m layer, the value of the richness around Chesterfield/Bellona was similar to the value in shallower layers, but it was lower than in the surrounding area at 250-600m, and more generally richness was higher in the south than in the north (Figure 4.5A). When averaging richness on 0-600m, the richness was higher than in surrounding seascape for two seamounts alignments north of the Chesterfield reefs and north of the Loyalties Islands (Figure 4.5B). This richness enhancement was mainly due to 80-250m and 250-600m layers. The mean richness in the southeast trench was low as well as around the Chesterfield/Bellona reefs.

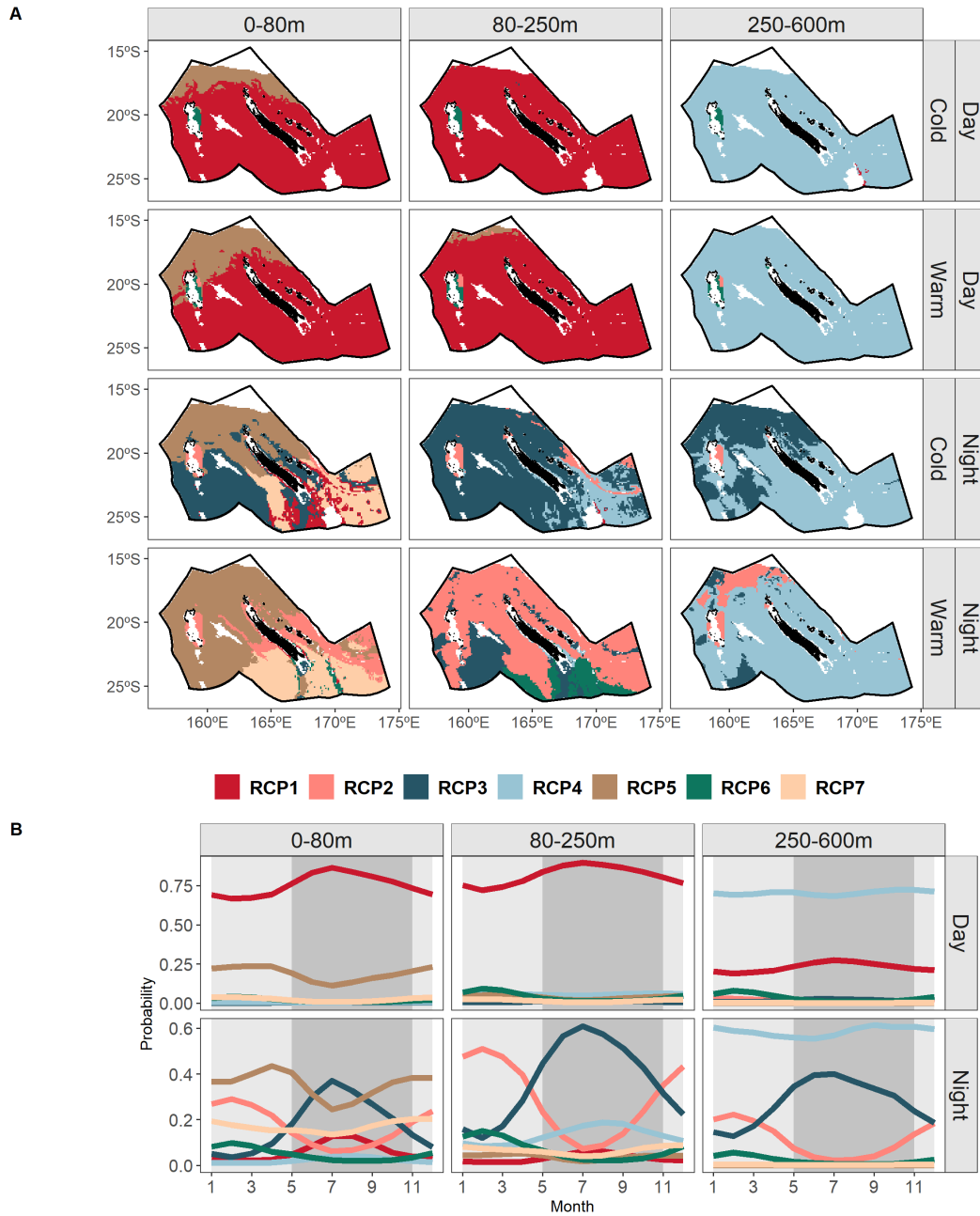


FIGURE 4.4 – Most probable predicted RCP (Region of Common Profile), for three different vertical layers : 0-80, 80-250 and 250-600m (columns) and for day and night periods during cold and warm seasons (rows) for the whole New Caledonian EEZ (panel A) and mean probabilities of each RCP by month with warm season in light grey and cold season in dark grey (panel B). See Figure 1 for the location of the various reefs and islands names.



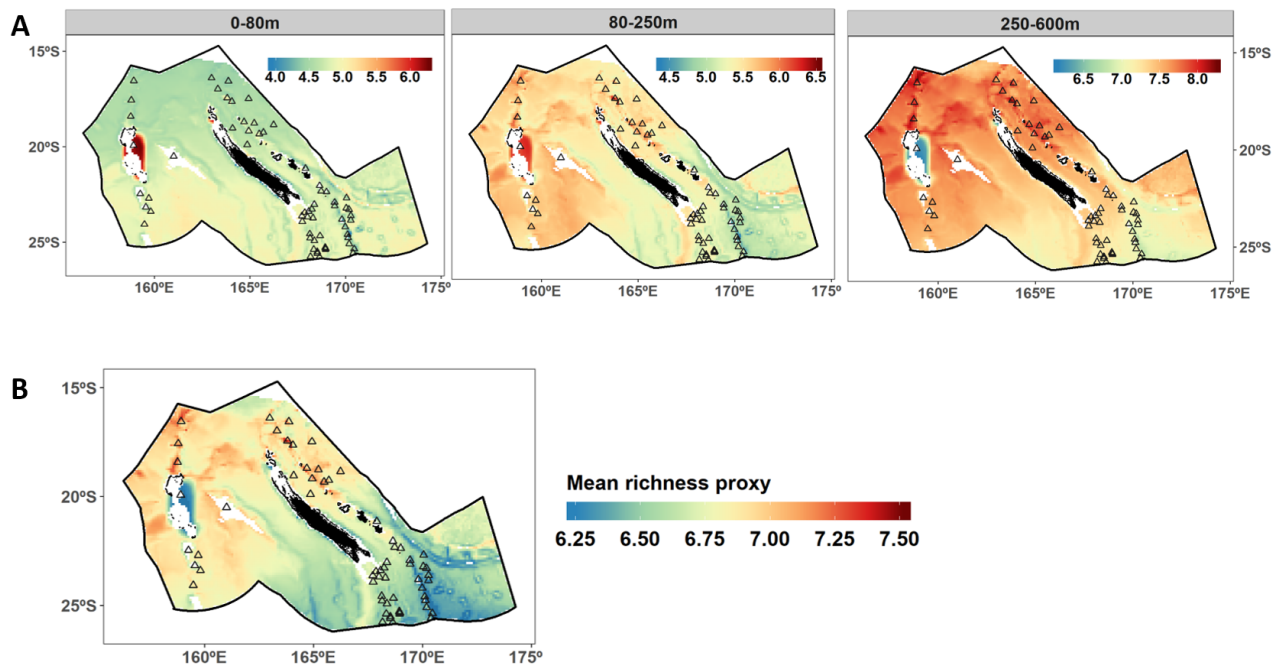


FIGURE 4.5 – Proxy for the species richness predicted in the whole studied area, for three different vertical layers (panel A) and on average between 0 and 600m (panel B). Black triangles indicate the location of seamounts according to Allain *et al.* [2008].

#### 4.3.5 Vertical and spatial distribution per species

The diel vertical behaviour of the 22 focus species was studied using the day and night occurrence profiles (Figure 4.6) to identify resident (overlay of day and night curves); migrant (differing day and night curves differed); and weakly migrant species (night curve only slightly different from the day curve, assuming that only part of the population migrated).

The previously described DVM behaviour of some species were confirmed by comparing results from this study with literature results (Table 4.2). For instance, *Thysanopoda tricuspoidata* was found to have a migrant behaviour from 400-600m at day to 0-200m at night as previously shown by Grandperrin [1975] and Legand *et al.* [1972]. Similarly, two *Pterygioteuthis* species were classified as migrant from day 200-500m to night 0-200m, as mentioned by Roper & Young [1975] and in the Tree of Life website (<http://tolweb.org/Cephalopoda>). The resident behaviour in waters deeper than 300m for the three hatchetfish *Argyropelecus* species and the highly migrant behaviour below 600m at day to 0-200m at night for the lanternfish *Hygophum reinhardtii* and *Symbolophorus evermanni* were confirmed (Davison *et al.* 2015b; Grandperrin 1975; Legand *et al.* 1972). Fishbase (<https://www.fishbase.se/search.php>) assigns the lanternfish *Lobianchia gemellarii* as migrant (juveniles in the 25-100m layer and adults in the 200-300m layer at night), and we identified for this species slightly larger probabilities in the 200-400m layer at night, likely indicating the presence of adult specimens.

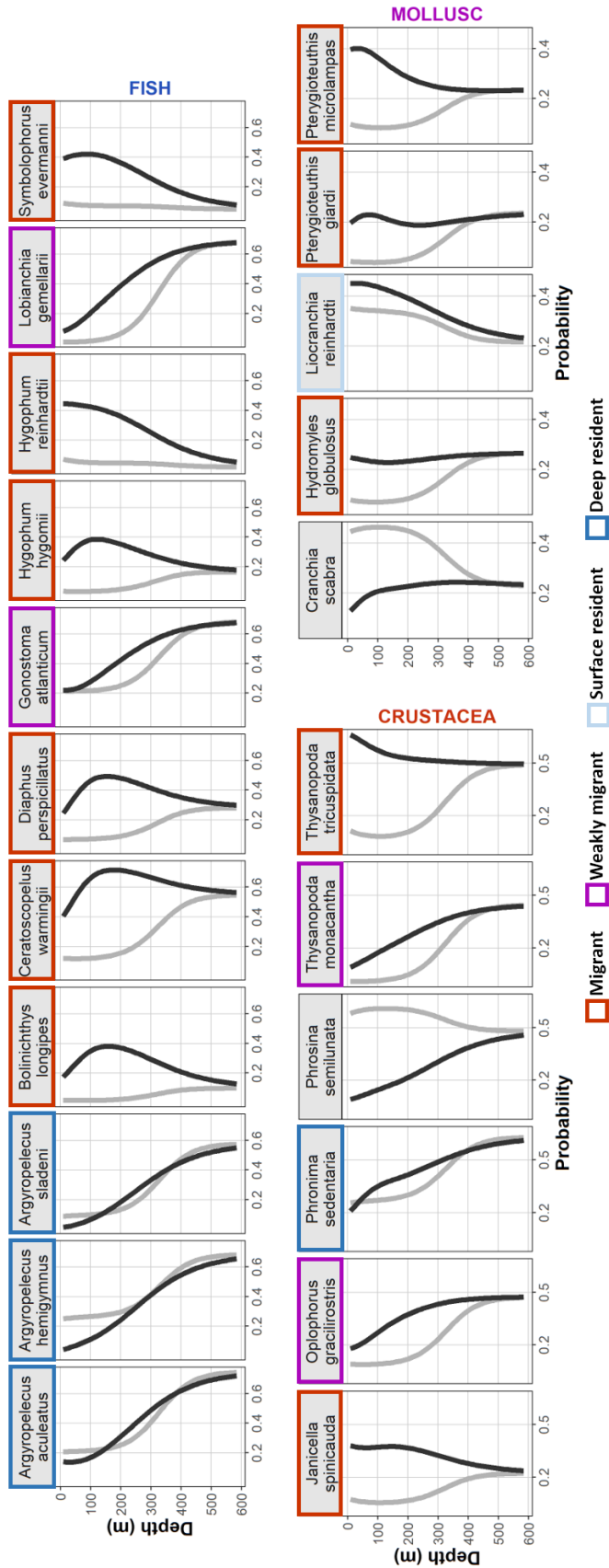


FIGURE 4.6 – Response of each species to depth according to day (light grey line) and night (dark grey line). Coloured box around species name indicate the identified migratory behaviour and no clear vertical behaviour identified has no colour.

TABLEAU 4.2 – Comparison of the vertical behaviour per species between our results and the literature , ordered and coloured by taxonomic group. For migrant species, the first depth range given is during the day and the second one during the night. Green colour indicate agreement between our results and the literature review.

|                                    | Species                          | Own results                        | Literature results                                      | Literature reference  |
|------------------------------------|----------------------------------|------------------------------------|---|---|
| C                                  | <i>Janicella spinicauda</i>      | Migrant 400-600 to 0-200m          | -   | -   |
|                                    | <i>Oplophorus gracilirostris</i> | Weakly migrant 400-600 to 200-400m | -   | -   |
|                                    | <i>Phronima sedentaria</i>       | Deep resident                      | Migrant 225-450m to 0-110m                              | (Grandperrin, 1975; Legand et al., 1972)                            |
|                                    | <i>Phrosina semilunata</i>       | ?                                  | Migrant 200-500m to 0-200m                              | (Grandperrin,1975)  |
|                                    | <i>Thysanopoda monacantha</i>    | Weakly migrant 400-600 to 200-400m | Resident 300-800m                                       | (Grandperrin, 1975; Legand et al., 1972)                            |
|                                    | <i>Thysanopoda tricuspidata</i>  | Migrant 400-600 to 0-200m          | Migrant 400-800m to 0-200m                              | (Grandperrin, 1975; Legand et al., 1972)                            |
|                                    | M                                | <i>Cranchia scabra</i>             | ?   | Deep resident   |
| <i>Hydromyles globulosus</i>       |                                  | 0-400m, mostly day                 | -   | -   |
| <i>Liocranchia reinhardti</i>      |                                  | Migrant 400-600 to 0-100m          | -   | -   |
| <i>Pterygioteuthis giardi</i>      |                                  | Surface resident                   | Migrant   | (Young, 1978)   |
| <i>Pterygioteuthis microlampas</i> |                                  | Migrant 400-600 to 0-200m          | Migrant 200-500m to 0-200m                              | (Roper and Young, 1975)   |
| F                                  | <i>Argyropelecus aculeatus</i>   | Migrant 400-600 to 0-100m          | Migrant 200-500m to 0-200m                              | Tree of Life webpage  |
|                                    | <i>Argyropelecus hemigymnus</i>  | Deep resident                      | Non migrant 200-500m                                    | (Grandperrin, 1975; Legand et al., 1972)                            |
|                                    | <i>Argyropelecus sladeni</i>     | Deep resident                      | Non migrant 200-500m                                    | (Davison et al., 2015; Grandperrin, 1975; Smith and Heemstra, 1986) |
|                                    | <i>Bolinichthys longipes</i>     | Deep resident                      | Non migrant 200-500m                                    | (Grandperrin, 1975; Legand et al., 1972)                            |
|                                    | <i>Ceratoscopelus warmingii</i>  | Migrant +600m to 0-200m            | Migrant +500 to 0-200m                                  | Fishbase  |
|                                    | <i>Diaphus perspicillatus</i>    | Migrant 400-600m to 0-200m         | Migrant +500 to 0-200m                                  | (Grandperrin,1975; Legand et al., 1972)                             |
|                                    | <i>Gonostoma atlanticum</i>      | Migrant 400-600m to 0-200m         | Migrant 300-400 to 0-200m                               | (Brodeur et al., 2005; Grandperrin, 1975; Legand et al., 1972)      |
|                                    | <i>Hygophum hygomii</i>          | Weakly migrant 400-600 to 200-400m | Migrant +500 to 0-200m                                  | (Grandperrin,1975; Legand et al., 1972)                             |
|                                    | <i>Hygophum reinhardtii</i>      | Migrant 400-600m to 0-200m         | Migrant 600-800m to 0-200m                              | Fishbase  |
|                                    | <i>Hygophum reinhardtii</i>      | Migrant + 600m to 0-200m           | Migrant +1,000m to 0-200m                               | Fishbase  |
|                                    | <i>Lobianchia gemellarii</i>     | Weakly migrant 400-600 to 200-400m | Migrant 300-800m to 25-100m (juv) and 200-300m (adults) | Fishbase  |
|                                    | <i>Symbolophorus evermanni</i>   | Migrant + 600m to 0-200m           | Migrant 700-900m to 0-200m                              | (Brodeur et al., 2005; Grandperrin, 1975; Legand et al., 1972)      |

For other species, findings provided information differing from information available in the literature. It was for instance the case for the crustacean *Thysanopoda monacantha*, classified as resident in the literature, and defined as a weak migrant according to our data. *Phronima sedentaria* was identified as migrant [Grandperrin, 1975; Legand *et al.*, 1972], but was found to be resident in the present study. On the contrary, *Liocranchia reinhardti* was classified here as surface resident whereas it was previously classified as migrant in Young [1978]. The probability of presence of the two species *Phrosina semilunata* and *Cranchia scabra* was higher during the day than during the night in the 10-200m layer, precluding their classification as surface resident, contrary to Boyle & Rodhouse [2008] who classified *Cranchia scabra* as deep resident and to Grandperrin [1975] who classified *Phrosina semilunata* as migrant.

Finally, the average spatial distribution over the 10-600m depth layer and over day and night was investigated for each of the 22 species (Figure 4.7).

First, regarding crustacean species, *Janicella spinicauda* was predicted to be more abundant in shallow waters, especially around Chesterfield reefs and in the north of the main island. On the contrary, *Oplophorus gracilirostris* and *Thysanopoda monacantha* were predicted to be absent around Chesterfield reefs, with the former more abundant north of 20°S and the latter south of 20°S. *Phrosina semilunata* was found in shallow waters close to the coast, and more abundant in the south than in the north. Finally, *Thysanopoda tricuspidata* was mainly predicted in the extreme north of the EEZ.

Second, regarding molluscs, *Cranchia scabra* had higher probability of presence in the southern part of the EEZ, with a homogenous repartition in the south. *Pterygioteuthis giardi* was also predicted to be more abundant in the south, but with a more patchy distribution and especially in deeper waters. To the contrary, *Hydromyles globulosus* was predicted to be more abundant in the north. Spatial patterns were weaker for *Liocranchia reinhardti* and *Pterygioteuthis microlampas*, with the first one being slightly more abundant north of 20°S and the second around Chesterfield reefs.

Finally among fishes, three hatchetfish *Argyrolepecus aculeatus*, *A. hemigymnus* and *A. sladeni* were predicted to have the same spatial patterns, with a higher abundance in regions characterized by high bathymetry slope and lower abundance around Chesterfield. Specifically, regarding the Chesterfield, *Bolinichthys longipes*, *Ceratoscopelus warmingii*, *Diaphus perspicillatus*, *Hygophum hygomii*, *Hygophum reinhardtii* and *Symbolophorus evermanni* were mainly predicted as abundant in this region whereas *Gonostoma atlanticum* and *Lobianchia gemellarii* were predicted to be absent. The two latter species had similar spatial distribution, found homogeneously all over in the New Caledonian EEZ but with a slightly higher probability in the southwest corner of the EEZ. *Ceratoscopelus warmingii*, *Diaphus perspicillatus* and *Hygophum hygomii* were predicted as rare almost everywhere but with slightly higher probability of presence in the south of the EEZ. To finish, *Bolinichthys longipes*, *Symbolophorus evermanni* and *Hygophum reinhardtii* were predicted as more abundant in the northwest compared to the southeast.

Based on the AUC criterion (Table 4.3), predictions of spatial distribution should be considered with caution for a number of species. For instance, *Cranchia scabra*, *Oplophorus gracilirostris*, *Janicella spinicauda* and *Phronima sedentaria*. *Thysanopoda monacantha* and *Hydromyles globulosus* had the smallest AUC of all species. In general, the spatial distribution of fish species were better fitted than crustacean and molluscs species. In particular, observations badly fitted predictions for *Phronima sedentaria*, *Thysanopoda tricuspidata* and *Ceratoscopelus warmingii* (indicated as grey points on Figure 4.7).

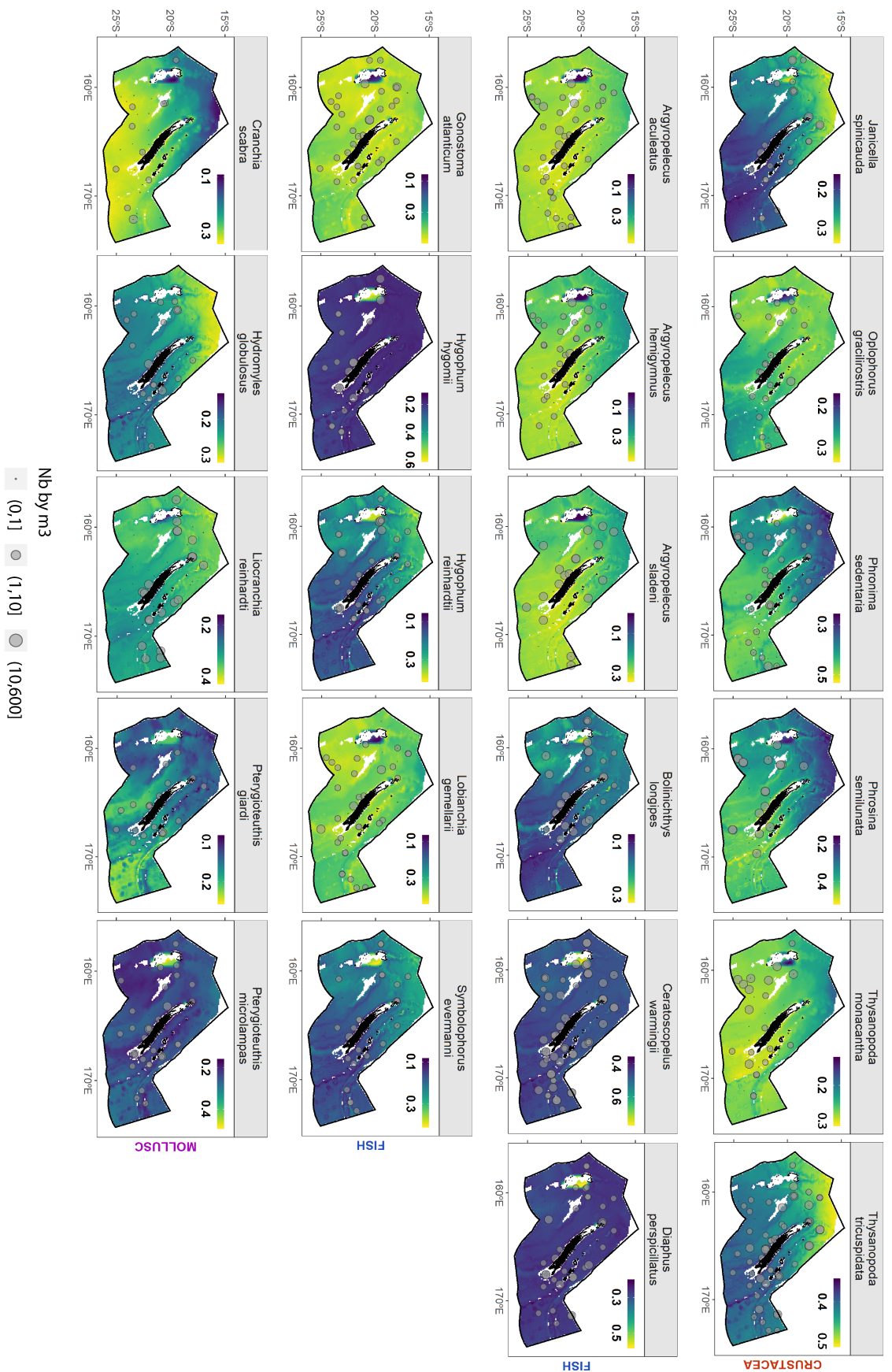


FIGURE 4.7 – Spatial distribution of occurrence probability predicted per species, on an average between day and night and for all depth with a 10m vertical resolution between 10 and 600m. Grey points show raw observed data in number of specimens per m<sup>3</sup>.

TABLEAU 4.3 – AUC (Area Under the Curve) values by species, higher the AUC, better the model is at predicting species occurrence. Species name are coloured by taxonomic group (blue for fish, purple for mollusc and orange for crustacean).

| <b>Species</b>              | <b>AUC</b> |
|-----------------------------|------------|
| Argyrolepecus aculeatus     | 0.91       |
| Argyrolepecus hemigymnus    | 0.90       |
| Bolinichthys longipes       | 0.88       |
| Hygophum hygomii            | 0.88       |
| Argyrolepecus sladeni       | 0.86       |
| Diaphus perspicillatus      | 0.84       |
| Pterygioteuthis giardi      | 0.84       |
| Symbolophorus evermanni     | 0.84       |
| Hygophum reinhardtii        | 0.81       |
| Ceratoscopelus warmingii    | 0.80       |
| Pterygioteuthis microlampas | 0.80       |
| Thysanopoda tricuspida      | 0.80       |
| Lobianchia gemellarii       | 0.79       |
| Phrosina semilunata         | 0.78       |
| Gonostoma atlanticum        | 0.72       |
| Liocranchia reinhardti      | 0.70       |
| Cranchia scabra             | 0.69       |
| Oplophorus gracilirostris   | 0.69       |
| Janicella spinicauda        | 0.67       |
| Phronima sedentaria         | 0.67       |
| Thysanopoda monacantha      | 0.60       |
| Hydromyles globulosus       | 0.53       |

## 4.4 Discussion

Community ecology (species assemblages) and ecosystem ecology (physical processes driving interactions with species) are primordial to the understanding of complex ecosystem functioning [Loreau, 2010]. The present study described the richness and community structure of micronektonic assemblages and their habitat in the New Caledonian EEZ (southwest Pacific). A focus was made on the 22 most frequent species (out of 250 identified) to adequately model their spatial distribution. Seven major assemblages were identified, mainly driven by the moment of the day and the depth of sampling. Environmental variables such as mean oxygen concentration, mean temperature and bathymetry also influenced micronekton assemblages and induced a north/south distribution of those assemblages. Only two major day assemblages were identified, both covering the whole EEZ, but segregated by depth layers : one in waters shallower than 250m and the other one in deeper waters (down to 600m). The four night communities were more diverse with a more patchy spatial distribution and two community changes along depth, at approximately 50m and 200m. The predominant night northern assemblage (RCP5) at 30m was dominated by crustacean whereas the southern assemblage (RCP7) was dominated by one crustacean, three cephalopod and four fish species. The 150m night assemblages were characterized by more cephalopods and fish in the south than in the north. Generally, assemblages' spatial distribution indicated that the northwest part of the EEZ was more diverse than the southwest region. Finally, our data allowed to describe the spatial distribution of 22 frequent species, as well as their vertical behaviour.

### 4.4.1 Statistical framework

From our knowledge, previous studies on micronekton mostly used clustering methods based on various dissimilarity metrics [e.g. Drazen *et al.*, 2011; Eduardo *et al.*, 2018; Flynn *et al.*, 2018; Parker *et al.*, 2015]. An alternative is offered here to classify trawl data in homogenous groups and at the same time to study links between these groups and environmental drivers. We confirmed Hill *et al.* 2017 conclusions about capabilities of RCP method and we extended the application domain moving from demersal fish of Kerguelen Plateau to micronektonic communities in a subtropical region. RCP species profiles allowed to assess which species and environmental variables drive these assemblages. The method was especially useful for micronekton species that had a complex vertical habitat and behaviour. Indeed, the approach allowed to take into account the DVM signal by including moment of the day and trawl depth, as well as to look at the influence of oceanographic parameters on more subtle variations in assemblages. Moreover, the prediction of species occurrence probability was predicted for all 0-600m depths and therefore incomplete dataset composed by small observations number (e.g. missing sample depths) could be used to assess species vertical habitat. Hence, the model was no longer limited to the depth sampled only, as presented by Williams & Koslow [1997] or Nishikawa *et al.* [2001]. A complete description of vertical habitat by species could be especially useful to integrate in biogeochemical models for example [Aumont *et al.*, 2018].

Given that rare species (*i.e.* present in less than 33 trawls) had being removed from analysis, it was assumed that part of the information was missing when compiling richness. To verify the validity of the results using this limited dataset, the same methodology was applied on a dataset keeping all the

252 observed species. This resulted in richness map was very similar to Figure 4.5, which validated the spatial predictions of micronekton richness based on the most frequent species only.

There was no link between the total numbers of observations and the model ability to efficiently predict the probability of presence (quantified by AUC). For example *Phronima sedentaria* had the third worse AUC whereas it was the third most frequent species. It was assumed that species with small AUC, such as *Phronima sedentaria*, had large environmental tolerance, at least for variables included in the RCP model. This large tolerance windows complicated the fit of the relationships between environmental gradient and the probability of presence. Therefore, to improve predictions of spatial distribution for these species, sampling may need to be performed in more contrasted environmental conditions.

#### 4.4.2 Eco-regionalization of prey communities

It should be noted that the trawl used in this study did not allow to sample micronekton communities at the surface (*i.e.* the top 10m), resulting in the likely absence of an important community, as previously shown in the southern ocean [Flores *et al.*, 2014]. Moreover, mid-water trawls are known to select some species due to net avoidance behavior by some organisms and to select some specific size ranges of organisms [Heino *et al.*, 2011; Kaartvedt *et al.*, 2012]. This trawl selectivity will have to be tested by using different trawls to sample same layers [De Robertis *et al.*, 2017]. Finally, as the trawl stay open for setting and hauling, layers sampled could be mixed with other layers during these two periods.

During the night, communities of the northern region were relatively stable across seasons, as well as the ones in the southeast region but below 250m. To the contrary, communities in the southwest changed above 250m during the night across seasons. Those differences could be explained by environmental conditions, as the assemblages predicted in the south of 21°S were supported by high oxygen values and cold temperature whereas northern assemblage were supported by low oxygen and warm temperature.

The north-south transition observed between the communities RCP5 and RCP3-RCP7 at night in the surface layer around latitude 21°S appear to be mainly linked to a thermal gradient. Spatial patterns of the mean temperature in the New Caledonian EEZ showed a strong north-south gradient, well delimited around 21°S [Menkes *et al.*, 2015]. Mean temperature may therefore be a measure of hydrographic features that likely reflected different oceanographic conditions. Therefore, 0-600m mean temperature appeared to delimit large homogeneous regions rather than having a direct impact on organisms. The 0-600m averaged oxygen concentration was another important variable influencing community's probability of presence. The link between oxygen concentration and micronekton vertical distribution has been studied previously using acoustic estimates. For instance in the South Pacific, the lower vertical expansion of micronekton layers was found to be limited by the minimum oxygen depth [Bertrand *et al.*, 2010]. Bianchi *et al.* [2013b] demonstrated at a global scale that the higher the oxygen concentration at depth, the deeper the micronekton deep layer daytime depth. Results from the present study, as well as from Suntsov & Domokos [2013] in the north Pacific showed that oxygen also influenced the micronekton species composition with higher oxygen values linked to richer community with a larger proportion of molluscs.

In addition to oceanographic parameters, we observed that micronekton assemblages were influenced by bathymetry which is very diverse in New Caledonia with ridges, seamounts, trenches and sedi-



mentary basins [Gardes *et al.*, 2014]. Shallower waters offer lower-quality habitat for mesopelagic organisms and may induce an organisms densification in the upper layers of the water column [Escobar-Flores *et al.*, 2018]. Spatial predictions of richness showed a higher richness around seamounts in the north, especially in the 80- 600m depth layer.

Climate change will have a profound impact on ecosystem structure [Lotze *et al.*, 2019], but impacts on the micronekton component are largely unknown [St. John *et al.*, 2016]. Based on this study, the predicted decrease of oxygen concentration [Stramma *et al.*, 2008, 2010] should favour RCP2 and RCP5 in the future whereas the predicted temperature increase [Bopp *et al.*, 2013] should favour RCP3. Moreover, changes in oxygen minimal depth would change the vertical distribution of prey communities, potentially making them more vulnerable to epipelagic predators [Olson *et al.*, 2014; Stramma *et al.*, 2010]. As predictions of future marine oceanographic conditions are becoming more and more precise and realistic, one next step could be to forecast future communities by forcing the RCP model with climate change model outputs, both with present and future simulations to measure communities changes.

The stronger latitudinal shift in micronekton assemblages, compared to a longitudinal one, found in this study, mirrored Flynn & Marshall [2013] and [Flynn *et al.*, 2018] bio-regionalization of the eastern Australia region. Communities described here were in agreement with previous studies in the Coral Sea, with the dominant fish species belonging to the families Gonostomatidae, Sternoptychidae, and Myctophidae [Flynn & Paxton, 2012; Grandperrin, 1975; Sutton *et al.*, 2017]. However, the 22 most abundant species identified were completely different from the 20 most abundant species described in the southern of Tasmania, even if some species were found in both studies (*Argyropelecus aculeatus*, *Argyropelecus hemigymnus*, *Ceratoscopelus warmingii*) [Williams & Koslow, 1997]. Some other common species in this study were also found in Hawaiian waters (18°N-21°N) (e.g. *Bolinichthys longipes*, *Ceratoscopelus warmingii*, *Diaphus perspicillatus*, *Gonostoma atlanticum* and *Janicella spinicauda*) [De Forest, 2009; Drazen *et al.*, 2011; Reid *et al.*, 1991] or close to Papua New Guinea (0-20°N) (e.g. *Bolinichthys longipes*, *Cranchia scabra*, *Diaphus perspicillatus*, *Hygophum reinhardtii* and *Symbolophorus evermanni*). Given those similarities and differences, an analysis at the scale of the Pacific Ocean would be a large improvement for the understanding of prey distribution. The ability of RCP method to take into account a sampling artefact would allow to inter-calibrate various sampling tools, making such a regional study relevant.

#### 4.4.3 Micronektonic species behaviour

Vertical behaviours and spatial distribution of the 22 most frequent species were investigated in the New Caledonian EEZ. Specifically, regarding the vertical behaviour, previously described vertical behaviour was confirmed for nine species; new vertical behaviour was described for three species, and vertical behaviour was refined for the nine remaining species. This indicated that the RCP method appear to be a valuable technique to analyse micronekton species data and to determine their vertical behaviour. Predictions of the spatial distribution patterns were very similar to the bathymetry pattern, highlighting the importance of this parameter in species distribution, but also in assemblage composition.

Eleven species (*Argyropelecus aculeatus*, *A. sladeni*, *Cranchia scabra*, *Hydromyles globulosus*, *Lio-cranchia reinhardti*, *Oplophorus gracilirostris*, *Phronima sedentaria*, *Phrosina semilunata*, *Pterygioteu-*

*this giardia*, *P. microlampas*, and *Thysanopoda tricuspidata*) had been observed in predators' stomach content in the western and central Pacific Ocean database of the Pacific Community (SPC; <http://www.spc.int/ofp/PacificSpecimenBank>) [Sanchez *et al.*, 2018] (e.g. *Coryphaena hippurus*, *Kajikia audax*, *Katsuwonus pelamis*, *Lampris guttatus*, *Sphyræna barracuda*, *Thunnus albacares*, *Thunnus obesus*, and *Xiphias gladius*). Lanternfish species (or Myctophidae) are also a non-negligible part of predators' diet [Brodeur *et al.*, 2005; Williams *et al.*, 2014], and while Myctophidae are found very often in stomach contents (Elodie Vourey, *pers. com.*) their quick digestion limited their identification at the specific level and explained their absence in the previously cited species list.. The 22 most frequent micronekton species found in this study were also observed in other predators diet studies in the Pacific Ocean [Kuhnert *et al.*, 2012; Olson *et al.*, 2014; Portner *et al.*, 2017; ?], corroborating the importance of this group in the pelagic ecosystem and reinforcing the need for a better understanding of their dynamics [St. John *et al.*, 2016]. Understanding how sensitive all micronekton species are to oceanographic variables (physical and biogeochemical) is needed to fully evaluate the impact that climate change could have on top predators' food [Choy *et al.*, 2016].

#### 4.4.4 Link to acoustics

Two previous studies analysed the acoustic data from the same Nectalis surveys, to link the mean 20-120m acoustic echo-intensity and the 0-600m vertical acoustic profiles to environmental conditions [Receveur *et al.*, 2019, n.d.]. The latter proposed a bio-regionalization of New Caledonian EEZ based on the micronekton vertical distribution and identified 3 homogenous regions during the day : i) north of 21°S with a weak Deep Scattering Layer (DSL) and a weak Shallow Scattering layer (SSL); ii) south of 21°S and west of 165°E (intense SSL at 80m and very intense SSL at 30m); and iii) south of 21°S and east of 165°E (intense SSL and very intense DSL at 550m). The spatial extent of assemblages found in the present study corresponded to the three homogenous regions defined based on acoustic profiles. This result reinforced the useful contribution of acoustics data to characterize mesopelagic organisms' distribution. However, gelatinous organisms are known to be responsible of a significant part of the acoustic signal [Proud & Brierley, 2018; Warren, 2001]. Therefore the development of methods capable to include gelatinous organisms in trawl analyses is crucial to compare acoustics and trawl data. Therefore, a study focusing on the direct link between trawl content and multi-frequency acoustic signal is needed to fully understand these complex links and to be able to quantify a total micronekton biomass for the region. For this type of study, it will be necessary to group species that respond in the same way acoustically (e.g. 'fluid-like', 'no gaz'...). However, in order to compile biomass estimation from acoustic data, the knowledge of community's species composition and of their target strength is primordial. Given the high species richness found in this study, going further into transforming acoustic signal into biomass appeared very complex in the region [Fielding, 2004; Godo *et al.*, 2009].

#### 4.4.5 Natural Park of the Coral Sea management

The creation of the Natural Park of the Coral Sea is recent (2014) and the management plan is still under development, specifically more focus have been made on isolated reefs and islands and less focus on the oceanic areas (<https://mer-de-coraile.gouv.nc/en>). Recently, Chesterfield, Bellona, Entre-

casteaux, Petrie and Astrolabe (see Figure 4.1 for location of those features) have been classified as strict nature reserves (category I of “no human activities authorized” according to IUCN protected area classification or “1-No take-No go” according to [Horta e Costa \*et al.\* \[2016\]](#) classification), but this only includes shallow waters inside reefs (Appendix 4.13). Based on results from this study, Petrie, Astrolabe and Entrecasteaux reefs seem to aggregate a high number of mesopelagic organisms’ in the 0-80m layer. Hence, these areas appear to be good candidates to implement a higher degree of protection level on offshore areas as well. For instance, it could be done by extending the existing “strict nature reserve” classification to the pelagic domain around reefs/atolls. The southeastern part of the EEZ (south of 22°S and east of 165°E) could be another area of interest for management as the RCP7 micronekton assemblage was composed of a large number of species identified as preys for top predator species, important for the pelagic ecosystem.

#### 4.4.6 Conclusion

By analysing the abundance of the 22 most frequent species collected in 123 pelagic trawls, and with the help of an innovative multivariate statistical approach, variability in micronektonic assemblages around New Caledonia was measured and linked to oceanographic drivers. The largest variability highlighted was function of depth due to DVM. Further, the method must help to isolate areas that may be regarded as priority conservation areas. The method must finally be a valuable contribution to assess the climate change impact on micronektonic assemblages and distribution, a crucial knowledge consequently for the whole pelagic ecosystem.

## Appendix

TABLEAU 4.4 – Family found in trawls arranged by alphabetic order with ‘N’ the total number of individuals, ‘W’ the total weight (g).

| Family                   | N    | W       | Family                   | N     | W        |
|--------------------------|------|---------|--------------------------|-------|----------|
| <i>Acanthephyridae</i>   | 28   | 110,6   | <i>Melamphaidae</i>      | 1     | 0,9      |
| <i>Amarsipidae</i>       | 2    | 2,1     | <i>Molidae</i>           | 9     | 1,14     |
| <i>Ancistrocheiridae</i> | 7    | 11,3    | <i>Monacanthidae</i>     | 7     | 2        |
| <i>Anoplogastridae</i>   | 1    | 0,6     | <i>Myctophidae</i>       | 20529 | 31702,48 |
| <i>Bathylagidae</i>      | 3    | 2,9     | <i>Nemichthyidae</i>     | 2     | 1,5      |
| <i>Bathysauridae</i>     | 1    | 5,2     | <i>Nomeidae</i>          | 24    | 241,6    |
| <i>Benthesicymidae</i>   | 38   | 18      | <i>Notosudidae</i>       | 40    | 137,9    |
| <i>Bramidae</i>          | 34   | 250,3   | <i>Ommastrephidae</i>    | 123   | 4046,5   |
| <i>Bregmacerotidae</i>   | 1    | 1,5     | <i>Onychoteuthidae</i>   | 11    | 17,3     |
| <i>Carangidae</i>        | 302  | 4316,1  | <i>Opisthoproctidae</i>  | 22    | 132,7    |
| <i>Carinariidae</i>      | 5    | 6,7     | <i>Oplophoridae</i>      | 903   | 638,53   |
| <i>Cavoliniidae</i>      | 13   | 3,31    | <i>Ostraciidae</i>       | 9     | 4,7      |
| <i>Chiasmodontidae</i>   | 3    | 2,7     | <i>Oxycephalidae</i>     | 51    | 5,46     |
| <i>Chlopsidae</i>        | 14   | 98,3    | <i>Pandalidae</i>        | 1     | 0,4      |
| <i>Chtenopterygidae</i>  | 2    | 2,1     | <i>Paralepididae</i>     | 18    | 60,8     |
| <i>Cirrhitidae</i>       | 7    | 1       | <i>Penaeidae</i>         | 151   | 172,9    |
| <i>Cliidae</i>           | 55   | 4,85    | <i>Pholidoteuthidae</i>  | 9     | 66,4     |
| <i>Cranchiidae</i>       | 393  | 451,24  | <i>Phosichthyidae</i>    | 249   | 104,15   |
| <i>Cystisomatidae</i>    | 7    | 9,6     | <i>Phronimidae</i>       | 191   | 25,8     |
| <i>Dalatiidae</i>        | 11   | 1375,8  | <i>Phronimidae</i>       | 630   | 210,37   |
| <i>Derichthyidae</i>     | 1    | 0,5     | <i>Platyscelidae</i>     | 207   | 42,97    |
| <i>Diretmidae</i>        | 15   | 13,9    | <i>Priacanthidae</i>     | 8     | 10,9     |
| <i>Emmelichthyidae</i>   | 14   | 19,3    | <i>Pronoidae</i>         | 8     | 1,4      |
| <i>Engraulidae</i>       | 116  | 123,2   | <i>Pterotracheidae</i>   | 3     | 5,8      |
| <i>Enoploteuthidae</i>   | 349  | 730,2   | <i>Pyroteuthidae</i>     | 1471  | 626,59   |
| <i>Epigonidae</i>        | 3    | 2,8     | <i>Radiicephalidae</i>   | 2     | 2,7      |
| <i>Euphausiidae</i>      | 6642 | 1115,16 | <i>Scinidae</i>          | 40    | 3,7      |
| <i>Evermannellidae</i>   | 1    | 0,8     | <i>Scombridae</i>        | 4     | 26,2     |
| <i>Fistulariidae</i>     | 1    | 0,6     | <i>Scombrolabracidae</i> | 5     | 160,8    |
| <i>Gempylidae</i>        | 200  | 247,39  | <i>Scopelarchidae</i>    | 12    | 46,1     |
| <i>Gonostomatidae</i>    | 765  | 1530,2  | <i>Sergestidae</i>       | 86    | 22,85    |
| <i>Grammicolepididae</i> | 3    | 4,4     | <i>Spirulidae</i>        | 29    | 113,8    |
| <i>Histioteuthidae</i>   | 7    | 69,7    | <i>Sternoptychidae</i>   | 3829  | 2660,72  |
| <i>Howellidae</i>        | 3    | 9,9     | <i>Stomiidae</i>         | 288   | 811,2    |
| <i>Hydromylidae</i>      | 378  | 9,46    | <i>Syngnathidae</i>      | 2     | 1        |
| <i>Lampridae</i>         | 1    | 0,7     | <i>Thalassocarididae</i> | 119   | 10,8     |
| <i>Lanceolidae</i>       | 1    | 0,2     | <i>Thysanoteuthidae</i>  | 1     | 6,9      |
| <i>Lycoteuthidae</i>     | 1    | 1,6     | <i>Xiphiidae</i>         | 1     | 55,9     |

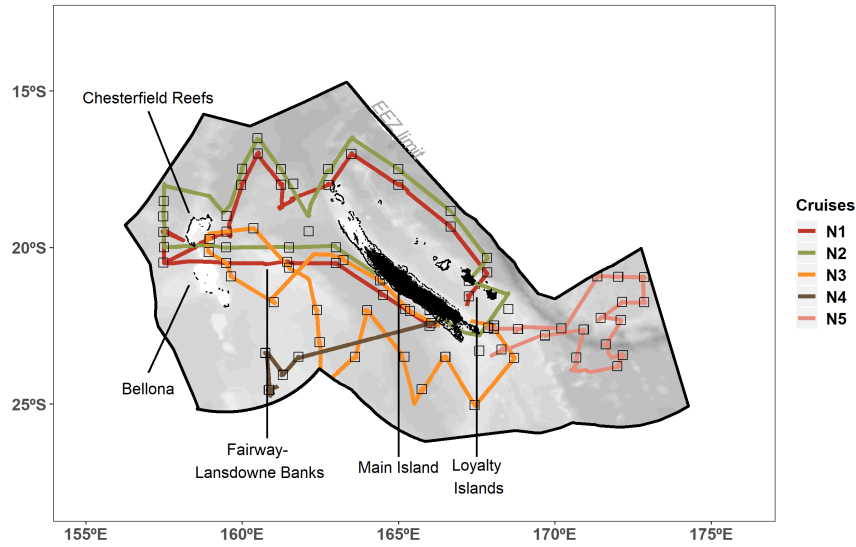


FIGURE 4.8 – Tracks of the 5 Nectalis cruises.

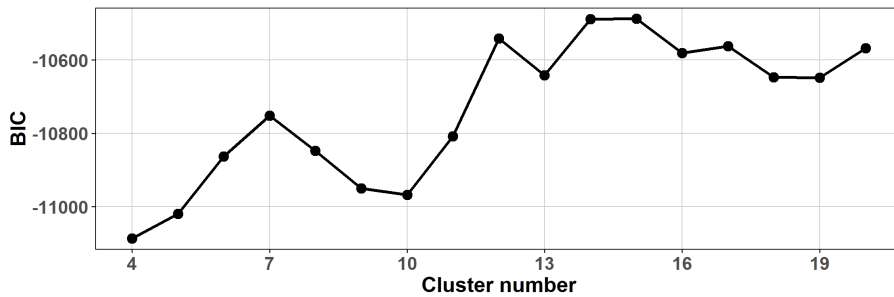


FIGURE 4.10 – BIC (Bayesian information criteria) function of number of clusters or RCPs.

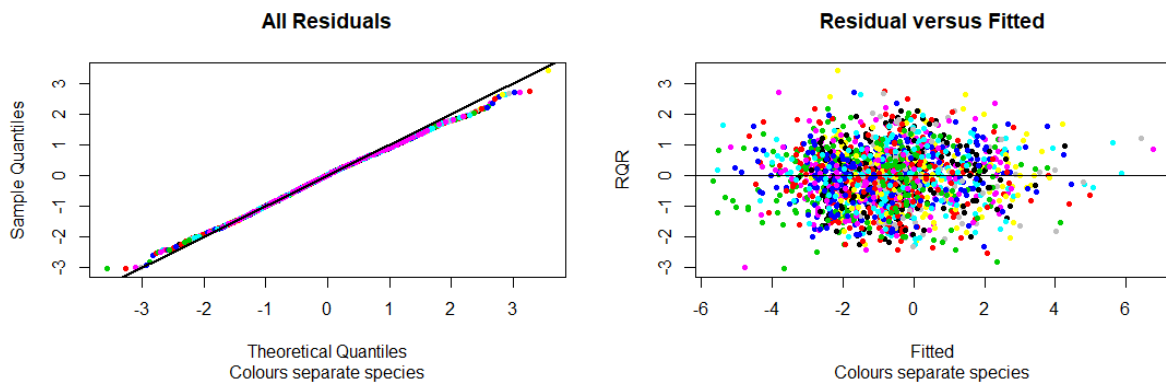


FIGURE 4.11 – Residuals plots checking : qqline (left) and residuals function of fitted values (right).

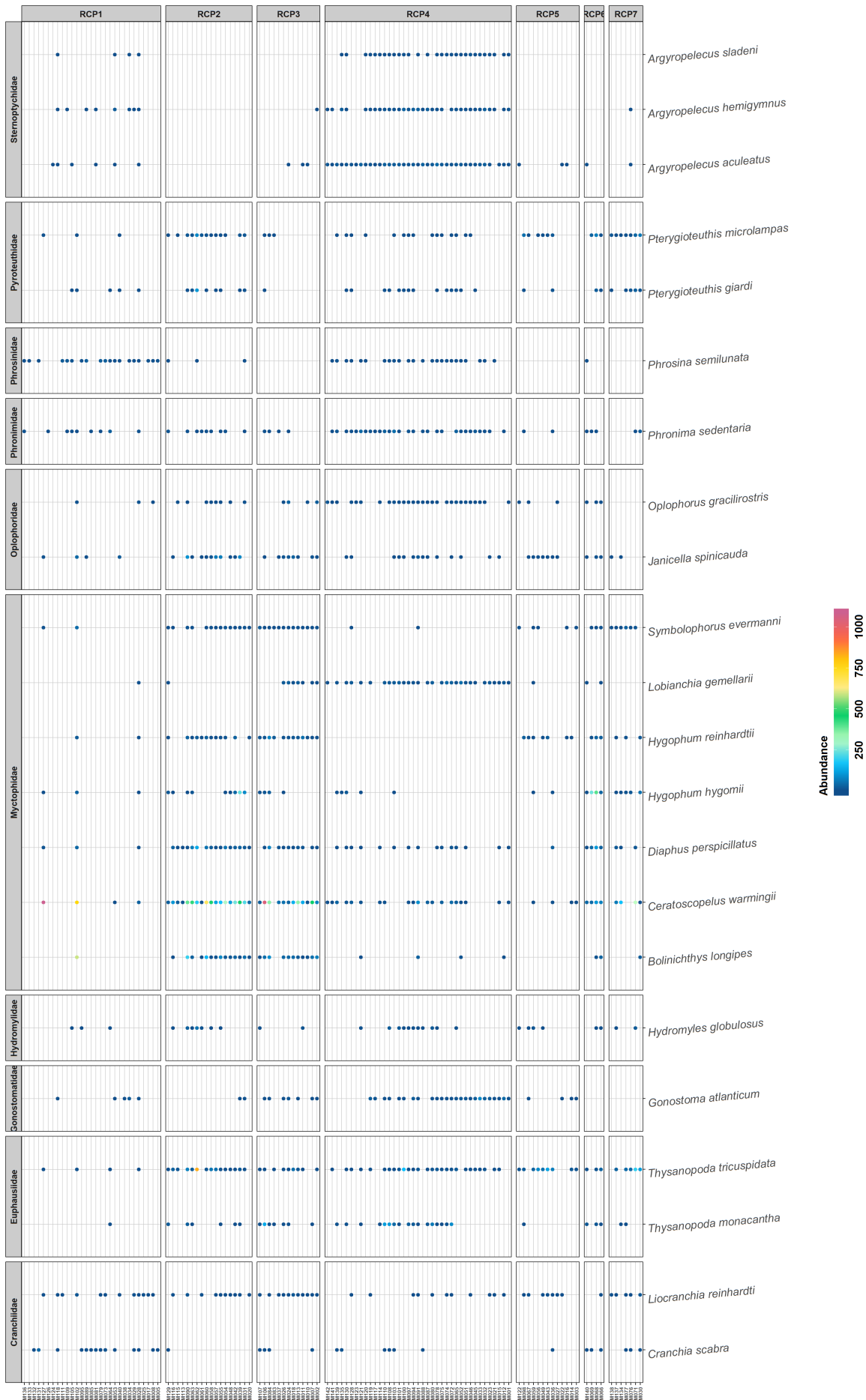


FIGURE 4.9 – Raw trawls data species composition and their RCP corresponding.

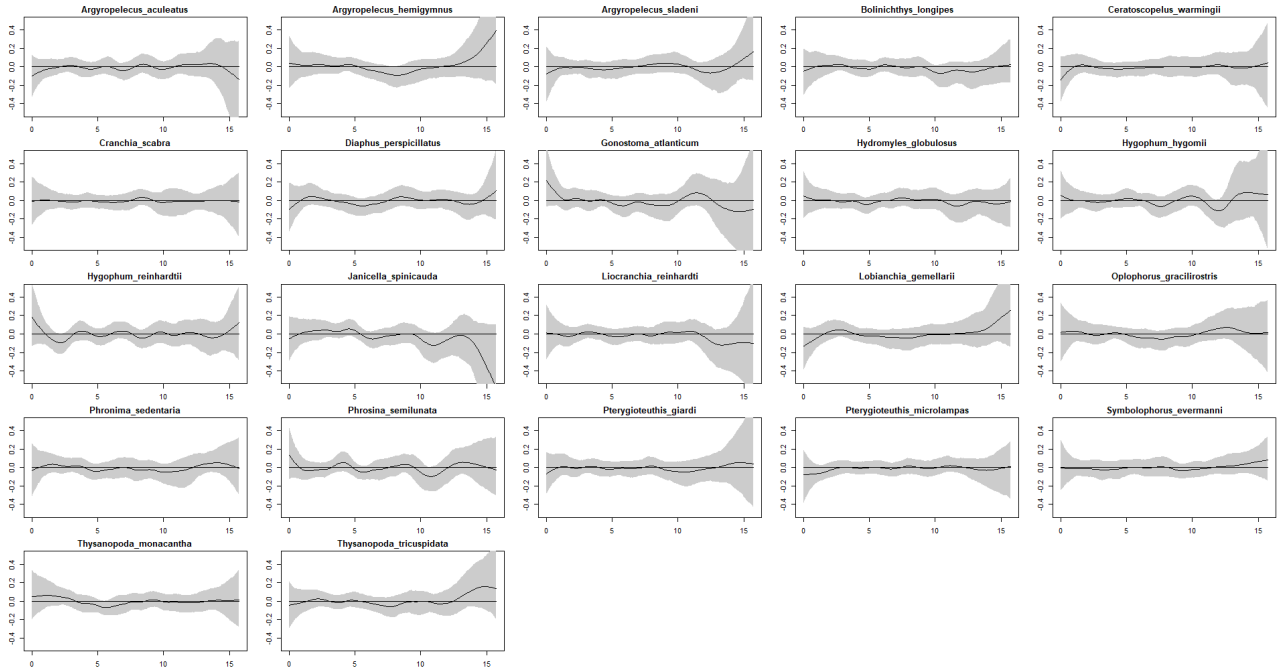


FIGURE 4.12 – Spatial auto-correlation by species, horizontal axis is the distance in km.

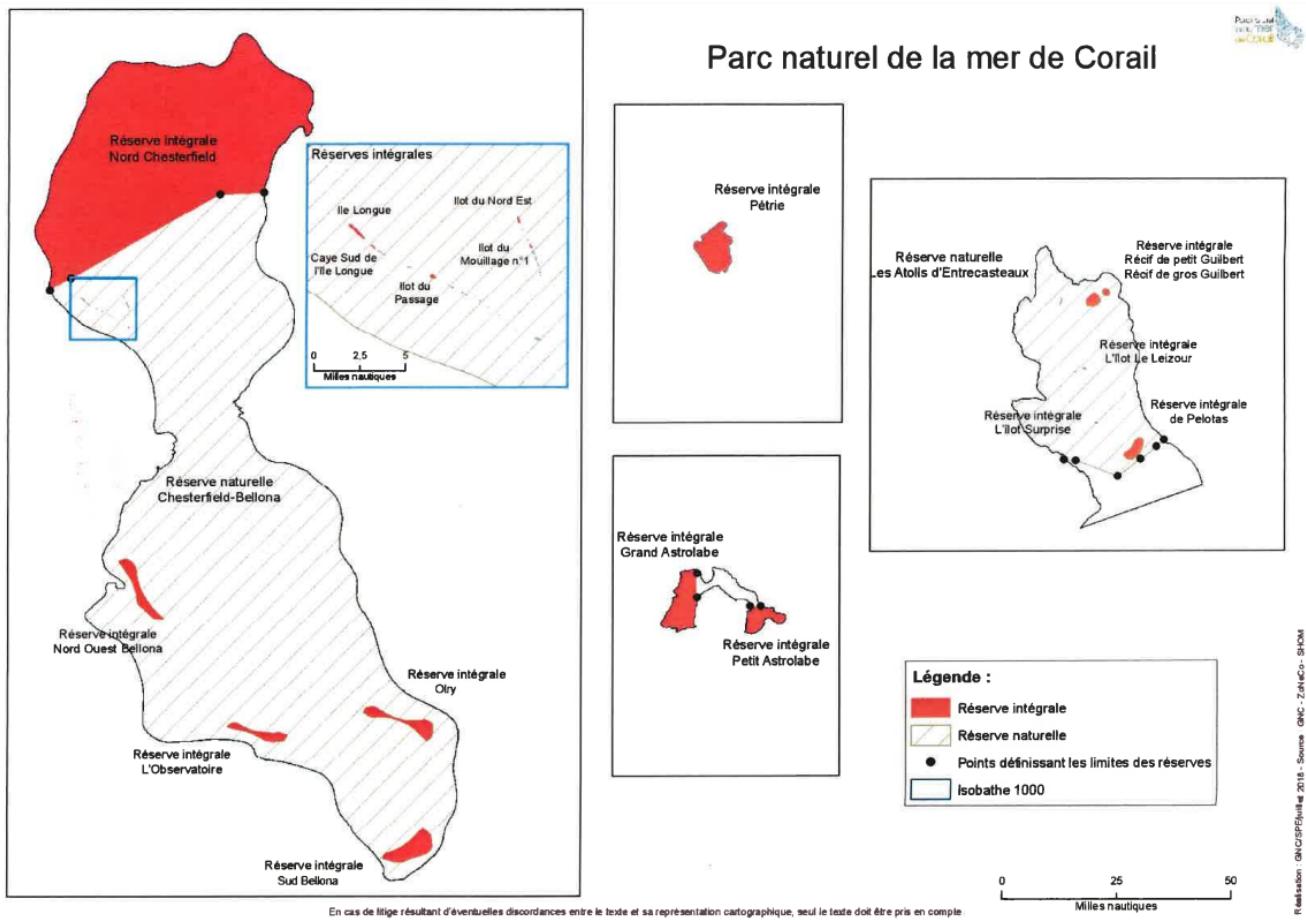
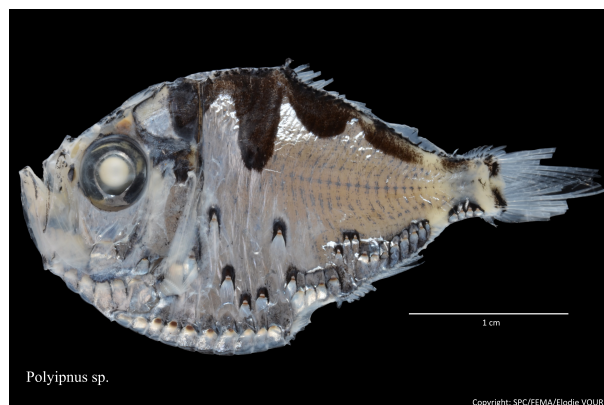


FIGURE 4.13 – Last decree (16-08-2018) identifying strict nature reserve (category I, none human activities authorized, according to IUCN protected area classification or 1-No take-No go according to [Horta e Costa et al. \[2016\]](#)) in the Natural Park of the Coral Sea in New Caledonia (from <https://mer-de-coraill.gouv.nc/en>) .ReferredtoFigureA1forlocalization.

# Inter-chapter

Chapter 4 described spatial variability of micronekton species assemblages. We analyzed, with a multi-variate method, data from 123 trawls done in the New Caledonian EEZ between 2011 and 2016. As for the analyses of acoustic data, time of day was one of the most influential variables on species composition, together with trawl depth. Other environmental variables such as mean oxygen, mean temperature and bathymetry, also influenced micronekton assemblages and induced a north/south distribution pattern of those assemblages. The two day-time assemblages were relatively invariant spatially, one in waters shallower than 250m, and the other one in deeper waters. The four night-time assemblages were also mostly different function of depths, with two community changes at approximately 80m and 250m. Globally, northern assemblages were dominated by crustacean species whereas southern assemblages were more dominated by cephalopods and fish species. The spatial distribution of fitted assemblages were closely similar to the spatial predictions of acoustics classes. The three first chapters focused on analysing data to fully understand micronekton dynamics, spatially, vertically, temporally and in term of species assemblages. The next two chapters place micronekton in a broader context. The next chapter compares two approaches to predict micronekton abundance in a climate change context.







# Chapitre 5

## Exploring the potential future of the Coral Sea micronekton

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## Abstract

Despite its predominant role in the pelagic ecosystem and its potential role as proteins source, studies about the mesopelagic organism at global scale are recent and insufficient to fully understand its dynamic. Due to this weak understanding of the mesopelagic organisms present dynamics, the potential impact of climate change is even less known and understood. The complexity to measure these organisms could explain this lack. Bias-adjusted regional climate simulations of ocean dynamics had been performed with the coupled model NEMO-PISCES in present-day and future conditions (RCP8.5 scenario). The future surface and lateral oceanic boundary conditions were generated from four CMIP5 models. Then, using these simulations, 1) ecosystem climate simulations have been performed from the ecosystem model SEAPODYM, and 2) a 3D statistical model based on present-day acoustic data was used to explore the future of micronekton. The NEMO-PISCES simulations showed a good representation of main oceanic characteristics (*i.e.* temperature, salinity, oxygen concentration), condition necessary for the micronekton growth. The 3D statistical model projected a decrease of micronekton abundance in epipelagic layer and an increase in bathypelagic layer. The main drivers of these changes for the Coral Sea were the change in 20°C isotherm depth and in salinity. The SEAPODYM projections were coherent with statistical projections for epipelagic layer, but the trend was opposite for the micronekton abundance change in mesopelagic and bathypelagic layers. The difference projections between the two modelling tools highlighted the need of more analyze to explore the changes of micronekton abundance in global warming context. Nevertheless the possible decrease of micronekton abundance in epipelagic layer predicted by both tools highlighted the crucial need to establish management areas for this potentially important resource in the future.

**Keywords :** *Micronekton, echosounder, Coral Sea, climate change, SEAPODYM model*

## 5.1 Introduction

Recently, mesopelagic community have been highlighted as a potential food resource, especially for aquaculture with large uncertainty of its global biomass ranging from 0.5 to 19.5 billion metric tons [*e.g.* Anderson *et al.*, 2019; Irigoien *et al.*, 2014; Proud *et al.*, 2017, 2018b]. Mesopelagic species play a central role in the pelagic ecosystem too, acting noticeably as food for predators that include commercially targeted species [Bertrand *et al.*, 2002a; Duffy *et al.*, 2017; Olson *et al.*, 2014] as well as emblematic marine species [Lambert *et al.*, 2014; Miller *et al.*, 2018]. Some of the mesopelagic species compose the micronekton, which is known to migrate daily between the surface layer (0-200m), where they stay during the night, and the mesopelagic layer (200-1000m), where they stay during the day to avoid visual predation. Thus, micronekton largely participate to the downward flux of nutrients and particulate organic matter via respiration and excretion processes [Ariza *et al.*, 2015; Drazen & Sutton, 2017]. This well-known migrating compartment is called Diel Vertical Migration (DVM) and is observed at the global scale [Bianchi & Mislán, 2016; Klevjer *et al.*, 2016].

The Coral Sea ecosystem has been classified as a hotspot of species richness [Tittensor *et al.*, 2010] found in prey communities [*e.g.* Allain *et al.*, 2012; Olson *et al.*, 2014; Williams *et al.*, 2014; Young *et al.*, 2010] and in top predators communities with cetaceans [Mannocci *et al.*, 2014b], sharks [Boussarie *et al.*,

2018] and seabirds [Weimerskirch *et al.*, 2017]. The Coral Sea is located in the southwest Pacific and covers more than 4 700 000 km<sup>2</sup>, making it the second largest tropical area marginal sea after the Philippine Sea [Ceccarelli *et al.*, 2013]. The South Equatorial Current (SEC), entering between New Caledonia and the Solomon Islands, dominates Coral Sea oceanic circulation. When reaching the Australian coast, waters above the thermocline diverge into two branches around 15°S : one forming the Gulf of Papua Current (GPC) flowing northward along the coast of Queensland and the other feeding the southward flowing East Australian Current (EAC) [Cravatte *et al.*, 2015; Kessler & Cravatte, 2013]. Water are mainly regarded as oligotrophic, with a higher productivity zone south of 22°S [Dandonneau & Gohin, 1984]. Its food web included in the ARCH (Archipelagic Deep Basins) region, was expected to have a low in 2035 and a moderate in 2100 vulnerability to climate change [Bell *et al.*, 2013].

Despite its predominant role in the pelagic ecosystem and its potential role as proteins source, studies about the mesopelagic at global scale are recent (Figure 1 from Hidalgo & Browman 2019) and insufficient to fully understand its dynamic [Glover *et al.*, 2018; St. John *et al.*, 2016]. Most of the micronektonic species are currently not commercially exploited and hence scientific cruises are needed to collect data. The large intrinsic diversity level including crustaceans, molluscs, gelatinous organisms and fish [Olivar *et al.*, 2017] makes it challenging to have a complete understanding of micronektonic species ecology [Duffy *et al.*, 2017]. Species are usually sampled with mesopelagic trawls and calibrated echosounders that are complex and difficult to compare. The transformation of acoustic backscatter into mesopelagic biomass needs the knowledge of the species composition, their size and the target strength of each species detected [Davison *et al.*, 2015a; Proud *et al.*, 2018b]. Therefore, extracting relationships between mesopelagic organisms' biomass and environment is hard with acoustic. Trawl data are size and/or species dependent and because of net avoidance behavior of organisms, obtaining an unbiased quantitative estimate with trawls is even more challenging than with acoustic data [Heino *et al.*, 2011; Kaartvedt *et al.*, 2012]. Moreover, trawl data are temporally and spatially discrete, and understanding a relationship between one micronektonic species and its environment would require a very high number of trawls. For these reasons, the actual understanding of the optimal environmental conditions for the micronekton, even for small spatial region, is poorly developed [St. John *et al.*, 2016]. Despite the above mentioned limitations, analyzing the whole micronekton vertical distribution rather than the integrated backscatter echo intensity value, allows us to develop an innovate statistical framework to assess the 3D distribution of micronekton from environmental conditions [Receveur *et al.*, 2019]. The latter studies thus provide a technical framework to explore how changes in the future environmental conditions may change micronekton distribution in the future.

Upper trophic levels models are another solution to assess the evolution of micronekton biomass and spatial distribution. Micronektonic compartment is implemented in some ecosystem models. For instance, a fully coupled end-to-end ecosystem model combining the ocean general circulation model NEMO [Madec & team, 2008] for the ocean dynamics, PISCES for the biogeochemistry and lower trophic level organisms (phytoplankton and zooplankton) [Aumont *et al.*, 2015] and APECOSM for the upper trophic level organisms [Maury, 2010] was developed. An end-to-end model was used in Aumont *et al.* [2018] to study the impact of DVM on carbon cycle and oxygen concentration. Lefort *et al.* [2015] used a similar modeling framework (NEMO-PISCES-APECOSM) to predict the evolution of biomass, maximum body size and spatial distribution of pelagic communities in 2100. The latter study showed a global decrease of biomass with a spatial shift to Arctic region, a decrease of growth rate and maximum size for

epipelagic and mesopelagic communities in central oceans. Spatial Ecosystem and Population Dynamics Model (SEAPODYM) is another model implementing a micronekton compartment [Lehodey *et al.*, 2015, 2008, 2010]. This model uses the simulated micronekton mainly to predict tuna biomass and spatial distribution following climate change scenarios in support of pacific islands resource management [Johnson *et al.*, 2018; Senina *et al.*, 2016]. To the authors knowledge, these upper trophic levels models have never been used in published literature to study changes in micronekton spatial distribution or quantity.

To predict these changes, the ocean dynamic models composing the fully coupled end-to-end ecosystem models need to be forced by atmospheric fields, which are generally extracted from the Coupled Model Intercomparison Project (CMIP) database [Taylor *et al.*, 2011]. Unfortunately the CMIP5 models exhibit substantial present-day climatological biases in the Pacific : an equatorial cold tongue penetrating too far westward [Li & Xie, 2013; Li *et al.*, 2015; Richter, 2015; Zuidema *et al.*, 2016] and a South Pacific Convergence Zone (SPCZ) too zonal and extending too far eastward [Brown *et al.*, 2010; Grose *et al.*, 2014]. Therefore directly forcing an ocean model with the CMIP atmospheres boundary conditions will induce systematic biases as those seen in the ocean models of CMIP5. Theses biases also impact upper trophic levels predictions [Payne *et al.*, 2016]. In the atmosphere, a commonly-used strategy to partly alleviate this problem is to add “climate change anomalies” to the observed signal over the present day [e.g. Dutheil *et al.*, 2019].

Hence, in the present study, we developed a framework to project the change of micronekton spatial distribution and quantities in 2100 based on realistic physical simulations. For that, we performed four climate simulations with the NEMO-PISCES model, one present-day simulation, and four climate-change simulations forced with the climate trends extracted from four CMIP5 models. Based on these simulations, we extracted the future oceanic conditions (*e.g.* temperature, salinity, dissolved oxygen concentration) to simulate micronekton spatial distribution change with two highly different tools : the SEAPODYM mid-trophic levels model and an acoustically based statistical model. This methodology allows to address the following questions : What are the changes in micronekton spatial distribution in the Coral Sea? What are the parameters driving these changes? And what are the differences in the micronekton projections between the SEAPODYM model and an acoustically based statistical model?

## 5.2 Material and Methods

The predictions of future evolution of micronekton requires the future dynamical and biogeochemical states of the ocean as a prerequisite. The method used to derive future ocean states was described in section 5.2.1. SEAPODYM was then used to compute future micronekton biomass following the set-up described in section 5.2.2. In addition to the projection made using the SEAPODYM model, the present study also used [Receveur *et al.*, 2019] analyzes to produce another projected future micronekton biomass from a statistical model. As acoustic data collection, statistical methods and validation were presented in details in Receveur *et al.* [2019], section 5.2.3 presented only the main information needed to comprehend the method.

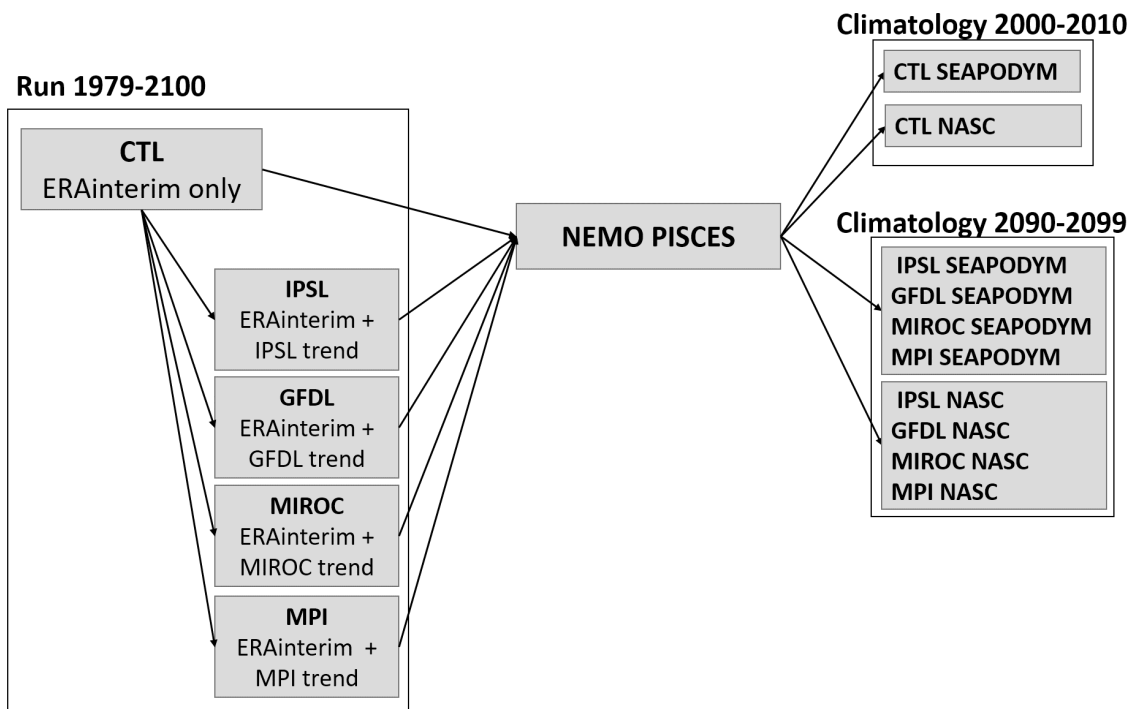


FIGURE 5.1 – Modeling framework.

### 5.2.1 Dynamical and Biogeochemical ocean future states

Despite their ability in producing a consistent global warming trend for the future, global coupled climate models are known to display significant biases in the mean state as well as in the variability of the ocean for the historical and present periods along with regional discrepancies for the future climate. Those discrepancies, particularly significant for biogeochemical projections, arise from dynamical model differences [Wang *et al.*, 2014] and from biogeochemical model differences [Laufkötter *et al.*, 2015]. Therefore, their projected dynamical and biogeochemical ocean states should be used with caution at regional scale. To be able to pin point changes of realistic biogeochemical regional structures in response to future climates, we proposed an alternative method using a single physical-biogeochemical ocean model. This model, NEMO-PISCES [Aumont *et al.*, 2015], was forced with mixed forcing fields composed of realistic atmospheric forcings, based on an improved ERA-interim reanalysis (DFS5 : Drakkar Forcing Sets, Brown *et al.* 2010) to which atmospheric trends extracted from global coupled climate models for the RCP8.5 scenario were added for the future climate. With this method, we produced simulations of the dynamic and biogeochemical state of the ocean for the future (2011-2100) period using different atmospheric trends from different climate coupled models applied to the same physical-biogeochemical model. The method advantages were to constrain the mean spatial patterns of the ocean forcing fields to remain close to the observations and to retain the desired observed modes of variability while having the changes induced by the anthropogenic perturbations. In this study, we choose to focus on the long term climatic trends leaving out any inter-annual to decadal climate modulation. To that end, we removed variations equal to shorter than 15 years by using a 31-years Hanning filter applied on the four selected coupled climate models (Table 5.1) atmospheric outputs (*i.e.* zonal and meridional wind stresses, air temperature and humidity at 2 meters, shortwave radiation and longwave radiations, snowfall and precipitation). We then constructed four sets of atmospheric forcing fields, in which the low frequency trends

TABLEAU 5.1 – Ocean-Atmosphere coupled models and their related modelisation centers used in this study.

| Modeling centers  | Coupled models |
|---|----------------|
| Institut Pierre Simon Laplace (IPSL)  | IPSL-CM5A-MR   |
| Geophysical Fluid Dynamics Laboratory (NOAA GFDL)   | GFDL-ESM2G     |
| Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies (MIROC) | MIROC-ESM      |
| Max Planck Institute for Meteorology (MPI-M)  | MPI-ESM-MR     |

from the four coupled-models had been added to the atmospheric reanalysis product DFS5 (cycled 3 times to cover the 90 years future period). Thus, the seasonal to decadal variability of this forcing dataset was fully constrained by the reanalysis and was repeated unchangingly in the future while the climatic trends over the 2011-2100 period were imposed from the coupled models. A control simulation (CTL) using unaltered atmospheric reanalysis product DFS5 cycled three times had also been run to account for model drifts. These atmospheric inputs were then used to force our physical-biogeochemical model. We finally obtained five simulations of the dynamics and biogeochemistry covering the 1979-2100 time period : one control (CTL) without including any climate change scenario and four simulations corresponding to the four atmospheric forcings built from four CMIP5 climate models projections (Table 5.1 and Figure 5.1).

### 5.2.2 SEAPODYM simulation

The sub-model of SEAPODYM-MTL (for Mid Trophic Level) simulates several functional groups of micronekton for the oceanic epi, meso and bathy pelagic layers [Lehodey *et al.*, 2015, 2010]. The spatial and temporal dynamics of production and biomass are modelled with a system of advection-diffusion-reaction equations driven by ocean temperature, horizontal currents, primary production and euphotic depth (Table 5.2). Currently, there are six groups of micronekton defined according to the Diel Vertical Migration (DVM) patterns of mesopelagic organisms between three broad epipelagic, upper and lower mesopelagic vertical layers. The euphotic depth  $Z_{eu}$  is used to define the depth boundaries of the vertical layers, *i.e.*,  $0-1.5*Z_{eu}$  for the epipelagic layer,  $1.5-4.5*Z_{eu}$  for the mesopelagic layer and  $4.5-10.5*Z_{eu}$  for the bathypelagic layer. The average euphotic depth for the region, as calculated from the historical simulation NEMO-PISCES is 105m, therefore  $1.5Z_{eu}$  corresponds to about 160m,  $4.5Z_{eu}$  to 470m and  $10.5Z_{eu}$  to 1100m. During the day, only the epipelagic group inhabits the epipelagic layer and during the night, it also includes the migrant upper-mesopelagic and highly migrant lower mesopelagic groups. The mesopelagic layer is inhabited by the mesopelagic and the migrant mesopelagic during the day and the mesopelagic and migrant bathypelagic during the night. Finally, the bathypelagic is inhabited by bathypelagic, migrant bathypelagic and highly migrant bathypelagic during the day and only by bathypelagic during the night (see Figure 1.26 in PhD Introduction).

SEAPODYM simulations were forced by the five physical-biogeochemical outputs obtained from the method presented in section 5.2.1 : CTL, IPSL, GFDL, MIROC and MPI (Figure 5.1). Complementing the control simulation without climate change trend, we carried out four climate change simulations from the four climate models spanning the future under the RCP8.5 scenario, all over the 2000-2100 period. From those, we calculated one present climatology over the 2000-2009 period from the CTL simulation,

TABLEAU 5.2 – Covariates used as forcing for SEAPODYM and for the acoustic modeling.

| Variable           | SEAPODYM                  | Acoustic model      |
|--------------------|---------------------------|---------------------|
| Currents           | Average by vertical layer | -                   |
| Winds              | -                         | Surface             |
| Temperature        | Average by vertical layer | Average over 0-600m |
| Oxygen             | Average by vertical layer | Average over 0-600m |
| Salinity           | -                         | Average over 0-600m |
| Primary production | Surface                   | Surface             |
| Euphotic depth     | To define layers          | Yes                 |
| Isotherm depth     | -                         | Yes                 |
| Bathymetry         | -                         | Yes                 |
| Sun inclination    | To define periods         | Yes                 |

and four futures climatology over the 2090-2099 period calculated from the four climate change simulations. Spatial resolution was 1°.

### 5.2.3 Acoustic modeling

#### Data collection

The steps of that section are similar to [Receveur et al. \[2019\]](#) in which the detailed methodology is given. In short, we gathered data from six cruises on board the R/V Alis between 156°E–175°E and 14°S–27°S from 2011 to 2017. During cruises, *in situ* acoustic data were recorded continuously using an EK60 echosounder (SIMRAD Kongsberg Maritime AS, Horten, Norway) connected to four split-beam transducers, we only used in the present study the 38 kHz. EK60 calibration was performed according to [Foote et al. \[1987\]](#) for each cruise. After data processing, the echo-integration was done providing the volume backscattering strength  $S_v$  data (dB.R.1.m<sup>-1</sup>) referred to echo intensity hereafter), the linear measure of the volume backscattering strength  $s_v$  (m<sup>-1</sup>) ( $s_v = 10^{\frac{S_v}{10}}$ ) and the Nautical Area Scattering Coefficient (NASC),  $s_A$  (m<sup>2</sup>nmi<sup>-2</sup>) a proxy for the micronekton biomass [[Irigoiien et al., 2014](#)][[MacLennan et al., 2002](#)]. The final dataset was then composed of 16715 vertical profiles ranging between 10 and 600m, with a 4m vertical bin and a 0.1nm horizontal bin.

Transition periods at dawn and dusk had voluntarily been excluded from the final dataset, when organisms' orientation changes as organisms actively swim up or down, creating strong variability in backscatter [[McGehee et al., 1998](#); [Zedel et al., 2005](#)].

#### Statistical analysis of acoustic vertical profiles

The vertical dimension of acoustic profiles was reduced with a Principal Component Analysis (PCA) [[Jolliffe, 2011](#)] : from 146 depths per profile to 11 coordinates. Then vertical profiles were classified using their PCA coordinates based on density points : each cluster was centered where the observations density was the highest [[Fraley & Raftery, 2002](#)]. Based on the Bayesian Information Criteria [[Raftery, 1995](#)], 10 clusters were done. Only frequent clusters were shown and discussed in the present study.

Finally, we calculated climatology for the physical CTL simulation over the 2000-2009 period. The



10 clusters were statistically linked to 9 environmental covariates extracted from the previous described climatology through XGBoost algorithm (eXtreme Gradient tree Boosting) : sun inclination, bathymetry, chlorophyll-a, depth of the 20°C isotherm, euphotic depth, norm of the winds, and the mean 0-600m values of oxygen, temperature and salinity.

We then used the XGBoost model as a predictive tool. As for SEAPODYM, we calculated the four futures climatology over the 2090-2099 period calculated from the four climate change simulations of all explanatory variables on a regular spatial grid with a resolution of  $\frac{1}{4}^\circ$ . The model predicted the probability to belong to each acoustic cluster (*i.e.* a vector of 10 probabilities). Two alternative approaches were considered to finally allocate one acoustic profile per cell : 1) we selected the acoustic cluster with the highest probability and 2) we calculated each mean vertical profile by cluster, and then we averaged the mean vertical profiles of clusters weighted by their predicted probability. The second option allowed us to predict acoustic values for all EEZ cells by month, during day and night, and at each depth. We then estimated acoustics values for the whole EEZ and produced maps of the integrated acoustic value for different vertical layers for the present period as well as for the future period.

To rank the importance of environmental covariates, SHapley Additive exPlanation (SHAP) values were computed [Lundberg *et al.*, 2018]. SHAP values indicated how much a given covariate value could change the predicted value compared to the prediction done without this covariate [Lundberg & Lee, 2017]. For instance, a high SHAP value for a given covariate value indicates a strong significance on the prediction. By averaging SHAP values by covariate across all predictions, we could rank the explanatory variables for the present predictions and the four models climate change predictions.

#### 5.2.4 SEAPODYM and acoustic estimates comparison

The 38 kHz NASC values was used as a proxy of micronekton biomass for the present study [Irigoién *et al.*, 2014] and predicted spatial patterns were directly compared to SEAPODYM-MTL biomass outputs. We assumed that even if NASC was not a direct measure of micronekton biomass, they could be used for qualitative comparisons between the future and the present period for example, or between vertical layers.

SEAPODYM vertical epi, meso and bathypelagic layers are calculated as a function of the euphotic depth (section 5.2.2). We similarly integrated modelled acoustic values over the same vertical layers for comparisons. Climate change anomalies were calculated by subtracting future from present values. Correlations were calculated.

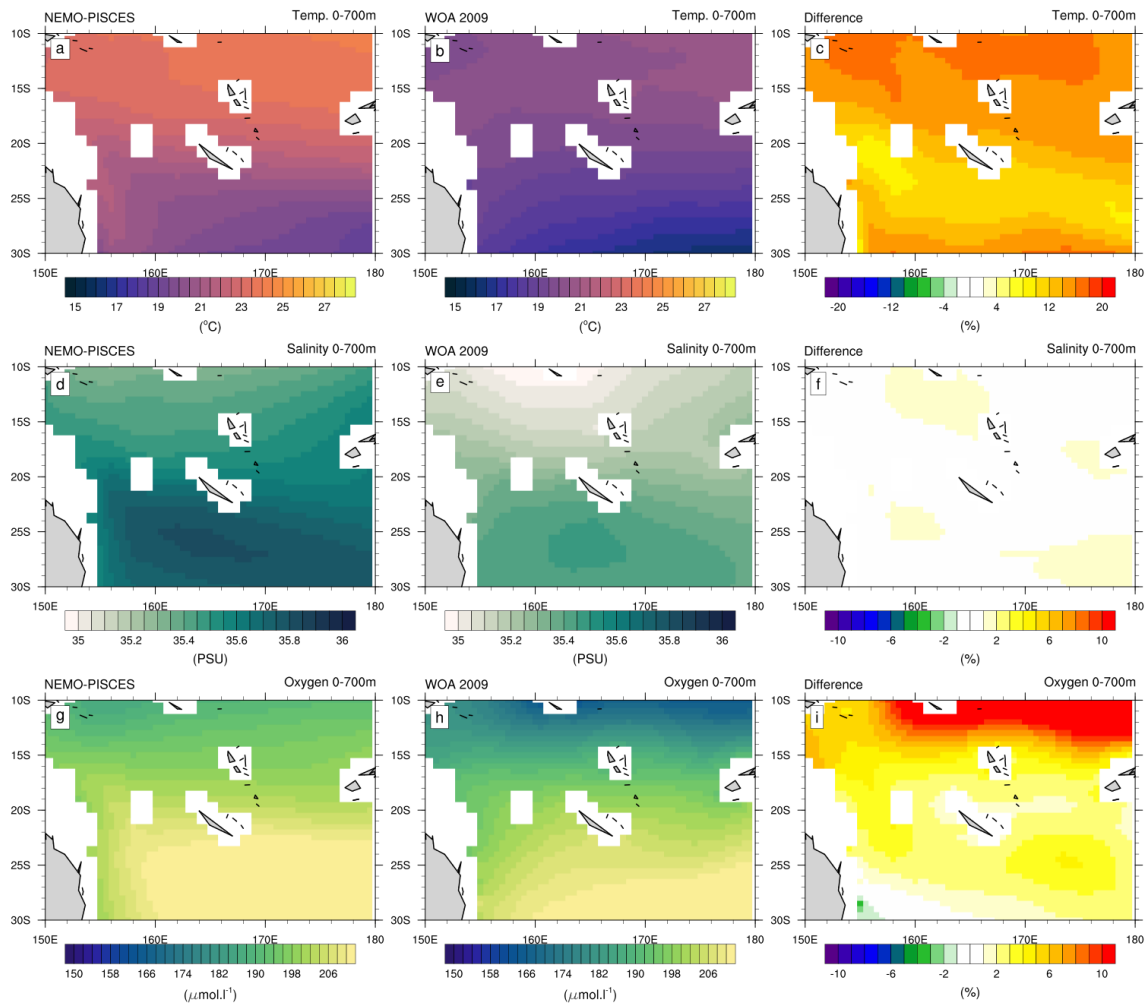


FIGURE 5.2 – Comparison between the NEMO-PISCES outputs (first column) and the WOA2009 (World Ocean Atlas, extrapolated observed data, [https://www.nodc.noaa.gov/OC5/WOA09/pr\\_woa09.html](https://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html)) (second column) dataset for three variables : the temperature (first row), the salinity (second row) and the oxygen concentration (third row), averaged over the top 700m of the ocean. Difference in percentage between two are shown too (third column).

## 5.3 Results

### 5.3.1 Climate experiments

#### Control of the biogeochemical simulation

In this subsection we aimed at validating the NEMO-PISCES simulation over the present-day period by comparing NEMO-PISCES to WOA2009 real data. In the southwestern Pacific, the observations showed a maximum south of New-Caledonia, and a south-north gradient for temperature, salinity and oxygen concentration (Figure 5.2). The three variables showed modeled values and spatial structures in good agreement with observations. Nevertheless, the NEMO-PISCES simulation tended to overestimate about 10% temperature observed values (Figure 5.2c), about 5% oxygen concentrations (Figure 5.2f), while the difference between salinity modeled values and observations was less than 2% (Figure 5.2i).

#### Future oceanographic conditions in the Coral Sea

Generally, the four climate experiments agreed on future evolution compared to the CTL situation for the environmental covariates, especially for the oxygen, the chlorophyll-a, the euphotic depth, the temperature and the 20°C isotherm depth (Figure 5.3). IPSL and MIROC predicted more pronounced changes than GFDL and MPI. Oxygen was predicted to decrease in the 4 experiments, chlorophyll-a was predicted to increase slightly in the north of the Coral Sea and to decrease below 25°S as well as in the small northwest corner (close to the Papua New Guinea). Changes in euphotic depth were naturally anti-correlated to chlorophyll changes : a deeper euphotic depth south of 25°S and for Papua New Guinea EEZ where the chlorophyll-a decreased and a shallower euphotic depth in the remaining part of the Coral Sea where increased chlorophyll were simulated. Expectedly, mean temperature was predicted to increase almost everywhere in climate change experiments, with an anomaly reaching or exceeding 2°C. 20°C isotherm depth was predicted to deepen with a higher trend (> 100m) in the south of the Coral Sea. Salinity predictions were more variable among climate experiments : GFDL forcing predicted an increase of the salinity for almost all the studied region whereas the three other models predicted a salinity drop for almost all the region, with only a small rise in the south for IPSL and MPI and also a small rise in the northeast for IPSL. Winds were predicted to reinforce strongly for MIROC and MPI, slightly for GFDL and a strong increase in the south and a weak decrease in the north were simulated for IPSL.

### 5.3.2 Micronekton vertical distribution

#### Modeling framework validation

The classification step for observed profiles separated almost perfectly day and night profiles into different acoustic clusters (Figure 5.4A). Among day clusters, we observed persistent detections located at 20-100m, which were composed of non-migrant micronekton staying within surface zone during the day. These detections would correspond to SEAPODYM-MTL epipelagic resident group. DSLs (Deep Scattering Layers) were located between 450 and 600m depth at day. Cluster 10 displayed an interme-

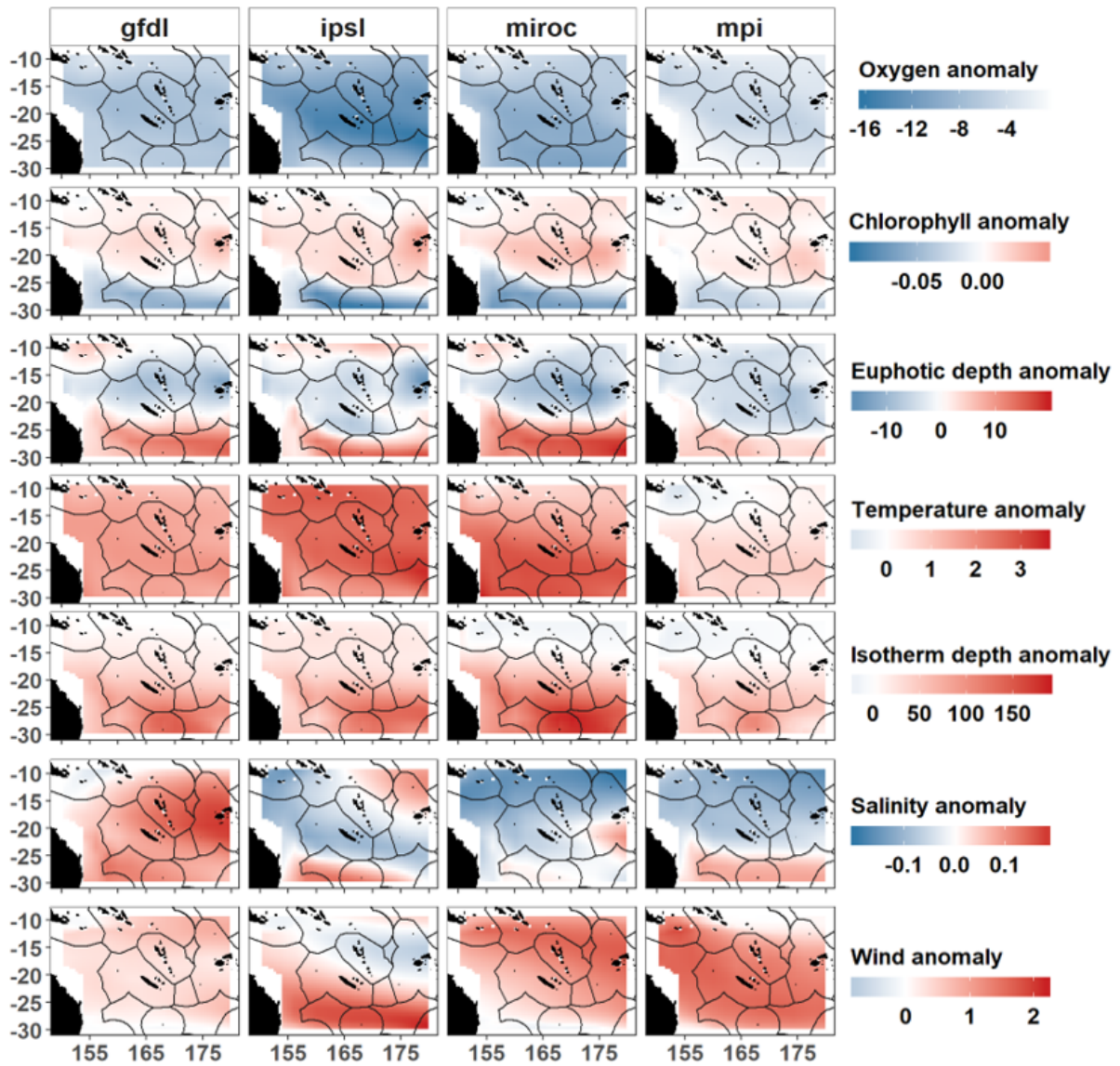


FIGURE 5.3 – Spatial anomalies (future – present) of environmental variables for the 4 climate models.

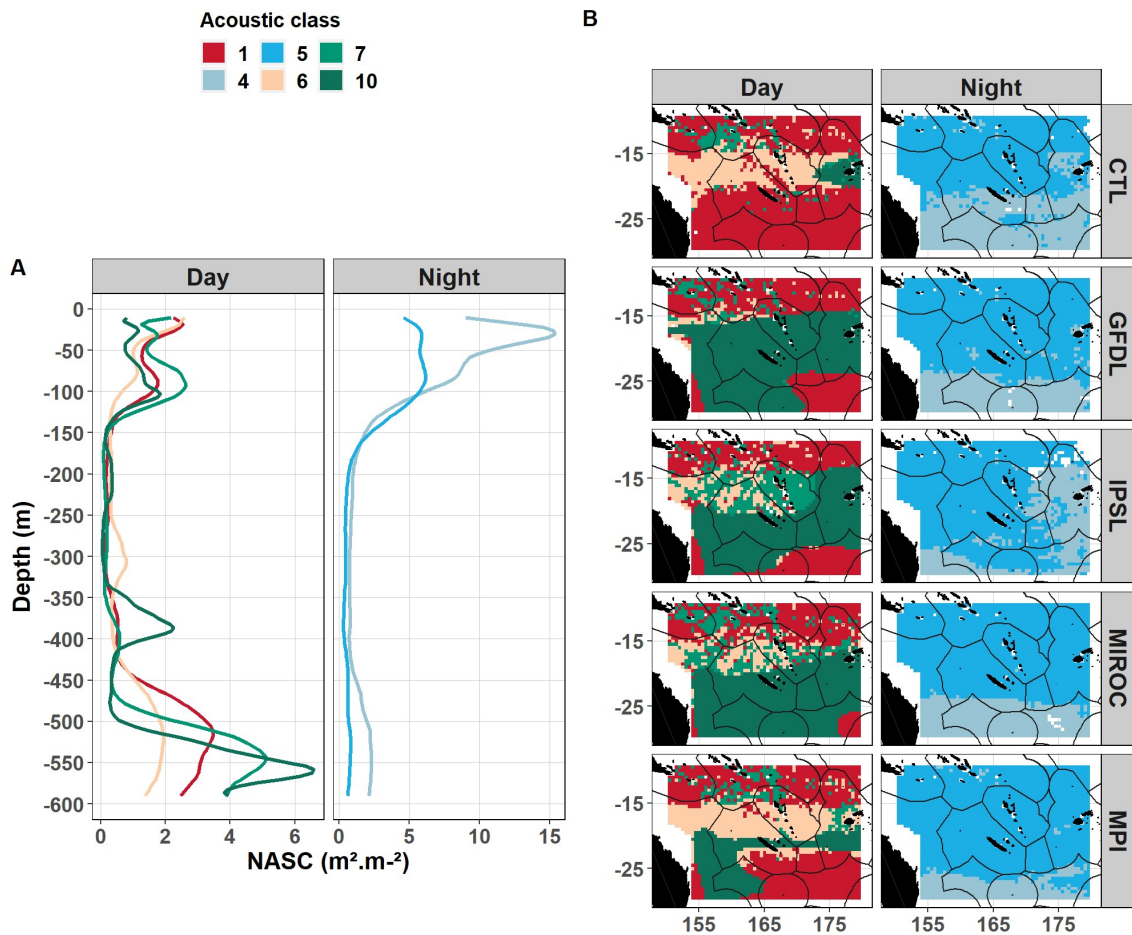


FIGURE 5.4 – Main vertical acoustic classes (panel A) and spatial pattern of these classes for the present (first row) and for the CTL simulation and the 4 climate models (panel B) during day (left column) and night (right column).

TABLEAU 5.3 – Correlations between SEAPODYM outputs and acoustic modeling outputs. (\*) indicates significant results for a 0.01 threshold.

|                | Epipelagic | Mesopelagic | Bathypelagic |
|----------------|------------|-------------|--------------|
| <b>Control</b> | 0.74 (*)   | 0.16 (*)    | -0.1         |
| GFDL           | 0.64 (*)   | 0.12 (*)    | -0.01        |
| <b>Future</b>  |            |             |              |
| IPSL           | 0.48 (*)   | -0.27 (*)   | -0.24 (*)    |
| MIROC          | 0.58 (*)   | -0.28 (*)   | -0.1         |
| MPI            | 0.71 (*)   | 0.02        | 0.25 (*)     |

diate layer in the 350-400m range. The variability of the vertical profiles shapes among the night clusters was concentrated in the epipelagic zone (0-200m). The two most important had two SSL (Shallow Scattering Layer).

As explained in the section 5.2.3, the relationships between acoustic clusters and environmental covariates were examined using XGBoost modelling. Covariates used to fit the model were extracted from the control simulation. Then, the most probable cluster was predicted over an area covering the whole Coral Sea based on CTL simulation variables and on the four future simulations variables (Figure 5.4B). The XGBoost modeling predicted the cluster number with a success rate of 84% in cross validation, *i.e.* 84% of the observations were well-classified in the validation dataset. We also showed previously that the model was able to predict main patterns of the micronekton vertical distribution [Receveur *et al.*, 2019].

The CTL simulation showed a dominance of clusters 6 in the north and 1 in the south for day-time and clusters 5 in the north and 4 on the south for night time (Figure 5.4B). Future predictions agreed on the spatial expansion of cluster 10 during the day and of cluster 5 during the night. GFDL, IPSL and MIROC showed a large expansion of cluster 10 in the south and small changes in the north. MPI also showed a movement of cluster 6 spatial distribution southward. IPSL and MIROC showed a small southward expansion of cluster 7. For the night, the four climate models showed a southward expansion of cluster 5.

Concerning future vertical distribution, during the day, the most predicted cluster (10) showed weaker SSL and narrower but more intense DSL compare to CTL vertical distribution. This future cluster also had a supplementary layer at 380m. The other cluster in expansion in the future (7) had also a more intense DSL as well as a more intense SSL. For the night, acoustic vertical profiles mostly predicted in the future showed (cluster 5) both weaker DSL, weaker SSL at 80m and especially a significantly weaker SSL at 30m than present vertical profiles (cluster 4) (Figure 5.4A). In conclusion, climate change seemed to consistently favor some acoustic vertical distributions (7, 10 and 5) and to disadvantage others (1 and 4).

**Future change according to acoustic modeling and SEAPODYM**

The importance order of forcing variables changed between the present and future acoustic simulation (Figure 5.5). Wind was the most important covariate structuring the present predictions whereas the 20°C isotherm depth became the most important for three future predictions (GFDL, IPSL and MIROC) over four. The mean salinity took the second place for the same 3 climate models despite it was only the fourth for CTL. Finally, the mean 0-600m temperature became more important in future simulations than for the present-day simulation.

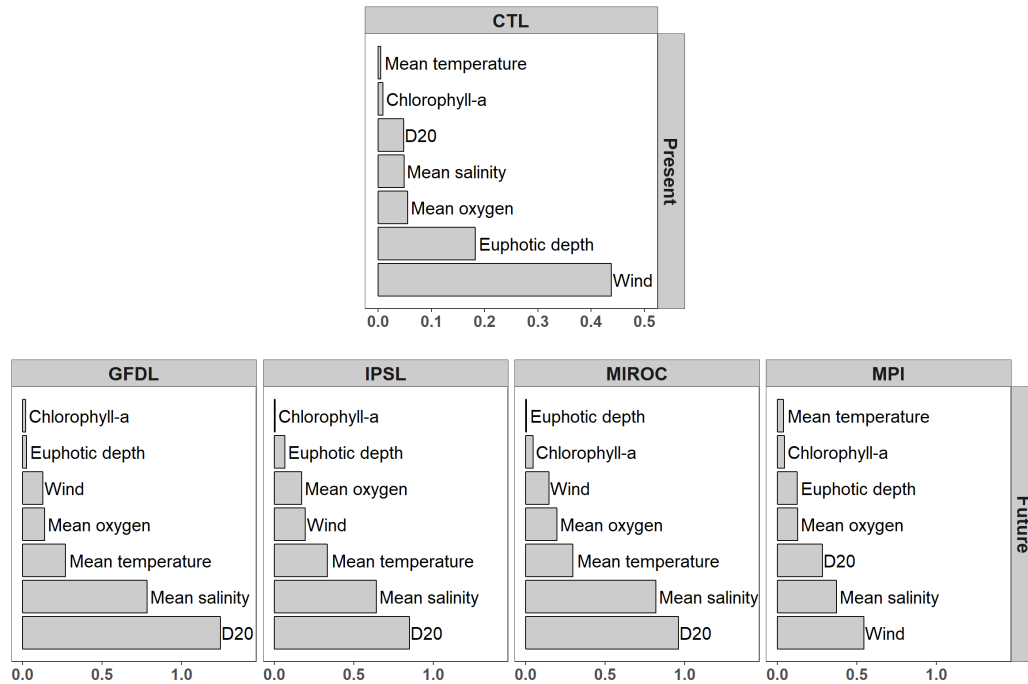


FIGURE 5.5 – Important variables represents by SHAP values (x-axis) in acoustics predictions for the present (first line) and for the 4 future predictions (second line).

As explained in section 5.2.3, the model predicted the probability to belong in each acoustic cluster for a given spatial cell. By averaging vertical profiles of clusters weighted by their probabilities, we rebuilt the 38 kHz complete vertical distribution for the whole zone (see also [Receveur et al. 2019](#) for additional information on the method). We integrated these predicted NASC values on the same vertical layers than SEAPODYM used to predict the forage biomass for the present and the future periods.

Predictions of SEAPODYM biomass and NASC values were well correlated in the control simulation in epipelagic layer, however correlations were smaller for mesopelagic and bathypelagic layers (Table 5.3). Therefore, we only found a consensus between SEAPODYM and acoustics predictions for the epipelagic layer.

On average for the three vertical layers, both SEAPODYM and acoustics modeling predicted a drop in micronekton quantities, ranged from -0.39 to -0.49 g/m<sup>2</sup> for SEAPODYM and from -0.06 to -0.45 m<sup>2</sup>/nmi<sup>2</sup> for predicted NASC values (Table 5.4). SEAPODYM and acoustics predictions agreed on the change sign for epipelagic and mesopelagic layers but strongly disagreed for the bathypelagic layer.

**Epipelagic layer** In general, both acoustics and SEAPODYM predicted a drop of values in the south of the Coral Sea and a rise in the north for the epipelagic layer (Figure 5.6) with good predictions agreement across climate models. Values between SEAPODYM and acoustics were correlated significantly for this layer in future simulations even if correlations for the future period were smaller than for the present for the four models (Table 5.3). Acoustic predictions showed a limit at 20°S for the four models. Maximum increase were predicted in Fijian economic zone for the IPSL model. GFDL predicted larger increases in the north of Vanuatu. MIROC and MPI mainly agreed with a slight increase between Vanuatu and Fiji. Below 20°S, the four models predictions showed a strong decrease except for the southeast corner

TABLEAU 5.4 – Coral sea mean anomalies (*i.e.* future – present) for the three vertical layers and on average for SEAPODYM and for acoustic modeling. The average value is also done in percentage (*i.e.* (future-present)/future).

|          |       | Epipelagic | Mesopelagic | Bathypelagic | Mean   | Mean (%) |
|----------|-------|------------|-------------|--------------|--------|----------|
| SEAPODYM | GFDL  | -0.072     | -0.064      | -1.3         | -0.48  | -29.5    |
|          | IPSL  | -0.089     | -0.049      | -1.28        | -0.47  | -26.7    |
|          | MIROC | -0.055     | -0.022      | -1.25        | -0.44  | -19.1    |
|          | MPI   | 0.0031     | 0.029       | -1.20        | -0.39  | -15.8    |
| Acoustic | GFDL  | -0.22      | -0.015      | 0.16         | -0.024 | -0.75    |
|          | IPSL  | -0.25      | -0.035      | 0.042        | -0.081 | -2.4     |
|          | MIROC | -0.38      | -0.055      | 0.14         | -0.099 | -3.1     |
|          | MPI   | -0.32      | -0.069      | -0.19        | -0.19  | -8.8     |

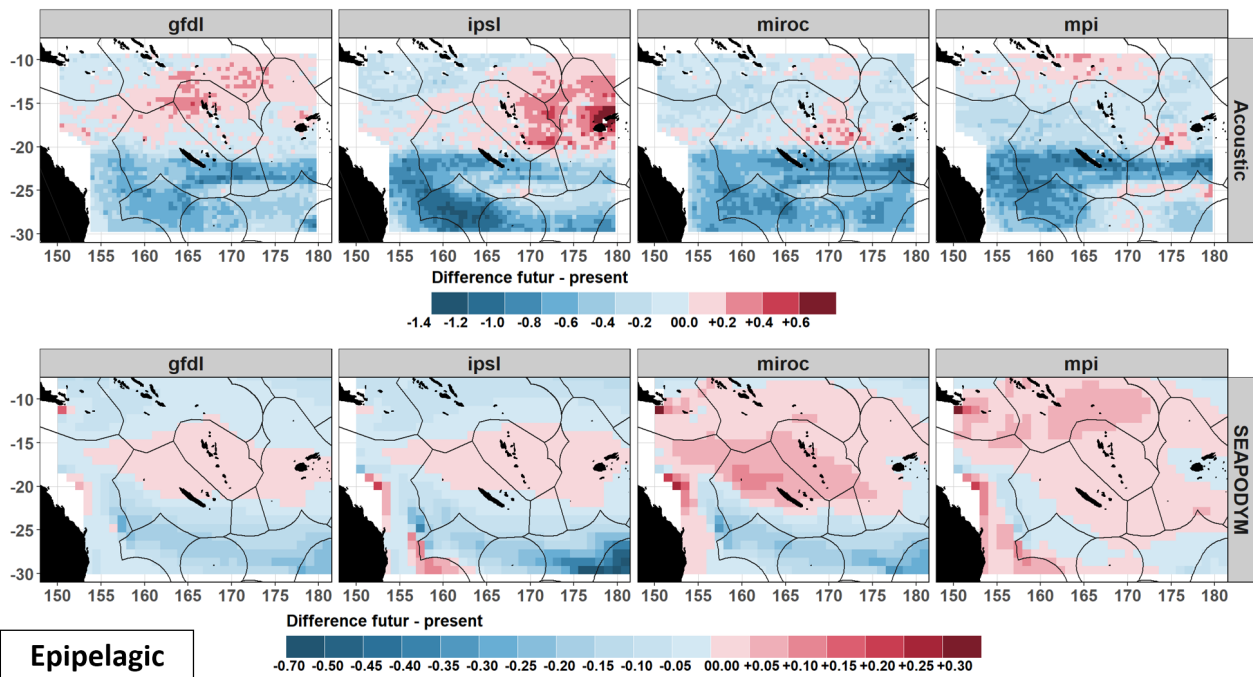


FIGURE 5.6 – Spatial anomalies (future – present) for the epipelagic zone (1.5\* euphotic depth) for the mean acoustic value (first row) and the SEAPODYM biomass (second row).

in MPI model. SEAPODYM predictions showed similar spatial patterns with the presence of the 20°S limit for GFDL, IPSL and MIROC predictions. GFDL and IPSL predicted an increase for New Caledonian, Vanuatu and Fijian EEZs and MIROC and MPI also predicted an increase for Solomon islands and Papua New Guinee EEZs (Figure 5.6). GFDL, IPSL and MIROC for the acoustic modeling and the four climate models for SEAPODYM showed a decrease of the biomass in the epipelagic layer (Table 5.4).

**Mesopelagic layer** Correlations were smaller for mesopelagic compared to epipelagic layer even if they were still significant for the future periods (Table 5.3). IPSL and MIROC were anti-correlated according to acoustics predictions. Acoustic predictions were also less heterogeneous between models than for the epipelagic layer (Figure 5.7). GFDL and MIROC showed an increase in the southeast corner not shown by the two other models. IPSL was the only model showing an increase in the north. SEAPODYM predictions were more consistent among models with a large northwest increase, mainly around Solomon Islands. The rise pattern spread toward the southeast until New Caledonian EEZ. Like for the epipelagic layer, GFDL, IPSL and MIROC for the acoustic modeling and the four climate models for SEAPODYM showed a



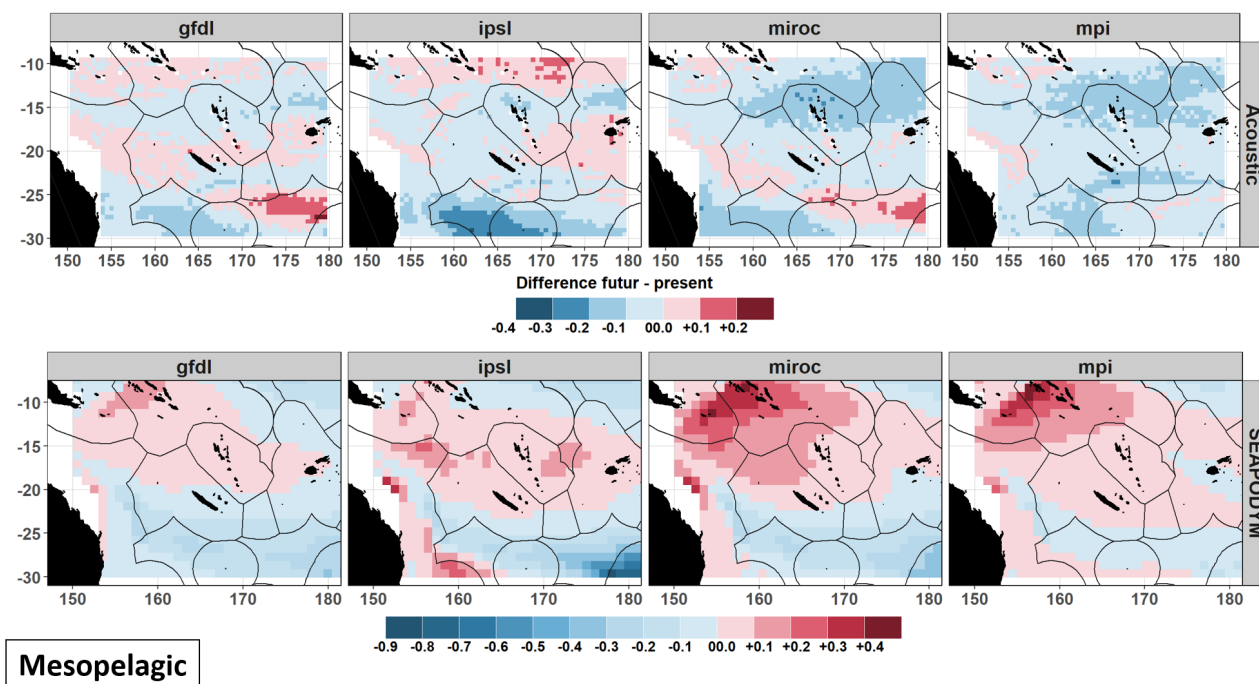


FIGURE 5.7 – Spatial anomalies (future - present) for the mesopelagic zone ( $1.5*Z_{eu} - 4.5*Z_{eu}$ ) for the mean acoustic value (first row) and the SEAPODYM biomass (second row).

decrease of the biomass (Table 5.4). For all decreases, the drop was smaller than for the epipelagic layer.

**Bathypelagic layer** Correlations were almost all null for models for the future periods in bathypelagic layer (Table 5.3). Spatial patterns were very different between SEAPODYM and acoustics predictions (Figure 5.8). The four models predicted a decrease of the micronekton biomass for the whole Coral Sea in SEAPODYM, with larger decrease in the north and in the south bands compare to the band comprised between 15°S and 25°S. On the contrary, acoustics predictions showed a strong increase of values, especially below 25°S for MIROC and GFDL, and between 15°S and 20°S for GFDL. IPSL also showed a crescent shape of increase around Fiji. This time, all SEAPODYM simulations had a negative drop and all acoustics modeling simulations had a positive drop except for MPI (Table 5.4).

**Seasonal cycle** By integrating predicted acoustic NASC between 10 and 600m, change in acoustics predictions according to the month were assessed. Increase above 20°S were stronger between March and September, *i.e.* during the austral winter. During the austral summer (November-March), the main change was a drop in the New Caledonian EEZ (Figure 5.9). There was no change in spatial distribution predicted by SEAPODYM across seasons, only differences in the biomass predicted (not shown).

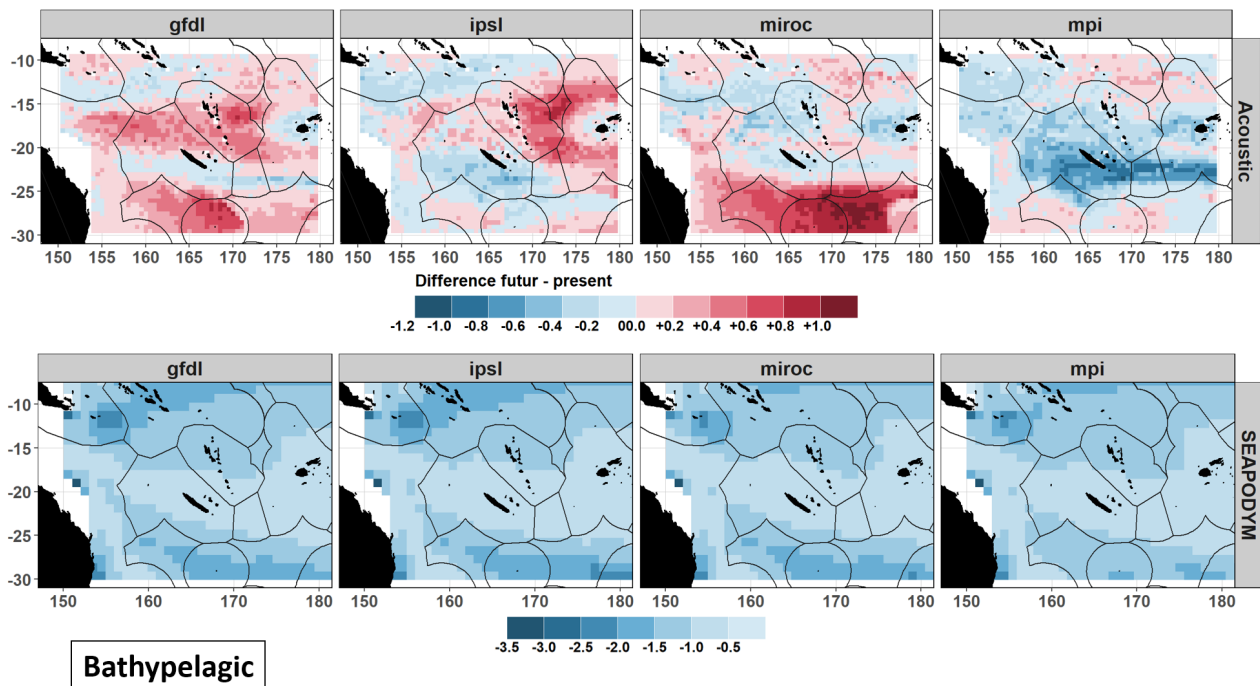


FIGURE 5.8 – Spatial anomalies (future – present) for the bathypelagic zone (4.5\* euphotic depth – 10.5\* euphotic depth) for the mean acoustic value (first row) and the SEAPODYM biomass (second row).

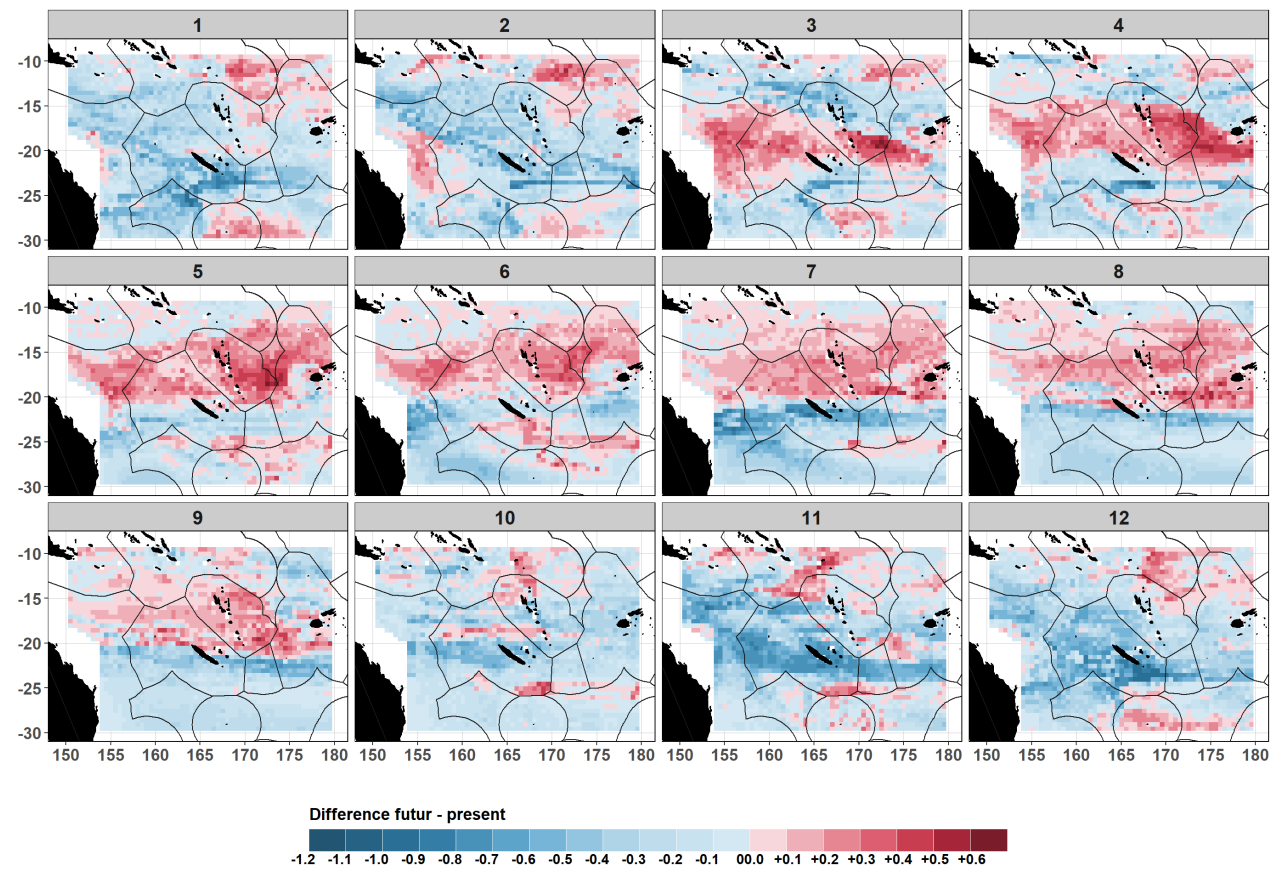


FIGURE 5.9 – NASC spatial anomalies (future – present) by month averaged over the complete vertical layer (10-600m).

## 5.4 Discussion

We used bias-adjusted atmospheric outputs of four (IPSL, GFDL, MIROC and MPI) climate models for the next 100 years under RCP8.5 scenario to force the PISCES-NEMO dynamical-biogeochemical model. These model outputs were then used as inputs of two ecosystem models of micronekton to understand the potential futures of this trophic compartment. The first model was a statistical model linking observed profiles of acoustic relative abundance of micronekton. The second one was the micronekton component of the population dynamics SEAPODYM model. With these two models, we evaluated the response of Coral Sea marine micronekton to changes of temperature, oxygen, salinity, winds, 20°C isotherm depth, euphotic depth and primary production resulting from a range of climate change forcings. In agreement with previous climate modeling studies, we reported profound modifications of the ecosystem structure, such as micronekton biomass decrease and geographical shift predicted both by SEAPODYM and acoustic modeling albeit with uncertainties related to the different models and forcings. The strongest difference between SEAPODYM and acoustic predictions occurred for the bathypelagic vertical layer both in term of biomass and of spatial patterns. Changes in the water column vertical structure seemed to create change in acoustic vertical structure. Uncertainties within climate model forcings were reported to be less impacting than differences between micronekton model types.

### 5.4.1 Main limitations

#### Acoustic modeling

The acoustic modeling framework created depth-dependent acoustic clusters by linking observed acoustic vertical profiles and the present-day environment. That model constrained the micronekton future projections as we predicted the probability to belong to the present-day clusters given the evolution of the environment under climate change. Hence, the method could not create new vertical distributions in the future but could only show increased or decreased proportion for each cluster given future environments.

Moreover, the XGBoost model predicted the probability of belonging to a given acoustic cluster based on a vector of covariate values, therefore the range of covariate values used for the model prediction had to be similar to the range covered by the initial data used to build the model. Globally, the dataset used for control predictions was reasonably sampled with observed covariates values whereas future conditions were less sampled. Future values of low mean oxygen, high mean temperature and deep isotherm depth were the most badly sampled covariates for future predictions. By using determinist equation, SEAPODYM overpassed this issue.

In addition, the 38kHz frequency detected mostly organisms with a swimbladder (mostly fish) while excluding other organisms without gas-filled swimbladders [Davison *et al.*, 2015a,b]. Foote [1980] even showed that more than 95% of the organisms' backscatter at 38 kHz was produced by gas-filled swimbladders of fish and gas-filled pneumatophores of siphonophores. If climate change favors some species compared to others, our analysis of acoustics cannot capture such effect. We used the 38 kHz NASC to have an overview of the micronekton total biomass in the Coral Sea and the NASC predicted would cer-

tainly slightly change if species composition changed. However, we assumed that spatial patterns and the sign of the change were realistic.

The next step to validate our acoustics prediction would require an extensive program of *in situ* sampling with appropriate trawls to identify the species composition of the different layers. This would allow to link species to their environmental tolerances and so predict species distribution in a climate change context. However, new conditions may be physiologically tolerable, allowing acclimatization (an adjustment of physiology like oxygen tolerance by individual) or adaptation (increased abundance and reproduction with some genotypes changes over generations), or may be intolerable, creating migration, change in phenology, or local extinction [Parmesan, 2006]. So far, given the micronekton species diversity already observed [Ceccarelli *et al.*, 2013; Payri *et al.*, 2019], it is unlikely that the climate change effect understanding on individual species can be met in the near future in the Coral Sea.

### SEAPODYM modeling

SEAPODYM-MTL is a complex model based on advection-diffusion equations and we could not directly link biomass changes to oceanographic changes as we did with acoustic modeling.

SEAPODYM bathypelagic layer is comprised between  $4.5Z_{eu}$  and  $10.5Z_{eu}$ , *i.e.* on average 470m and 1100m for the Coral Sea. Acoustics vertical profiles ranged from 10m to 600m. Therefore, the SEAPODYM ‘bathypelagic layer’ has 500m more than the acoustics ‘bathypelagic layer’, that could explain the large differences between NASC predictions and SEAPODYM outputs. However, Receveur *et al.* [2019] concluded that for the region, vertical profiles until 600m were enough to take into account the complete DSL compartment.

Overall, to the authors knowledge the present study provided a first assessment of the possible change of the mesopelagic compartment in the future in the Coral Sea.

#### 5.4.2 Change in physical oceanography

By using realistic atmospheric forcings to which climate change trends were added, the common biases of fully coupled climate models at regional scale were minimized. The future simulations forced by those “hybrid” atmospheric forcings were therefore minimizing the ocean biases in the Coral Sea region.

Predicted change of mean temperature mostly agreed with previous published work about temperature changes, even if most of the studies were about SST change [Le Borgne *et al.*, 2011]. For example, Ceccarelli *et al.* [2013] reported a SST rise of 3.2°C by 2100, which was in accordance with present results.

Spatial patterns of chlorophyll-a change showed a delimitation at about 25°S that more or less matched the limits described by Jitts [1965]. He divided the Coral Sea into two regions based on their productivity, with a boundary at 20°S; the central Coral Sea ( $264\text{mgC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) and the less oligotrophic southern Coral Sea ( $360\text{mgC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). Menkes *et al.* [2015] confirmed this spatial pattern with more chlorophyll-a below 22°S. Based on this study results, the oligotrophic waters were predicted to become less oligotro-

phic to the north and on the contrary, relatively richer waters to the south were predicted to become poorer. Therefore, the Coral Sea was predicted to become more homogenous in term of primary production (*i.e.* the rich south was predicted to become poorer in the future and the poor north was predicted to become richer in the future).

The decrease of chlorophyll-a in the Coral Sea south deepened the euphotic depth and the increase in the north resulted in a shallower euphotic depth. For the region, [Bopp \*et al.\* \[2013\]](#) mapped a decrease of the integrated net primary productivity change of about  $100\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$  by 2100 for the RCP8.5 scenario, with an homogeneous decrease for the whole Coral Sea. The present study showed that such pattern may be more contrasted than previously published : the chlorophyll-a increase found above  $25^{\circ}\text{S}$  has never been shown before to our knowledge.

We found a decrease of about 3.4% of mean oxygen by 2100 on average among the 4 climate models, which was coherent with the 5% given by [Ceccarelli \*et al.\* \[2013\]](#). [Bopp \*et al.\* \[2013\]](#) mapped a decrease of about  $10\ \mu\text{mol/L}$  at 200-600m that was fully coherent with our oxygen predictions.

We did not find any study showing climate change effect on salinity and wind that were also the most spatially variable covariates among the 4 climate models for the future (Figure 5.2). Mean salinity was also the second most driving covariate in micronekton future spatial change for the four climate models. For the future, validate the evolution of these two variables in climate change is crucial.

### 5.4.3 Change in micronekton

As said in the section 5.4.1, climate change could create favorable or un-favorable environmental conditions for the mix of species composing micronekton [[Pecl & Jackson, 2008](#); [Pecl \*et al.\*, 2017](#)]. If a habitat becomes unsuitable for a given population, population size may decline as eco-physiological performance (*e.g.* metabolic rates or growth) is negatively affected [[Hillebrand \*et al.\*, 2018](#); [Portner, 2001](#)] or species may shift their distribution to cooler waters [[Pecl \*et al.\*, 2017](#)]. The large diversity of species strongly complicated the assessment of climate change impact on micronekton.

Strong discrepancies appeared between SEAPODYM and acoustics modeling, across the four climate models and across vertical layers in the present study. SEAPODYM and acoustics modeling agreed on the predicted decrease of micronekton abundance on average for the whole Coral Sea. They both showed an increase of micronekton abundance in the north of the Coral Sea and a decrease in the south for the epipelagic layer. They also agreed to conclude that climate change impacts were completely different between epipelagic and bathypelagic layers. [Bryndum-Buchholz \*et al.\* \[2019\]](#) predicted a biomass decrease of about 15% for organisms with a length ranged from 0 to 30cm for the whole South Pacific Ocean and [Lefort \*et al.\* \[2015\]](#) an approximately 20% decrease for the whole Pacific Ocean. SEAPODYM predicted changes (-13.2%, -2.6% and -70.4% respectively for the epipelagic, mesopelagic and bathypelagic layers) and acoustics predicted changes (-6.6%, -5.7% and +2.6% respectively for the epipelagic, mesopelagic and bathypelagic layers) globally agreed on the sign of the change, but showed a large variability. However, unlike our study, these previous studies did not include the vertical structure of the micronekton that was shown to be important.

The increase of epipelagic micronekton biomass matched the region that predicted higher chlorophyll-

a by 2100 (Figures 5.3 and 5.6). We suggested that the enhancement of primary production could be associated with enhanced zooplankton production, leading to an increase in micronekton density in that part of the water column. The trophic link of a positive relationship between primary production and mesopelagic organisms had been found previously [Escobar-Flores *et al.*, 2013; Irigoien *et al.*, 2014]. Positive anomalies NASC values in the epipelagic layer also matched with relatively high salinity anomalies values (Figures 5.3 and 5.6). Salinity is often linked to water mass, and so this positive link between high salinity and high NASC values could be due to the enhancement of a specific water mass as it had already been demonstrated in other places [e.g. Behagle *et al.*, 2016; Jungblut *et al.*, 2017; Sutton & Beckley, 2017]. A focused analysis on water masses and their links to micronekton would be needed to validate this hypothesis.

Largest change in acoustics modeling for the bathypelagic layer (Figure 5.8) coincided spatially with a deeper 20°C isotherm depth predicted (stronger for the MIROC simulation as for acoustics' prediction) together with low wind. Weak winds and deep isotherm are often linked to oceanic conditions characterized by small mix rate between mixed layer and deeper layer. We assumed that deep isotherm could create a physical barrier for micronekton, which more stay in the epipelagic layer. However, this effect was not shown by SEAPODYM MTL model.

By doing niche modeling, spatial distribution of top predators in climate change could be assessed [Block *et al.*, 2011; Hazen *et al.*, 2012]. However, these studies did not take into account the potential change in predators prey spatial distribution that could highly influence predators spatial distribution [e.g. Hazen *et al.*, 2009; Lambert *et al.*, 2014; Miller *et al.*, 2018; Schick & Lutcavage, 2009]. We have shown in the Coral sea that the prey spatial distribution are likely to change. Spatial predictions of predators with climate change would hence need the integration of their prey spatial distribution in the future.

#### 5.4.4 Improve prediction reliability

Correlations between SEAPODYM predictions and acoustic modeling predictions were good (significant and superior to 0.5) for the epipelagic layer both for present and future periods but were small (inferior to 0.3) for the mesopelagic and bathypelagic layers. The large difference between SEAPODYM and acoustics predictions in the mesopelagic layer highlighted the need to develop tools assessing climate change impact on mesopelagic components.

More and more recent articles published global analyses of the climate change impact on ocean biomass and trophic interaction. They showed a decline of the global marine animal biomass under all scenarios, and a stronger decline for high trophic level organisms (*i.e.* top predators) [Bryndum-Buchholz *et al.*, 2019; Cheung *et al.*, 2016; Lotze *et al.*, 2019]. For that, they all used ensemble projections from several global marine ecosystem models forced with several Earth system models under at least two climate change scenarios. Studies using ecosystemic models size structured concluded for the same decrease [Blanchard *et al.*, 2012; Carozza *et al.*, 2019; Christensen *et al.*, 2014; Fernandes *et al.*, 2013; Lefort *et al.*, 2015]. Tittensor *et al.* [2018] offered a method to homogenous forcing oceanographic data to be able to compare outputs from different ecosystem models and so to measure the predictions variability across different ecosystem models. However, large uncertainty gap remained in these models [Payne *et al.*, 2016].

Studies about biodiversity changes in marine ecosystem using real *in situ* data are more common than studies about quantity potential change using *in situ* data [Garcia Molinos *et al.*, 2016; Hillebrand *et al.*, 2018; Worm & Lotze, 2016]. *In situ* diversity data are often easier to understand and to analyze regarding to environmental data than *in situ* quantity data for micronekton. However, more study using *in situ* data are needed to improve our understanding of marine ecosystems, their services and their possible change in climate change [St. John *et al.*, 2016]. We argue that, before developing ensemble model as advised by Chen & Guestrin [2016], it is essential to first develop predictions based on real data. It is also crucial to enhance knowledge about micronekton species physiological tolerance to environmental data to predict potential changes in species compositions.

We assumed for our study that the NASC was directly proportional to the biomass of all micronekton organisms included in SEAPODYM functional groups and we found a good match between the two products for the epipelagic layer, which provided confidence in the results of the ecosystem model. However, the common spatial patterns for the mesopelagic and bathypelagic layers were weak, even for the present period. To fully be able to compare acoustics data and ecosystemic models outputs as SEAPODYM MTL, it seemed essential to characterize the community of micronekton species in these different vertical layers, and the target strengths of dominant species. It is possible for instance that the observed discrepancy between these model outputs was due to a dominant species with strong acoustic resonance but low energy (carbon) content that dominated NASC values [Davison *et al.*, 2015a; Proud *et al.*, 2018b]. Conversely large biomass of mesopelagic fish without gas-filled swimbladders can be present but transparent to the acoustic signal [Foote, 1980]. SEAPODYM-MTL model structure also may appear too simple to take into account the spatial variation of observed micronekton distribution across seasons, based on our acoustic estimates. For instance, implementing a zooplankton compartment in SEAPODYM-MTL may improve that model by giving more flexibility to the model to better fit with our predicted NASC values.

#### 5.4.5 Conclusions and perspectives

We predicted a decrease of micronekton biomass in the Coral Sea by 2100 both in an ecosystemic model and based on statistical models working with acoustics data. For that, we used an innovative physical modeling based on the NEMO-PISCES coupling. Future predictions for the epipelagic mostly agreed whereas SEAPODYM and acoustics data hugely differed for the bathypelagic layer, even for the present period. We emphasized the necessity to do more predictions about micronekton that has a key role in the pelagic ecosystem in a climate change context. Ecosystem models have to be tuned with external data [Lehodey *et al.*, 2015] and predictions have to be compared with real *in situ* data. We reinforced Handedgard *et al.* [2013] conclusions for the development of observation models and for the improvement of observation-model links.

# Inter-chapter

Chapter 5 offered two 3-dimensional techniques to predict micronekton evolution in response to climate change, using four different oceanographic models to ensure conclusions were robust to the underlying physical predictions. We used an innovative oceanographic regional simulation from a coupled dynamical-biogeochemical model (NEMO-PISCES) to force biological modeling. One method was based on statistical modelling using available acoustic data and the other one on the outputs of SEAPODYM, an end-to-end ecosystemic model. A deeper 20°C isotherm depth and salinity change drove micronekton change in the Coral Sea by 2100. The two methods predicted a mean decrease of micronekton abundance, though uncertainty in predictions varied depending on the vertical layer considered. Micronekton's epipelagic SSL abundance increased north of 21°S and decreased south of this limit, both for acoustic and SEAPODYM predictions. Predictions of mesopelagic layer micronekton abundance increased by 2100 according to SEAPODYM, whilst no clear patterns were apparent based on acoustic data. Finally, there was a large inconsistency in predictions for the bathypelagic layer. We concluded on the importance to develop more frameworks and methods to compare between acoustic data and forage ecosystemic model outputs in order to be able to predict micronekton change. Chapter 6 also compares, in a certain way, the use of forage ecosystemic model outputs and acoustic based prey layers but in the context of prey-predator relationships. In the next chapter, we conducted a similar analysis but using acoustics values to incorporate prey relative abundance into nine predators' niche models.







## Chapitre 6

# Habitat predictive modelling of nine top predators with respect to the abundance of pelagic prey in the southwest Pacific

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## Abstract

Developing habitat predictive models of both predators and prey species is a fundamental goal in marine spatial ecology, as marine species are often highly mobile and difficult to monitor. In this study, the spatial distribution of nine top-predator groups was analyzed throughout the New Caledonian pelagic waters, including three fish species, three cetacean guilds and three seabird species : albacore tuna (ALB), yellowfin tuna (YFT), dolphinfish (DOL), Delphininae (DELPH), Globicephalinae (GLOB), Ziphiidae (ZIPH), wedge-tailed shearwater (WTSH), Tahiti petrel (TAPET) and red-footed booby (RFBO). Spatial distribution and environmental relationships were analysed using catch per unit effort for tuna and dolphinfish, aerial counts for cetaceans, and tracking data identifying foraging behaviour for seabirds. Predator distributions were modelled in relation to static predictors (bathymetry), dynamic predictors (SST, chlorophyll and 20°C isotherm depth) and acoustically derived preyscapes. Preyscapes influenced six out of nine predator distributions (ALB, YFT, DOL, DELPH, WTSH and RFBO). Therefore, it appears that acoustically-derived prey abundance estimates can improve distribution models for some predators. Predicted spatial distributions of fishes (ALB, YFT and DOL) did not overlap, whereas those of cetacean (DELPH, GLOB and ZIPH) were more similar. WTSH, TAPET and RFBO spatial distributions slightly differed, even if conclusions are limited by the relatively small datasets collected for TAPET and RFBO. By combining the predicted maps of distribution for the nine predators, we identified regions concentrating a number of predators that may be regarded as interesting areas for management purposes. This study constitutes a first step towards an integrated description of marine top predators' distribution in the New Caledonian pelagic ecosystem.

**Keywords :** *Micronekton, top predators, Southwest Pacific Ocean, niche modeling, habitat, Natural Park of the Coral Sea*

## 6.1 Introduction

Ecosystem based fisheries management (EBFM) aims at developing relevant knowledge on ecological mechanisms and processes that shape predator-prey interactions [Christensen *et al.*, 1996; Koslow, 2009]. It values habitat, embraces a multispecies perspective, and is committed to understanding ecosystem processes [Garcia *et al.*, 2003]. However, one of EBFM's major challenge is the definition of efficient and comparable indicators integrating the ecosystem complexity [Garcia & Cochrane, 2005; Garcia *et al.*, 2003]. This pelagic ecosystem complexity results both from the numerous interactions across species, and from the variability of spatiotemporal scales at which interactions take place. Understanding ecological processes at an ecosystemic level that underpin species distribution patterns and their oceanographic drivers remains challenging [e.g. Briscoe *et al.*, 2016; Carroll *et al.*, 2017; Wiens, 1989].

In addition, the variety of observation systems complicates the production of relevant EBFM indicators. Within marine top predators, commercially exploited fish species are often studied using catch data [e.g. Lan *et al.*, 2018], non-target species using by-catch data [e.g. Escalle *et al.*, 2018] and on-board observer data [e.g. Lopez *et al.*, 2003]. For species of special interest like cetacean or seabirds, datasets also comprise detailed counts carried out by scientific observers from boats or aircrafts, but are based on a great variety of sampling strategies. Data collection from citizen science is sometimes an alternative

approach to produce these datasets [e.g. [Delavenne et al., 2017](#); [Derville et al., 2018](#)]. The movements of marine predators are also followed with tagging approaches, which include a great variety of methods (e.g. spaghetti marks, archival marks, telemetry) [e.g. [Abecassis et al., 2015](#); [Block et al., 2011](#); [Leroy et al., 2016](#)]. All the above-listed data types measure different predators' behaviors (e.g. foraging, migrating, resting) at variable spatio-temporal scales : from a few seconds to several years, and from a few centimeters to thousands of kilometers. Scientific effort is needed to develop a modeling framework to fill data gaps in time and space, to undertake integrated analyses of species distributions, and therefore acquire a realistic overview of the pelagic ecosystem functioning [[Bax et al., 2019](#)].

In addition, while most of the predators vertical and horizontal movements are motivated by foraging behavior [[Lehodey & Maury, 2010](#)], measures of prey availability are often lacking in predators niche modeling [[Robinson et al., 2011](#)]. Most studies of predators' spatial distributions only rely on oceanographic (e.g. SST, oxygen, chlorophyll-a) and static (e.g. depth, bottom slope) variables. At fine spatial scale, predator-prey relationships have been studied with the use of acoustics [e.g. [Bertrand et al., 2002a](#); [Lezama-Ochoa et al., 2010](#)]; but to date, most of the studies assessing the influence of prey distribution on predator distribution at a regional scale used ecosystem models [e.g. [Briand et al., 2011](#); [Lambert et al., 2014](#); [Miller et al., 2018](#)]. The lack of real prey data in predators niche modelling could be explained by the large variability in predators diet [[Duffy et al., 2015](#); [Olson et al., 2014](#); [Potier et al., 2007](#)], as well as the difficulty to quantify prey abundance and characterize its dynamics.

Oceanic pelagic prey abundance and diversity are often investigated using meso-pelagic trawls ([Sutton et al., 2010](#)) and stomach content data [e.g. [Annasawmy et al., 2018](#); [Ménard et al., 2013](#); [Portner et al., 2017](#)]. However, the net avoidance behavior of organisms introduces a bias in abundance estimates derived from trawl data [[Heino et al., 2011](#); [Kaartvedt et al., 2012](#)]. In addition, trawls or stomach data estimations are spatially discrete, hampering extrapolation at scales larger than the surroundings of the sample position. For the last fifty years, net sampling has been supplemented with underwater sound measurement [[Benoit-Bird & Lawson, 2016](#)], scientific echosounders being a powerful tool to study prey distribution and behavior [[Cade & Benoit-Bird, 2015](#); [Kloser et al., 2002](#)]. Although species composition and species target strength have to be exactly known to calculate an absolute prey biomass [[Davison et al., 2015a](#); [Proud et al., 2018b](#)], the acoustic echo-intensity can be used as useful proxy of prey relative abundance [[Irigoién et al., 2014](#)]. As scientific echosounders record echo intensity continuously during surveys at sea, acoustic data have a larger spatial extent and are less scattered than trawl data.

To give an overview of predator-prey spatial distribution relationships, acoustic data can be interpolated on a regular grid, and then matched with various predators' distribution data. Moreover, the feeding habitats and vertical behaviors of predators through the water column are very diverse [e.g. [Benoit-Bird & McManus, 2012](#); [Choy et al., 2017](#)] and may change spatially, as a function of prey distribution or due to physiological tolerance to environmental parameters [[Houssard et al., 2017](#); [Schaefer & Fuller, 2010](#); [Schaefer et al., 2007](#)]. Taking into account the vertical structure of preys is therefore necessary to fully understand predator-prey relationships [[Louzao et al., 2019b](#)] as these are strongly layered in the ocean [[Opdal et al., 2008](#)].

In the present study, we developed a method to combine environmental variables and vertically-structured prey abundance with top-predator abundance/occurrence data. As a result, the influence of prey abundance on predator distribution was assessed in comparison with oceanographic drivers. We

used nine predators taxa in New Caledonian Economic Zone (EEZ), located in the Coral Sea at the southwestern edge of the Pacific Ocean. Around New Caledonia, a large species richness of top predators has been highlighted with for example the presence of 27 species of cetaceans [Garrigue & Poupon, 2013; Laran *et al.*, 2016a] or 17 species of seabirds [Borsa *et al.*, 2014, 2015; Laran *et al.*, 2016a; Weimerskirch *et al.*, 2017]. This high predator diversity is supported by a large diversity among prey species demonstrated through predator diet studies [Allain *et al.*, 2012; Olson *et al.*, 2014; Williams *et al.*, 2014; Young *et al.*, 2010] and trawl data analyses [Grandperrin *et al.*, 1999; Menkes *et al.*, 2015; Young *et al.*, 2011].

The recent creation of the Natural Park of the Coral Sea (Decree 2014-1063/GNC) covering the whole NC EEZ has led to a need for robust scientific information on the functioning of its remarkable pelagic ecosystem. In this context, distribution models were built for two tuna species and dolphinfish through catch data, three cetacean taxa through aerial survey count data and three seabird species through tagging data. Predators abundance/occurrence data were statistically modeled in relation to three main biophysical oceanographic variable (SST, chlorophyll, 20°C isotherm depth), bathymetry, as well as one biotic prey variable (acoustics echo intensity integrated over different depth layers). We described the importance of prey relative abundances on predator abundance/occurrence. Finally, the relationships were used to predict spatial distributions of the nine predators and the overlap between those were discussed to identify areas of special interest for management.

## 6.2 Methods

Statistical models were fitted over a measure of predators' occurrence or abundance as a function of explicative variables including oceanographic conditions and prey distribution. All data used in the models were gathered in the New Caledonian Exclusive Economic Zone (EEZ), covering the area between 156°E–175°E and 14°S–27°S (Figure 6.1).

### 6.2.1 Predator data collection

#### Tuna and dolphinfish

Daily catch rates of albacore (ALB) and yellowfin (YFT) tuna and dolphinfish (DOL) were obtained from the logbooks covering 100% of the longline fleets in New Caledonia [WCPFC, 2018] (Table 6.1). The logbooks provided information on a daily basis : name of vessel, date and location (latitude and longitude) of the fishing set, number of specimens captured according to commercial category and number of hooks.

#### Cetaceans

Cetacean counts were obtained from the REMMOA aerial surveys conducted in the New Caledonian EEZ between October and December 2014 (Table 6.1). More than 30 000 km were surveyed over a total surface area of 542 300 km<sup>2</sup> (39% of the EEZ) (see Figure 4 in Laran *et al.* 2016a) at a ground speed of 167 km.h<sup>-1</sup>. A line-transect methodology was used to count cetaceans [Buckland *et al.*, 2001],

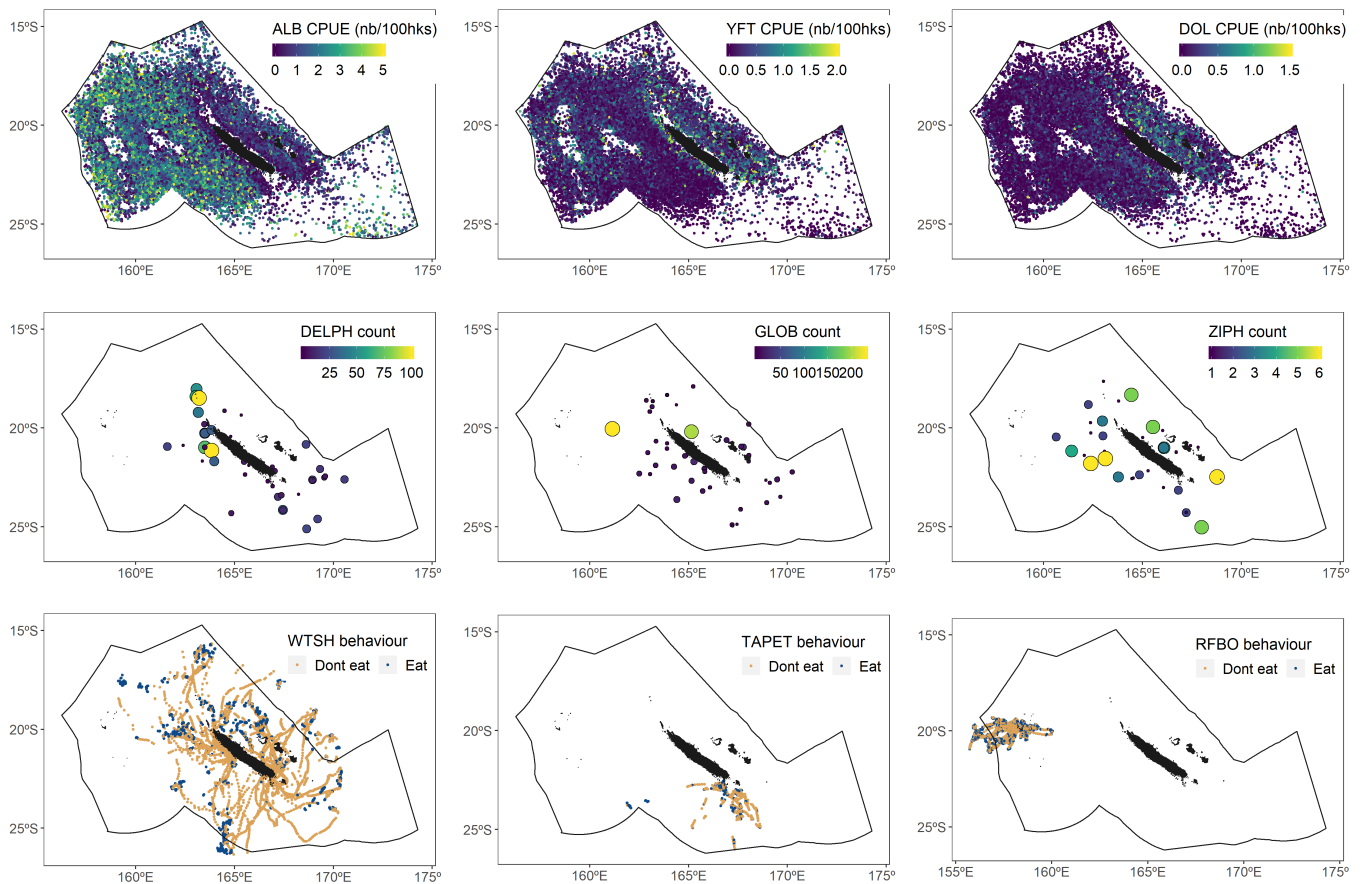


FIGURE 6.1 – Raw data for the nine predators included in the study. Top : Albacore (ALB) and yellowfin (YFT) tuna and dolphin fish (DOL) catch per unit of effort (CPUE) in number of fish caught per 100 hooks. Middle : Delphininae (DELPH), Globicephalinae (GLOB) and Ziphiidae (ZIPH) cetacean counts in number of animals. Bottom : wedge-tailed shearwater (WTSH), Tahiti petrel (TAPET) and red foot booby (RFBO) foraging behavior positions from tagging data.

TABLEAU 6.1 – Predators variable summary with the species, the code used for figures, the unit, the number of observations (N), the data source, the time of day, year and month sampled.

| Taxon                   | Code  | Unit                            | N     | Source        | Moment of the day | Year range | Month           |
|-------------------------|-------|---------------------------------|-------|---------------|-------------------|------------|-----------------|
| Albacore tuna           | ALB   | Number per 100 hook             | 13158 | Catch         | Unknown           | 2010-2017  | 1 to 12         |
| Yellowfin tuna          | YFT   | Number per 100 hook             | 13158 | Catch         | Unknown           | 2010-2017  | 1 to 12         |
| Dolphinfish             | DOL   | Number per 100 hook             | 13158 | Catch         | Unknown           | 2010-2017  | 1 to 12         |
| Delphininae             | DELPH | Number along 10km segment       | 47    | Aerial survey | Day               | 2014       | 10, 11 and 12   |
| Globicephalinae         | GLOB  | Number along 10km segment       | 46    | Aerial survey | Day               | 2014       | 10, 11 and 12   |
| Ziphiidae               | ZIPH  | Number along 10km segment       | 37    | Aerial survey | Day               | 2014       | 10, 11 and 12   |
| Wedge-tailed shearwater | WTSH  | Occurrence of foraging behavior | 7413  | Tagging       | Day and night     | 2017       | 3 and 4         |
| Tahiti petrel           | TAPET | Occurrence of foraging behavior | 745   | Tagging       | Day and night     | 2017       | 8, 9, 10 and 11 |
| Red-footed booby        | RFBO  | Occurrence of foraging behavior | 3588  | Tagging       | Day and night     | 2012       | 5 and 6         |

from high-wing double engine aircrafts equipped with bubble windows, allowing a vertical observation of the sea surface. For each observation, group sizes were recorded at the lowest taxonomic level possible, alongside observation conditions (Beaufort sea-state, glare severity, turbidity, and cloud coverage). Animal observations were summed over 10 km segments of effort with homogenous weather conditions. Only segments with good weather conditions allowing detection were kept. The angle to the track line was also recorded for each observation, used with the flight altitude to calculate the perpendicular distance from the track line. Data are available on the PELAGIS Observatory website (<http://www.observatoire-pelagis.cnrs.fr>).

As the number of observations per species was relatively small, we grouped observations into trophic guilds based on morphological features, as defined by [Lambert *et al.*, 2014]. These authors used diving abilities as a proxy for energetic requirements to classify cetacean species into three guilds : Ziphiidae (ZIPH), Globicephalinae (GLOB) and Delphininae (DELPH) [Mannocci *et al.*, 2014a,b]. The DELPH guild was composed of *Lagenodelphis hosei*, *Stenella attenuate*, *Stenella longirostris*, *Tursiops truncates*, *Tursiops aduncus* and large and small delphininae unidentified. The GLOB guild was composed of *Globicephala macrorhynchus*, *Grampus griseus*, *Pseudorca crassidens*, *Peponocephala electra* and *Pseudorca* sp.. Finally, the ZIPH guild was composed of *Indopacetus pacificus*, *Ziphius cavirostris*, *Mesoplodon* sp., and *Ziphiidae* sp..

## Seabirds

Seabird data were obtained from tagging programs carried out during the breeding season of each species, in 2012 for red-footed booby (RFBO), and in 2017 for wedge-tailed shearwater (WTSH) and Tahiti

petrel (TAPET) (Table 6.1). For wedge-tailed shearwater, GPS-loggers were put on breeding adults during the chick-rearing period at four breeding sites. One study colony was located on Main Island of New-Caledonia, Pindaï (21.354°S, 164.954°E), where 37 breeders were equipped. The two other study sites were located in offshore islets : Mato islet (22.55°S, 166.80°E), where 20 breeders were equipped, and Canard islet (22.31°S, 166.31°E), where 11 breeders were equipped. Tahiti petrel were tagged at Canard islet and red-footed booby in the Chesterfield reef complex (19.3°S, 158.2°E).

Breeding adults were fitted with either 4.5 g Ecotone, 6 g Lotek, 5 g Pathtrack or 12.5 g TechnoSmart GPS-loggers, all representing less than 3% of animals' body weight ( $413 \pm 40$  g), so as not to modify their behaviour. The lightest GPS-loggers (Ecotone, Lotek and Pathtrack) were attached to three tail feathers using Tesa® tape, while the heaviest GPS-loggers (Technosmart) were back-mounted to not unbalance their flight. Locations were recorded every 15 minutes. Birds were captured by hand at their burrow entrance before feeding their chicks. Colonies were monitored every night to recapture birds for logger recovery.

The Expectation Maximization binary Clustering (EMbC) algorithm [Garriga *et al.*, 2016] was used to determine bird behaviour during their foraging trips. EMbC is a variant of the Expectation maximization algorithm in Maximum Likelihood Estimation of Gaussian Mixture Models : it is a robust multivariate clustering algorithm based on trajectory sinuosity and speed to identify animal behaviour. It assumes that wide turning angles between consecutive locations indicate a foraging behaviour, while fast and straight bouts are associated with commuting movement. EMbC assigned one of the four behaviours to each GPS location : resting (low speed, small turning angle), commuting (high speed, small turning angle), extensive search (high speed, wide turning angle) or intensive foraging (low speed, wide turning angle). Movement bouts including at least three consecutive 'Intensive foraging' locations were then conserved as 'presence of foraging' locations, while the others were considered as 'absence of foraging' locations for further analysis.

### 6.2.2 Explicative variables

Table 6.2 displays the environmental variables (and their spatial resolution) selected to explore drivers of predator abundance or occurrence. For each predator value, environmental data were extracted/predicted at the date and position of the observations.

#### Enviromental data

Bathymetry data were extracted from the ZoNéCo database at a 500m spatial resolution [ZoNéCo, 2013]. Sea Surface Temperature (SST) was extracted from the NOAA OI SST High Resolution Dataset at a daily resolution [Reynolds *et al.*, 2007]. The depth of the 20°C isotherm was extracted from the Armor3D dataset [Guinehut *et al.*, 2012] available at a weekly time scale. Surface chlorophyll-a was extracted from GLOBCOLOUR [Saulquin *et al.*, 2009] at a daily resolution. All variables were extracted on a  $\frac{1}{4}^\circ$  spatial grid.



TABLEAU 6.2 – Environmental variable summary with unit, source and resolutions detailed for each variable.

| Variable name              | Unit                             | Source  | Temporal resolution | Spatial resolution |
|----------------------------|----------------------------------|---|---------------------|--------------------|
| Bathymetry                 | km                               | ZoNéCo 2013   | -                   | 500 m              |
| Sea Surface Temperature    | °C                               | Advanced Very High Resolution Radiometer (AVHRR) infrared satellite | Day                 | ¼ degrees          |
| Chlorophyll-a              | mg/m <sup>3</sup>                | GlobColour-Processors versions : MODIS 2014.0.1/VIIRS 2014.0.2      | Day                 | ¼ degrees          |
| Depth of the 20°C isotherm | m                                | ARMOR3D   | Week                | ¼ degrees          |
| NASC                       | m <sup>2</sup> /nmi <sup>2</sup> | Receveur <i>et al.</i> 2019   | Day                 | ¼ degrees          |

### Prey data

Acoustic data (collection, processing, statistical models and outputs including validation) are presented in details in Receveur *et al.* [2019] (also Chapter 2). Hereafter, only the main information from those chapter are summarized.

Data were gathered from six cruises on board the R/V Alis in the New Caledonian EEZ over the period 2011 to 2017 where *in situ* acoustic data were recorded continuously using an EK60 echosounder (SIMRAD Kongsberg Maritime AS, Horten, Norway). Raw acoustic data were processed with the open-source Matecho software [Perrot *et al.*, 2018]. After data cleaning, the echo-integration of the 38kHz frequency was performed on cells of 1m-deep and 0.1nm-long, providing for each integrated cell the volume backscattering strength  $S_v$  data (dB.R.1.m<sup>-1</sup>) and the Nautical Area Scattering Coefficient (NASC)  $s_A$  (m<sup>2</sup>.nmi<sup>-2</sup>) a proxy for the prey biomass [Irigoien *et al.*, 2014] [MacLennan *et al.*, 2002]. The final dataset was composed of 16,715 vertical profiles ranging between 10 and 600m, with a 4m vertical bin and a 0.1nm horizontal bin only composed by day and night profiles (profiles from dawn and dusk were removed when organisms actively swim up or down, creating strong variability in backscatter values).

Acoustic vertical profiles were statistically linked to environmental conditions [Receveur *et al.*, 2019]. Using that model, a NASC vertical profiles were calculated, based on the environmental variables at a given position (in space and time). For each predator abundance/occurrence position, NASC profiles were predicted and then integrated over different vertical layers : 0-30m, 0-200m (*i.e.* epipelagic or ‘epi’), 200-400m (*i.e.* upper mesopelagic or ‘up\_meso’) and 400-600m (*i.e.* lower mesopelagic or ‘low\_meso’).

The vertical layer was then chosen depending on the predator. As the exact time of the day of catch data (ALB, YFT and DOL) was unknown, we first averaged NASC between day and night. Based on published knowledge of vertical habitats, epipelagic layer was kept for DOL [Furukawa *et al.*, 2014; Lin *et al.*, 2019], epipelagic and upper mesopelagic layers for YFT [Dagorn *et al.*, 2006; Schaefer *et al.*, 2009] and epipelagic and upper and lower mesopelagic layers for ALB [Williams *et al.*, 2014]. For cetacean (DELPH, GLOB and SIPH), aerial surveys were conducted during the day, so we took NASC values for the day period only. As vertical habitats of cetacean guilds were unknown, epipelagic, upper and lower mesopelagic layers were included. For seabirds (WTSH, TAPET and RFBO), GPS recorded the time of the day of locations. Based on their latitude/longitude, we calculated sun inclination at the time of each location [Blanc & Wald, 2012; Michalsky, 1988]. NASC values were then predicted based on this information and 0-30m integrated NASC layer was used, where seabirds dive and feed (Table 6.3).

TABLEAU 6.3 – Details of distribution models, with predator taxa, response variable, link function, distribution, offset to correct for sampling effort , explicative variables, and details of the nested model.

| Taxa                 | Response variable   | Link function | Distribution      | Offset               | Explicative variables  | Nested model  |
|----------------------|---------------------|---------------|-------------------|----------------------|--|---|
| ALB                  | Catch fish number   | log           | Negative binomial | Log(hooks number)    | SST, log_chlorophyll, d20, bathy, year, (lon,lat)<br>NASC_day_night by layer(epi, up_meso, low_meso) | Random effect by vessel                             |
| YFT                  | Catch fish number   | log           | Negative binomial | Log(hooks number)    | SST, log_chlorophyll, d20,bathy, year, (lon,lat)<br>NASC_day_night by layer(epi, up_meso)            | Random effect by vessel                             |
| DOL                  | Catch fish number   | log           | Negative binomial | Log(hooks number)    | SST, log_chlorophyll, d20, bathy, year, (lon,lat)<br>NASC_day_night_epi                              | Random effect by vessel                             |
| DELPH, GLOB and ZIPH | Animal count        | log           | Negative binomial | Log(sampled surface) | SST, log_chlorophyll, d20, bathy<br>NASC_day by layer(epi, up_meso, low_meso)                        | -   |
| WTSH, TAPET and RFBO | Foraging occurrence | cloglog       | Binomial          | -                    | SST, log_chlorophyll, d20, bathy<br>NASC_day_0-30m by moment(day, night)                             | Random effect by individual with an autocorrelation |

### 6.2.3 Statistical analysis

GAMs (Generalized Additive Models) [Hastie & Tibshirani, 1995] were used to examine relationships between predator abundance/occurrence and a suite of predictors. In GAMs, the response variable depends linearly on unknown smooth functions of some covariates, here the explicative variables described in Table 6.2 (e.g. bathymetry, SST, chlorophyll-a, d20 and NASC). Before constructing models, we confirmed that collinearity was not apparent among the predictors using Spearman correlations between each pair of covariates. We considered that covariates were not collinear when Spearman correlations were below 0.5 [Louzao *et al.*, 2011]. All variables were smoothed with cubic splines with a maximum knot number of eight to prevent overfitting. All GAMs were fitted in R (version 3.5.0, R Core Team 2018) using the *mgcv* package (Wood, 2017) .

Partial dependence plots were produced for each environment variable to visually explore their marginal effect on the response variable while other variables were fixed to their mean values [Friedman, 2001]. Models were fitted successively, excluding each of the remaining terms one at a time, to assess the percentage of variation explained by each predictor and to classify predictors according to the magnitude of their influence in the model. The nine GAMs were constructed differently depending on the nature of the response variable, and therefore were different for fish, cetacean and seabirds (Table 6.3).

## Tuna and dolphinfish models

For tuna and dolphinfish, the response variable was the number of animals caught. A negative binomial distribution was used and the mean of the response variable was related to the additive predictor by a log-link function (Table 6.3). To take into account the variability in fishing effort between trips, the logarithm of the number of hooks was added as an offset. A random effect by vessel was also fitted to deal with the variability in catchability between vessels. The year was also added as a continuous explicative variable to assess a possible change across years. Finally, a spatial smoothing in latitude and longitude was added to limit spatial autocorrelation. From this model, catch was predicted and then divided by the number of hooks in order to show CPUE, a fish abundance proxy.

## Cetaceans models

For cetaceans, the response variable was the number of animals counted along the track of the airplane segments of approximately 10 km. A negative binomial distribution was used and the mean of the response variable was related to the additive predictor by a log-link function (Table 6.3). For each guild, we used a unique effective strip width (ESZ) estimated by [Laran \*et al.\* \[2016a\]](#) [[Marques & Buckland, 2004](#)]. The ESZ could be interpreted as the effective distance from the plane at which animals could be detected. The sampled surface area for each single transect was the transect length multiplied by twice the corresponding associated ESW. The log-transformed sampled surface area was added as an offset in the model to account for the variability in sampled effort. Using this model, the number of individuals was predicted, and then divided by the surface in order to have an animal number by km<sup>2</sup>.

## Seabirds models

For seabirds, the response variable was the presence/absence of foraging behavior. We used a binomial distribution and the mean of the response variable was related to the additive predictor by a log-log-link function (Table 6.3). To account for autocorrelation between consecutive behaviors, we used a Generalized Additive Mixed Model (GAMM). We nested an autocorrelation structure of order three with a random effect fitted by individual to deal with the correlation structure [[Dormann \*et al.\*, 2007](#); [Wood, 2006](#)]. Using this model, the occurrence probability of animals foraging was predicted.

## 6.3 Results

### 6.3.1 Data collection

#### Predators data

ALB, YFT and DOL datasets were composed of 13,158 observations, ranging from 117 to 648 observations per month between 2011 and 2017. Number of fish caught by 100 hooks ranged between 0 and 5.5 (ALB), 0 and 2.4 (YFT) and 0 and 1.6 (DOL). The EEZ was used almost entirely by fishing vessels except

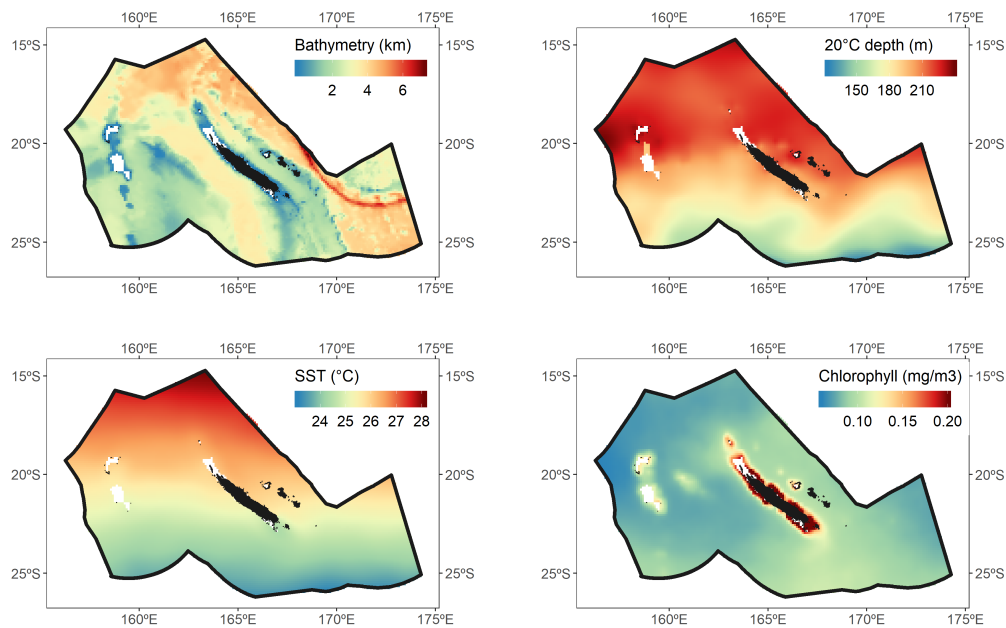


FIGURE 6.2 – Spatial patterns of environmental variables averaged from 2011 to 2017 and over all months.

for the southeast corner (Figure 6.1). Data for cetacean were more spatially sparse, with a lower spatial and temporal coverage than catch data. Number of animals counted for DELPH ranged from 1 to 100, from 1 to 230 for GLOB (with only two very large groups), and from 1 to 6 for ZIPH (Figure 6.1). Moreover, surveys only took place during three months in 2014. Concerning seabirds, month sampled were limited by the breeding season of each species, when animals were present in New Caledonia (Table 6.1). The number of foraging occurrences largely differed, with more than 7,000 observations for WTSH (including 2659 foraging behaviors), more than 3,000 for RFBO (including 1,064 foraging behaviors), and less than 1,000 for TAPET (including 234 foraging behaviors). The observations of TAPET and RFBO were spatially limited to the proximity of the unique colony where they were tagged (in the south for TAPET and in the northwest for RFBO).

### Environmental and prey layers

Mean 20°C isotherm depth was shallow in the south and deep in the north with deepest values found west of the Chesterfield reef complex (Figure 6.2). Waters had relatively warmer SST in the north and colder SST in the south. Chlorophyll concentrations were high close to coast and reefs, and generally higher in the south than in the north. Bathymetry is complex in the EEZ, with deep waters in the north and the southeast, shallower waters in the southwest corner and below Main Island.

NASC values were integrated over different vertical layers and for different time periods. As for SST and the 20°C isotherm depth, NASC spatial distribution showed a strong longitudinal gradient, especially during the night (Figure 6.3). During the day, between 0 and 30 m, the largest NASC values were close to the coast of the Main Island and the Loyalty Islands. The 0-200m and 400-600m integrated NASC were higher in the south than in north, with the exception of the waters southeast of the Main Island that had weaker NASC values than the rest of the southern region. At the opposite, this same area had higher NASC values than the surrounding southern region in the 200-400m vertical layer during the day. During

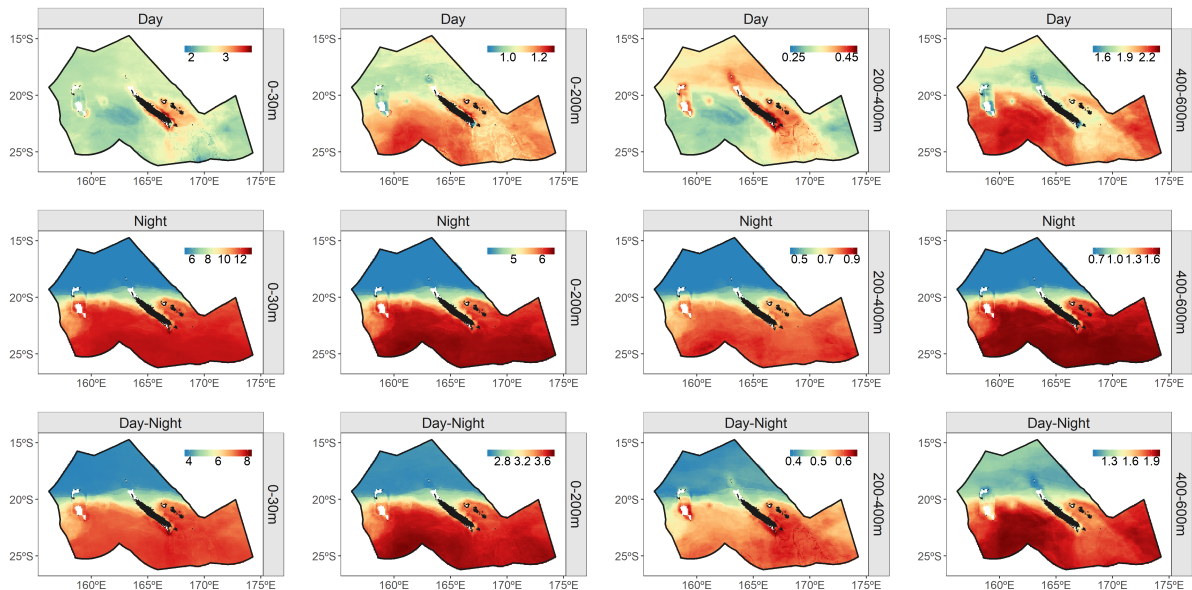


FIGURE 6.3 – Spatial patterns of NASC values during the day (first row), during the night (second row) and on average between day and night (third row) integrated over four vertical layers : 0-30 m (first column), 0-200 m (second column), 200-400 m (third column) and 400-600 m (fourth column).

the night, NASC values were higher in the south than in north for the four vertical layers considered, with values almost twice as high in south. After averaging day and night predictions, mean NASC night-day patterns were similar to night patterns.

### 6.3.2 Environmental drivers of predator distribution

#### Link to prey distribution

We checked residuals for the nine models using the quantile residuals [Dunn & Smyth, 1996] : residuals variances were constant, residuals were independent, and neither predicted values and residuals nor explicative variables and residuals were statistically linked.

Total deviance explained by model ranged from 10.7% (TAPET) to 58.6% (RFBO), with an average of 30% (Table 6.4). The NASC variable had a relatively small influence in all models. It ranked second for WTSH, three for DOL and RFBO. Then, it was at the fourth place for YFT and DELPH, and at the last position for ALB, GLOB (non-significant), ZIPH (non-significant) and TAPET (non-significant).

ALB and DOL had bell-shaped relationships to NASC values. ALB optimum were around 1.5 for the lower mesopelagic layer and around  $3.5\text{m}^2/\text{nmi}^2$  for the epipelagic layer. DOL optimum was  $3.2\text{m}^2/\text{nmi}^2$  for the epipelagic layers (Figure 6.4). The two YFT relationships to NASC were decreasing, more quickly for the upper mesopelagic than for the epipelagic. For the three species, the influence of NASC was relatively small compared to the total deviance explained (Table 6.4).

Relationships to NASC were weak and non-significant for GLOB and ZIPH (Figure 6.4) and deviance explained by NASC variable was low for the three cetacean taxa (Table 6.4). DELPH was linked to upper mesopelagic NASC with a positive relationship.

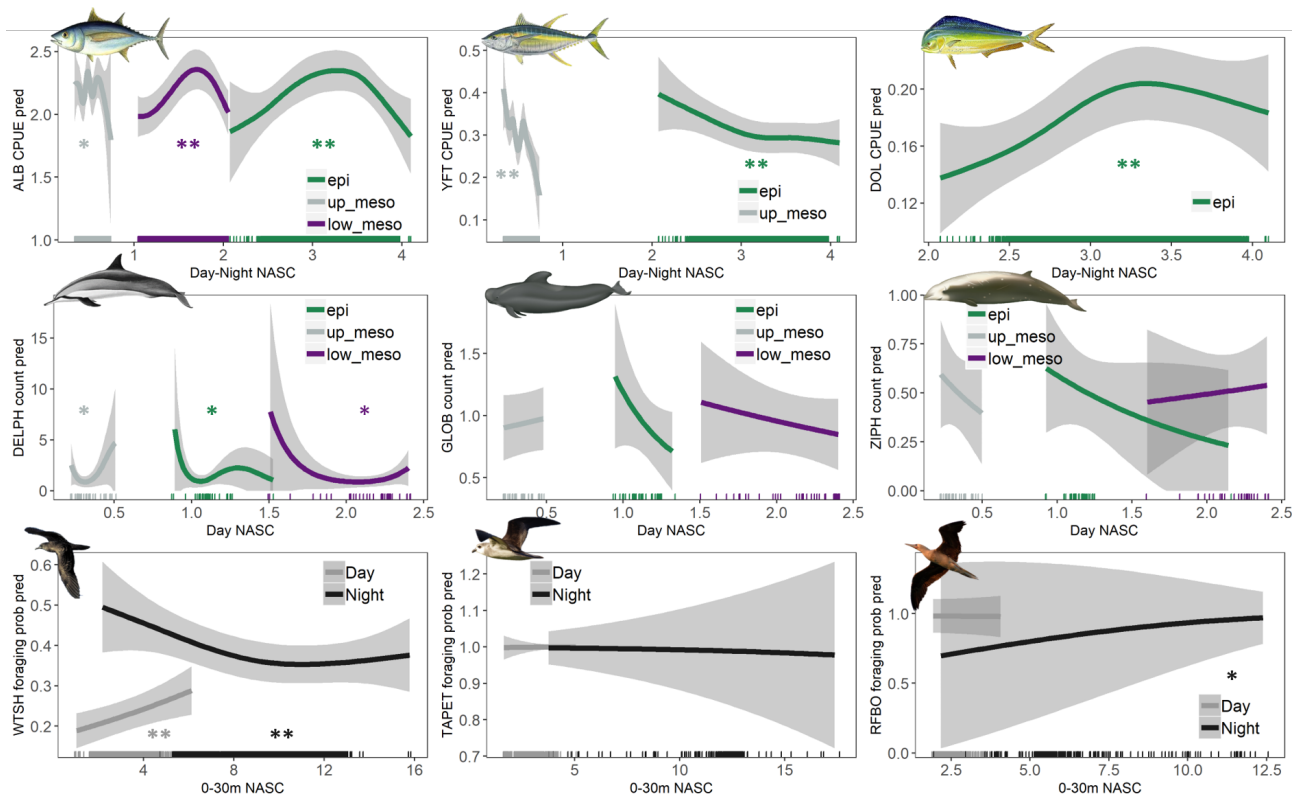


FIGURE 6.4 – Predators’ modelled responses to NASC variations (CPUE for tuna and dolphin fish, animal counts for cetacean, and foraging probability for seabirds). Colors indicate different vertical layers for tuna and cetacean, and time of day for seabirds. The solid grey ribbons show the confidence limits of the model and are twice the standard error. Stars colored by the factor (vertical layer or moment) show the significant level : two stars (\*\*) for highly significant (p-value < 0.01), one star (\*) for slightly significant (p-value between 0.01 and 0.1) and no star for non-significant.

TABLEAU 6.4 – Total deviance explained (second column) by model and for five explicative variables ordered by the importance of their influence. *Italic names show non-significant variables and bold names emphasize NASC's rank. All values are percentages.*

|       |      |                       |                       |                              |                       |                                 |
|-------|------|-----------------------|-----------------------|------------------------------|-----------------------|---------------------------------|
| ALB   | 22.8 | Bathymetry<br>(9.3)   | D20<br>(8.3)          | SST<br>(4.1)                 | Chlorophyll<br>(2.1)  | <b>NASC(1.1)</b>                |
| YFT   | 17.5 | Chlorophyll<br>(4.2)  | Bathymetry<br>(3.1)   | D20<br>(2.6)                 | <b>NASC<br/>(1.3)</b> | SST<br>(1.2)                    |
| DOL   | 29.5 | Chlorophyll<br>(19.3) | SST<br>(7.9)          | <b>NASC<br/>(2.0)</b>        | D20<br>(1.5)          | Bathymetry<br>(0.4)             |
| DELPH | 25.1 | Chlorophyll<br>(4.8)  | D20<br>(1.7)          | SST<br>(2.0)                 | <b>NASC<br/>(0.1)</b> | Bathymetry<br>(0.09)            |
| GLOB  | 33.9 | SST<br>(20.1)         | D20<br>(13.7)         | Bathymetry<br>(4.9)          | Chlorophyll<br>(4.2)  | <b>NASC<br/>(3.6)</b>           |
| ZIPH  | 51   | Bathymetry<br>(28.7)  | Chlorophyll<br>(18.9) | D20<br>(14.5)                | <i>SST<br/>(8.8)</i>  | <b>NASC<br/>(1.6)</b>           |
| WTSH  | 25.6 | Bathymetry<br>(14.7)  | NASC<br>(1.5)         | SST<br>(1.3)                 | D20<br>(0.8)          | <i>Chlorophyll<br/>(0.05)</i>   |
| TAPET | 10.7 | Bathymetry<br>(4.5)   | SST<br>(3.2)          | <i>Chlorophyll<br/>(0.5)</i> | <i>D20<br/>(0.2)</i>  | <b>NASC<br/>(0.1)</b>           |
| RFBO  | 58.6 | Bathymetry<br>(26.9)  | D20<br>(6.8)          | <b>NASC<br/>(0.5)</b>        | SST<br>(0.2)          | <i>Chlorophyll<br/>(0.0003)</i> |

Finally, there was no link between NASC values and TAPET foraging probability (Figure 6.4) and NASC ranked last by importance. WTSH had linear positive relationships to 0-30m NASC values during the day and a negative relationship with a large confidence interval during the night. NASC variable had the second place in term of importance for this species. RFBO was positively link to NASC values during the night, with higher foraging probability for high NASC values. Despite his third place, NASC relative importance in RFBO model was relatively weak (Table 6.4).

### Other oceanographic drivers

Among tuna species and dolphinfish, the four other environmental covariates were always significant but the importance of their influence ranked differently across species (Table 6.4). YFT and DOL were first driven by chlorophyll and ALB by bathymetry. The latter came second for YFT and SST came second for DOL.

Generally, optimal environments for the tested explicative variable were different across the three species (Figure 6.5) : ALB catches were predicted largest for intermediate bathymetry (around 4km), whereas YFT catches were highest for shallow bathymetry and DOL catches were highest for deep bathymetry. YFT catches were predicted maximal for intermediate chlorophyll values, whereas DOL catches were highest for low chlorophyll values. In the same way, cold SST were favorable to ALB catch whereas warm SST increased YFT and DOL catches; and deep 20°C isotherm depth for ALB and DOL catches, contrary to shallow depth for YFT catches (Figure 6.5).

Environmental variables influences among cetacean guilds were different : DELPH was mostly influenced by chlorophyll, GLOB by SST and ZIPH by bathymetry (Table 4). Higher occurrences of DELPH were predicted in waters with low chlorophyll concentration and a 20°C isotherm depth around 170m.

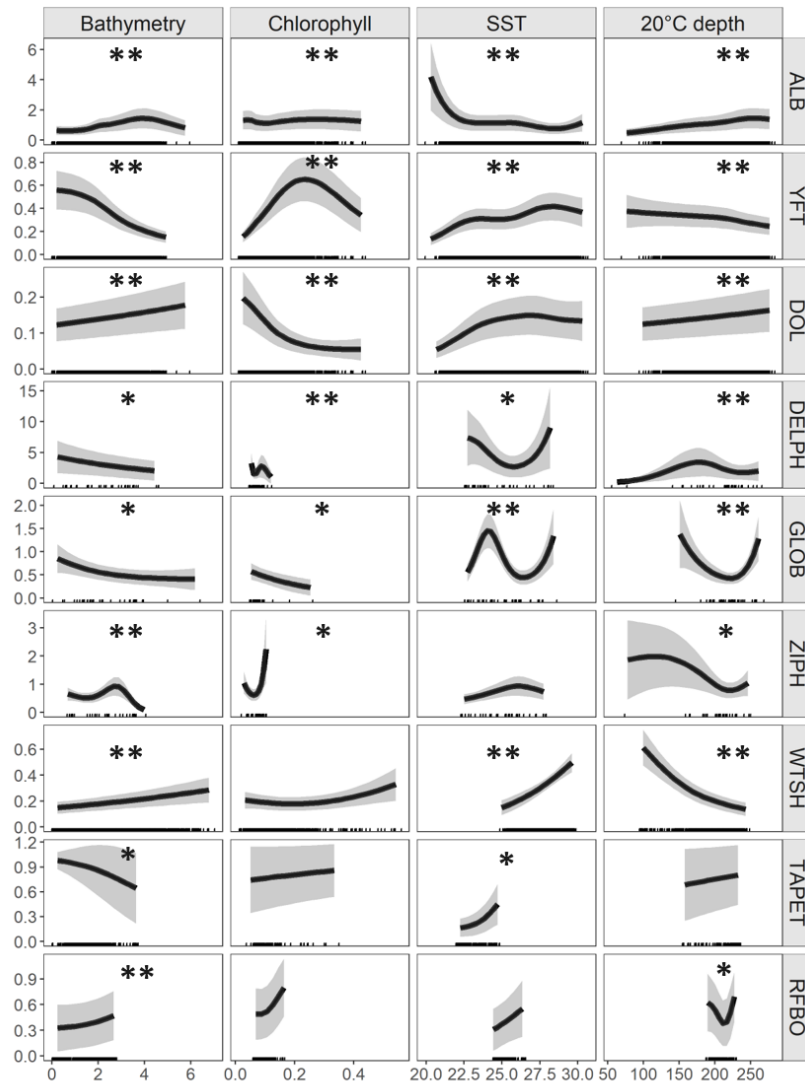


FIGURE 6.5 – Predators’ modelled responses (by rows) to four environmental variables (by columns). The solid grey ribbons show the confidence limits of the model and are twice the standard error. Stars show the significant level : two stars (\*\*) for highly significant ( $p$ -value < 0.01), one star (\*) for slightly significant ( $p$ -value between 0.01 and 0.1) and no star for non-significant.

GLOB were predicted to be more abundant when the 20°C isotherm depth was extreme (very shallow or very deep), and both in waters with SST around 24°C and with SST warmer than 27°C. Finally, ZIPH were predicted abundance was especially high in waters with a bathymetry around 3km and with large chlorophyll concentrations (Figure 6.5).

The three seabirds species foraging behavior were primarily influenced by bathymetry, but with contrasting optimal values : WTSH and RFBO mostly fed in deep waters while TAPET fed in shallow waters (Figure 6.5). Secondly, WTSH foraging behavior was influenced by NASC values integrated between 0 and 30m deep, and in a third place by warm SST. TAPET was also predicted to be more likely to feed in waters with warm SST. Finally, RFBO foraging behavior was also influenced by the 20°C isotherm depth, with more feeding predicted to occur in extreme values (very shallow or very deep isotherm).



### 6.3.3 Spatial distribution predictions

Based on environmental and NASC layers, we predicted the spatial distribution of the nine predators in the New Caledonian EEZ. In order to avoid predictive extrapolation, we limited predictions to sampled environmental variable ranges.

#### Predators spatial distribution

ALB, YFT and DOL CPUE spatial predictions did not spatially overlap. High ALB CPUE were predicted overall west of the diagonal marked by the Main Island. The largest CPUE were predicted west of Chesterfield reef complex (Figure 6.6), with the exception of a small area directly surrounding the Chesterfield and Bellona reefs. On the opposite, high predicted YFT CPUE were found in this small area. The highest YFT CPUE were predicted close to the lagoon, around the Main Island and to a lesser extent around the Loyalty Islands. Finally, the EEZ southeast corner, and around the Loyalty Islands were predicted favorable to DOL CPUE. Standard error predicted by models were larger in the southeast for YFT and DOL predictions, and in the south for ALB predictions (Figure 6.7).

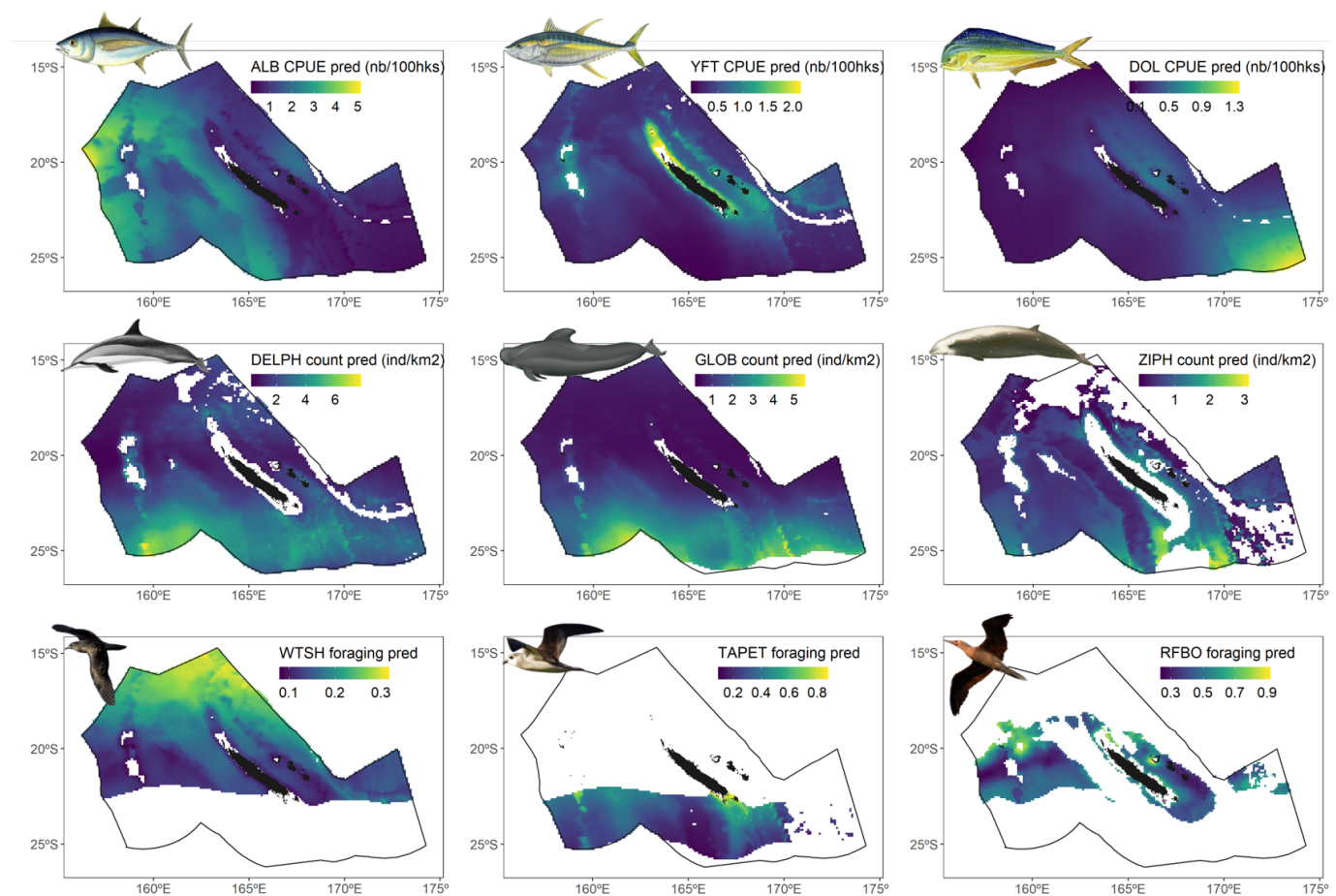


FIGURE 6.6 – Spatial predictions for the nine predators included in this study. Top : predictions of Albacore (ALB) and yellowfin (YFT) tuna catch per unit of effort (CPUE) in number of fish caught per 100 hooks. Middle : predictions of Delphininae (DELPH), Globicephalinae (GLOB) and Ziphiidae (ZIPH) cetacean count. Bottom : predictions of wedge-tailed shearwater (WTSH), Tahiti petrel (TAPET) and red footed booby (RFBO) foraging behavior probability.

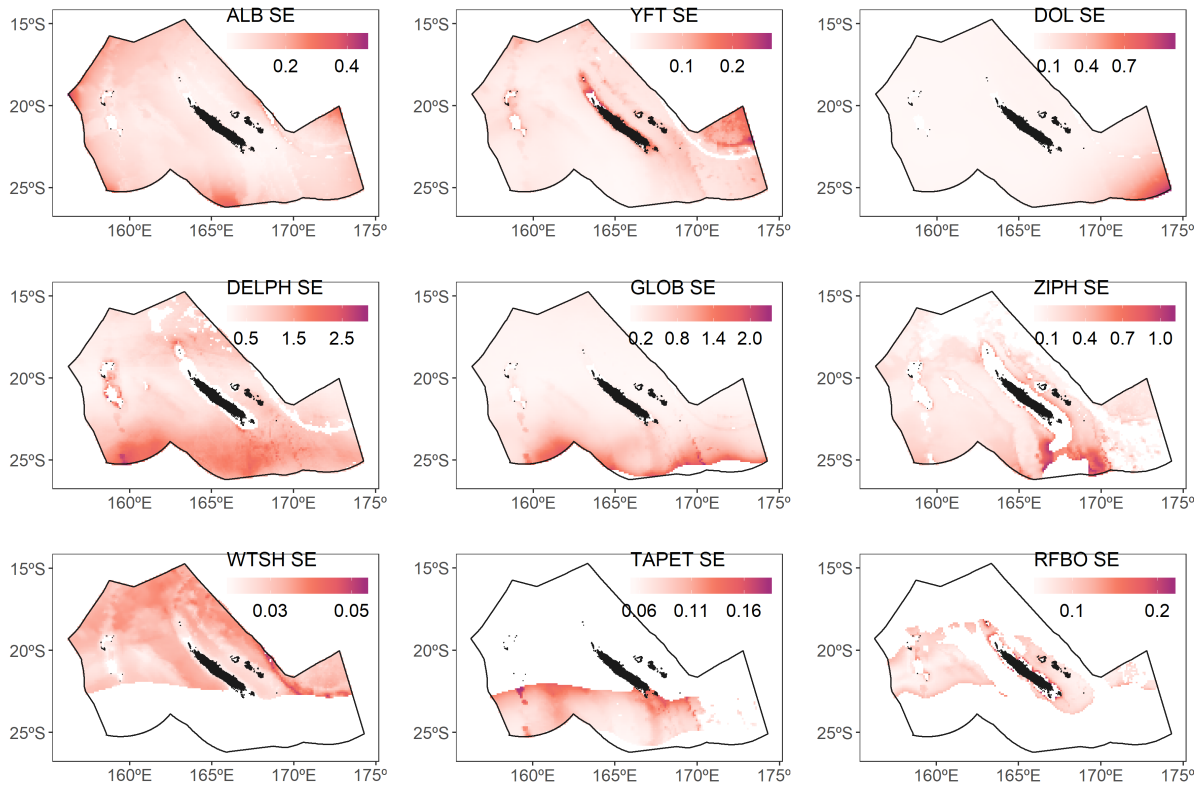


FIGURE 6.7 – Standard error (SE) predicted by the models (grey ribbons on Figure 2 and 3) for the nine spatial predictions in the same unit than for Figure 6.6.

For cetaceans, numerous DELPH were predicted in the EEZ southwest, with a hotspot south of Chesterfield and Bellona (Figure 6.6). Similarly, GLOB were concentrated in the extreme south of the EEZ. ZIPH predictions showed a tight link with bathymetry, as the highest number of ZIPH were predicted in waters with intermediate bathymetry in the south, identified in the GAM's output (Figure 6.3) to be approximately 3000m deep. For the three cetacean guilds, predicted standard error were large wherever the predicted values of abundance were high (Figure 6.7).

Finally, seabird spatial patterns of foraging probability were assessed (Figure 6.6). WTSH seemed to feed north of 19°S. TAPET was predicted to mostly feed in waters south of the Main Island and south of Bellona, but with a large standard error predicted for the latter area. None of the northern environmental conditions were sampled, limiting predictions to the EEZ southern part. Finally, RFBO predictions were scattered around the EEZ mid-latitudes, with two small feeding hotspots identified : around the northernmost Loyalty Island, Ouvea, and northeast of Bellona.

### Spatial overlap between predicted predator maps

The 75% and 50% kernel for each predator taxon were extracted from the predicted maps of abundance/foraging (Figure 6.8A). A predicted value overpassing the 75% quantile by taxa was classified as 'predicted occurrence'. Then for each spatial cell, the number of predicted occurrence was counted and divided by the total number of predictions of this cell to normalize. The resulting values were mapped to approximate the cumulated distribution of predator taxa and identify regions concentrating predators.

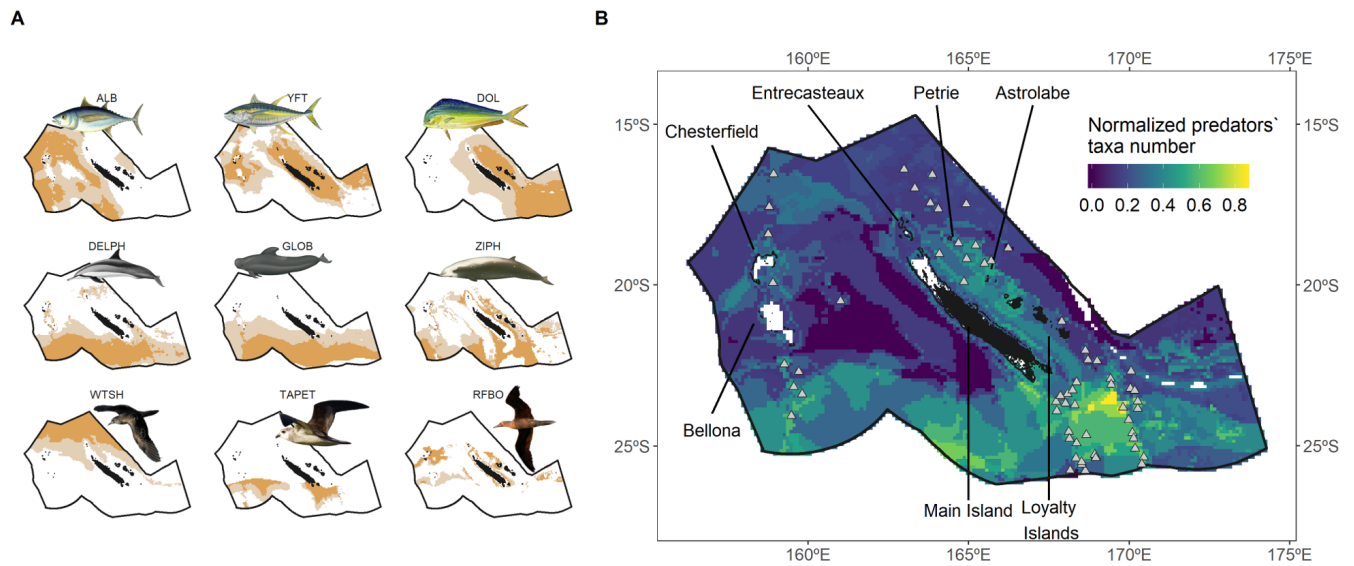


FIGURE 6.8 – 75% (dark brown) and 50% (light brown) kernel densities for each predators (panel A) and normalized predicted number of predators (*i.e.* number of 75% predator predicted occurrences divided by the total number of predicted occurrences per cell) (panel B). Grey triangles indicate the location of a selection of seamounts gathered from [Allain *et al.*, 2008].

Maps of the normalized predicted cumulated occurrence of taxa showed a slight north-south gradient, with relatively higher numbers of predators taxa in the south where there are numerous seamounts (Figure 6.8B). A large region northeast of the Main Island, covering the Petrie and Astrolabe reefs, was identified with a relatively high predicted occurrence of predator taxa, as well as in the region surrounding the Chesterfield reefs.

## 6.4 Discussion

Understanding the ecological processes that underpin species distribution patterns is a fundamental goal in spatial ecology. In the present study, the distribution of nine groups of top predators was modelled to provide a multi-trophic assessment of the ecological niches of pelagic communities. Previous studies in New Caledonia have focused on specific taxa, such as seabirds [Benoit & Bretagnolle, 2002; Robinet *et al.*, 1997], cetaceans [Derville, 2018; Garrigue *et al.*, 2015], shark [Boussarie *et al.*, 2018] and albacore [Briand *et al.*, 2011; Williams *et al.*, 2014]. This study therefore provides the first step towards an integrated view of multiple marine predator distributions across the New Caledonian pelagic ecosystem. Nine top predators were analysed at the same time : albacore tuna, yellowfin tuna, dolphinfish, Delphininae, Globicephalinae, Ziphiidae, wedge-tailed shearwater, Tahiti petrel and red-footed booby. Prey relative abundance data collected using acoustic methods (NASC) was tested together with static (bathymetry) and dynamic oceanographic descriptors (SST, chlorophyll and 20°C isotherm depth) to improve predator distribution models. Preyscape affected six predator distribution patterns out of nine (ALB, YFT, DOL, DELPH, WTSH and RFBO). Spatial distributions predicted for ALB, YFT and DOL did not overlap. DELPH, GLOB and ZIPH predictions were concentrated in the south whereas WTSH used the north of the EEZ to feed. The small datasets for TAPET and RFBO made complicated robust conclusions.

### 6.4.1 Sources of uncertainty

#### Predators' dynamics

Fishing vessels in New Caledonia are relatively homogeneous in term of fishing capabilities and only include long-liners [WCPFC, 2018]. By including vessel random effect, we took into account potential variability of fishing power between vessels due to different vessel sizes for example, or to more or less efficient hooks, or to differences in hooks fishing depth. By including the effort (number of hooks here) as an offset, we transformed catches into CPUE therefore used as a proxy of fish abundance accounting for effort. CPUE are also linked to fishing power of vessels and species catchability. Hence, large CPUE changes can be erroneously measured where only small abundance changes exist [Kleiber & Maunder, 2008]. However, given the large sample used and the precautions by including a vessels random effect, our CPUE predictions could constituted a robust proxy to species abundances.

Cetacean distributions were assessed through counting performed during the REMMOA aerial surveys [Laran *et al.*, 2016a]. This relatively low-cost method can be advantageously implemented with a great flexibility, which allows a quick reaction to changing weather conditions [Mannocci *et al.*, 2013]. However, compared to CPUE data for instance, REMMOA surveys only occurred once in New Caledonian EEZ and only spanned three months. The surveys gave a snapshot of animal presence and partial distribution over a short period. Moreover, cetaceans are highly mobile predators and their behaviors were not identified by observers. Animals could have been travelling between two favorable habitats when there were detected and therefore the oceanographic conditions attributed to that group were not necessarily optimal habitats. We assumed that to improve our niche modeling and therefore to have a better comprehension of species habitats, more cruises are needed to overpass the “snapshot problem”. Moreover, the aerial surveys had three other major limitations : observers do not detect animals under the surface, observers may miss some animals at the surface, and observers may miss-recognize species [Pollock *et al.*, 2006]. To deal with the miss-recognizing, planes could be equipped with camera taking pictures upon detection.

Finally, seabird feeding behaviors were analyzed with tracking data. As seabirds spend most of their time at sea in order to forage during the breeding season, we assumed that the foraging probability was a good indicator of seabird probability of presence and therefore of the seabirds' distributions during the breeding season. Another limitation of tagging data is the commonly small sample sizes that badly capture inter-individual behavioural variability. For instance, we used data from 47 individuals for WTSH, the largest seabirds' dataset, while up to 500,000 wedge-tailed shearwaters pairs are estimated to breed in New Caledonia. In addition, uncertainty may come from the clustering step (EMbC, Garriga *et al.* 2016) to identify the behavior of seabirds based on their sinuosity and speed. A sensitivity analysis of EMbC parameters would certainly help to identify robust foraging patterns. By selecting only the intensive foraging observations occurring for more than three consecutive positions, we offered an approach to filter-out the shortest foraging bouts and to ensure that the animals were truly foraging when classified as such.

## Prey layer distribution

Previous studies have emphasized the large added value in collecting acoustic data simultaneously with megafauna observations [Louzao *et al.*, 2019a], which is made possible by using monitoring systems such as integrated oceanographic surveys [Doray *et al.*, 2018]. Our study suggested an alternative whereby prey abundance is estimated during surveys focusing on low trophic levels, and then subsequently compared to a large number of predators observations coming from other surveys. Such approach is not applicable with other more discrete prey sampling techniques (Torres *et al.* 2008, trawling, *i.e.*). It provided a suitable dataset for modelling predator distribution in relation to their prey without observing predators and prey at the same time.

The strength of our acoustics modeling framework was the possibility to average prey relative abundances over different vertical layers. Therefore, prey layers could be adapted to the predators' vertical feeding habitats that most illuminate prey-predator relationships. The differences in spatial patterns during the day of integrated NASC values over layers 0-30 m and 0-200 m (Figure 6.3) supported the importance to extract specific vertical layers to analyze prey-predator relationships. Integrating more 3-dimensional biotic and abiotic variables in predator niche modeling is a necessity to be able to define 3-dimensional oceanographic habitats used by marine species [Brodie *et al.*, 2018; Lambert *et al.*, 2014; Louzao *et al.*, 2019b].

All prey layers were based on Receveur *et al.* [2019] methodology who used a statistical framework to link acoustics vertical profile to environmental variables. The present study assumed that predicted micronekton vertical distribution were realistic and so was the micronekton relative abundance variation. They showed that for a given observed acoustic value (measured through the backscatter echo intensity,  $S_v$ ), the predicted echo intensity could vary +/- 10dB, which could result in large biomass changes [Benoit-Bird, 2009; Proud *et al.*, 2018b]. They also demonstrated that predicted echo-intensity variations matched observed echo-intensity variations (see Figure 11 in Receveur *et al.* 2019) that were needed in the present study. Indeed, to assess NASC's influence on predators' behaviour, we presumed that realistic spatial, vertical and temporal NASC gradients were more informative than exact absolute NASC values. Receveur *et al.* [2019] noticed that the use of the 38kHz frequency favored detection of organisms with swimbladders (mostly fish) while excluding other organisms without gas-filled swimbladders [Davison *et al.*, 2015a], which may bias spatial variations of prey species composing predators' diets. Nevertheless, given the large diversity in predator's diets [Duffy *et al.*, 2015; Olson *et al.*, 2014; Williams *et al.*, 2014] and the difficulty to transform acoustic signal into species biomass [Davison *et al.*, 2015a; Proud *et al.*, 2018b], we used NASC values as an overall proxy of the relative abundance of prey available for all predators. Going further into acoustic signal separation into species groups (as fish, gelatinous, crustacean) would allow to link each predator to their favorite preys. However, given the diversity of preys present in the region (Chapter 3), assigning acoustic intensity to prey species will constitute a real challenge.

The last limitation was the potential absence of organism shoals. Indeed, our framework firstly clustered all vertical profiles into ten groups, allowing to keep only persistent structure in prey vertical distribution but removing less frequent features as shoals. Previous studies highlighted the importance of shoal formations in the feeding behavior of some predators [Benoit-Bird *et al.*, 2013; Bertrand *et al.*, 2002a, 2014; Carroll *et al.*, 2017; Ménard & Marchal, 2003; Williams *et al.*, 2014]. As we removed shoals

from our prey layers, we were not able to test their influence on predators' distribution. Moreover, we were not able to analyze the fine spatial scale that we removed from the acoustic signal, although it is known to be an important component of foraging behaviors [Benoit-Bird & Au, 2003; Bertrand *et al.*, 2014; Grados *et al.*, 2016].

Finally, developing predictive models of habitat use is challenging for species that forage in marine environments, as both predators and prey are often highly mobile and difficult to monitor. Previous studies incorporated SEAPODYM prey population dynamics outputs [Lehodey & Maury, 2010; Lehodey *et al.*, 2008] to their predator niche models for tuna [Briand *et al.*, 2011], seabird [Miller *et al.*, 2018] and cetacean [Lambert *et al.*, 2014]. The statistical method developed here based on observed acoustics is an alternative to using such modelled prey distribution from population dynamics model. The approach allowed to study predator-prey relationships at a regional scale, but required the acoustic observation at this vast spatial scale. Conducting more acoustic surveys would allow to refine prey distribution models and therefore would improve prey implementation into predator niche models.

#### 6.4.2 Environmental drivers of predators distribution

Tuna and dolphinfish species were strongly influenced by SST, as shown previously by Kleisner *et al.* [2010]. YFT and DOL preferred warm SST, whereas ALB's optimal temperatures were colder [Bertrand *et al.*, 2002b]. For foraging, ALB and DOL were linked to NASC values with a bell-shaped relationship whereas YFT was negatively linked to NASC values (Figure 6.2). ALB's relationships to NASC values were in total agreement with previous results found in the New Caledonian EEZ using the SEAPODYM outputs as prey data source. Briand *et al.* 2011 showed a negative relationship to upper mesopelagic layer (that they called 'mesopelagic') and a bell relationship to epipelagic layer. In order to explain the negative relationship to upper mesopelagic prey, they assumed that the increase in prey abundance induces a competition for baited hooks placed in this layer; a hypothesis confirmed by another albacore study in French Polynesia [Bertrand *et al.*, 2002b]. This hypothesis would explain the two YFT negative relationships to NASC values.

ALB, YFT and DOL were shown to utilize comparable foraging resources and have similar niches [Teffer *et al.*, 2015], especially for YFT and DOL in the Pacific [Young *et al.*, 2010]. We showed a different result with a relatively weak distribution overlap between the three species (except for DOL and YFT east of Main Island, Figure 6.8A) and different relationships to environmental predictors (Figures 6.2 and 6.3). We hypothesized that at the Pacific Ocean scale, ALB, YFT and DOL have similar large distribution but at a regional scale, the three species divided the space and the foraging resource. Bertrand *et al.* [2002a] showed that tuna were more abundant in waters rich in prey and with favorable hydrological conditions at a regional scale, and were attracted by small prey patches at a small scale in the southeast Pacific. We confirmed this result at a regional scale for ALB, but we found that YFT was more attracted by waters with relatively low prey abundance. Finally, the 20°C isotherm depth was relatively important for the two tuna species. The 20°C isotherm depth is a proxy for vertical habitat change, and is strongly linked to catchability changes. Therefore, part of the abundance changes linked to the 20°C isotherm depth may reflect catchability changes rather than a true ecological relationship.

REMMOA surveys of cetaceans were performed in several other places (French Polynesia, Mozam-

bique channel, Bay of Biscay, French Antilles...) and cetacean niche modeling has been published for all these other regions [Lambert *et al.*, 2016, 2014; Mannocci *et al.*, 2013, 2014a, 2015]. In New Caledonia, bathymetry strongly influenced GLOB and ZIPH distribution, as also shown by Laran *et al.* [2016b] in the bay of Biscay. Relationships to NASC values were non-significant for GLOB and ZIPH, whereas it was significant for DELPH, although only explaining a small part of the total explained deviance. Moreover, the shapes of the NASC relationships were different from those found by Lambert *et al.* [2014] in the Indian Ocean and in French Polynesia using SEAPODYM outputs. The cetacean dataset was certainly too small to fit relevant predator-prey spatial relationships. The positive relationships between epipelagic and upper mesopelagic NASC and DELPH and GLOB counts, and between mesopelagic and ZIPH counts suggests that vertical foraging habitats of ZIPH species were probably deeper than that of DELPH and GLOB. This result would confirm previous conclusions from the East Atlantic [Lambert *et al.*, 2014].

Finally, seabird relationships to oceanographic conditions were in agreement with previous results acquired nearby in Australia [McDuie *et al.*, 2018]. Bathymetry had the strongest influence on either of the three species [Catry *et al.*, 2009]. WTSH and RFBO seemed to have similar foraging habitats in deep waters and with high chlorophyll concentration, whereas TAPET preferred shallow waters. The three species were predicted to feed more in warm waters. Relationships to the 20°C isotherm depth were mostly negative for WTSH and RFBO. Fronts of oceanic eddies have been shown to largely influence seabirds' foraging behavior [Jaquemet *et al.*, 2014; McDuie *et al.*, 2018; McDuie & Congdon, 2016; Tew Kai & Marsac, 2010; Tew Kai *et al.*, 2009] and the 20°C isotherm depth is a proxy to characterize these meso-scale features.

WTSH relationship to NASC values was positive only during the day : the higher the NASC values, the higher the foraging probability was. This night-day difference in NASC relationships showed that WTSH may be visually searching for food during the day and can locate prey strong concentrations of prey at the surface, whereas during the night they might be using other feeding technics. TAPET did not target region with high prey abundance but stayed in shallows waters with high chlorophyll concentration. The facilitation of seabird foraging in association with other top predators has been observed in different regions, increasing seabirds' foraging probability when other predators are present [Miller *et al.*, 2018; Weimerskirch *et al.*, 2005]. At the regional scale, we did not find similar results with a globally low overlap between seabirds and tuna/cetacean spatial distributions.

### 6.4.3 Predator niche modeling

In addition to the uncertainty due to the source of predators and prey data, the nine GAMs also had their own limitations. For cetaceans, the small number of observations did not allow us to split analyzes at species level. In order to increase the dataset power to study cetacean-prey relationships, it was necessary to group cetacean species into three trophic guilds based on [Lambert *et al.*, 2014; Mannocci *et al.*, 2014b; Weimerskirch *et al.*, 2005]. This approach may be disadvantageous as it could smooth out some relationships to environmental conditions, by mixing together potentially different species-specific optimal habitats. In addition, even when pooling data into wider groups, the observations of cetaceans, TAPET and RFBO were too few to robustly evaluate the influence of NASC, resulting in a relatively low effect of NASC compared to other oceanographic variables.

In order to limit correlations between variables, to measure the influence of prey distribution and to compare this influence between species, we included the same four abiotic variables together with NASC for the nine predators. The models may have benefited from the inclusion of other environmental factors such as oxygen, which is known to be important for tuna habitat [Bertrand *et al.*, 2002a; Cayré & Marsac, 1993]. Increasing the number of environmental variables also may help to better model predators optimal habitats. Concerning prey, vertical integral of NASC values were included as a proxy of prey abundance. As the method used originally predicted vertical profiles, Receveur *et al.* [2019], relate predator abundance/foraging to the depth of NASC maximal value would be useful to understand vertical predator habitat- vertical prey habitat relationships [Boyd *et al.*, 2015].

Finally, we proposed a relatively simple method, the “quantile method”, to measure species’ niche overlap. In a recent review describing a large panel of metrics used to measure species niche overlapping [Carroll *et al.*, 2019], we found that all metrics needed the same quantity/variable for the two species to measure their distribution overlap (often presence probability Abrams 1980; Swanson *et al.* 2015). We did not find any metrics dealing with different responses measured for the two species of interest. We think that a crucial development would be to find new metrics allowing to deal with different data-sources, considering that current study methods are strongly species dependent. The ability to cross data from different domains has to be enhanced through new statistical frameworks.

#### 6.4.4 Conclusions and perspectives for the Natural Park of the Coral Sea

In the present study, we developed a methodological approach to implement preyscape predictors as well as oceanographic conditions into nine predator niche models. We managed to describe the relationship between prey and predator distributions only when the predators’ datasets were large enough. Based on the predicted spatial distributions of predators, we highlighted potential pelagic predator hotspots : around the Loyalty Islands, around Petrie reef, around the Chesterfield reefs, and in the seamount region southeast of the Main Island. More scientific surveys, especially for cetacean and seabird, are needed to confirm the relevance of these regions for conservation. Most of these areas (Chesterfield, Bellona, Entrecasteaux, Petrie and Astrolabe) have been classified into strict marine reserve (category I, none human activities authorized, according to IUCN protected area classification or “1-No take-No go” Horta e Costa *et al.* 2016), but only shallow waters up to 1000m bottom depth are protected. However, our results suggest that predators also aggregate in deeper pelagic waters. Those areas, therefore appear as good candidates to implement a higher level of protection into offshore waters. For instance, we suggest that protected areas could be extended from the existing strict marine reserves to the pelagic domain around reefs/atolls. Finally, the present analysis focused on nine predators, but a variety of other taxa are still lacking to provide an exhaustive overview of the pelagic ecosystem. Adding turtles, sharks, humpback whales, other seabirds such as frigates, and other commercially exploited fish species will be necessary for a complete management of the Natural Park of the Coral Sea.





# Chapitre 7

## Conclusions et perspectives

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L'objectif de ce travail de thèse était d'examiner le fonctionnement de l'écosystème pélagique dans le Pacifique sud-ouest et plus particulièrement la dynamique des organismes de niveaux trophiques intermédiaires (ou micronecton). A partir de l'analyse de données acoustiques, nous avons développé une méthode de suivi du micronecton dans l'espace et dans le temps en relation avec l'environnement. Cette méthodologie mise en place, nous l'avons utilisée pour décrire la dynamique spatiale et temporelle du micronecton autour de la Nouvelle-Calédonie et les facteurs environnementaux qui la contrôlent. Nous avons ensuite mis en évidence les espèces majoritaires de ce compartiment. Finalement, deux études ont replacé la dynamique de ce compartiment dans un contexte plus général : le devenir du micronecton de la zone face au changement climatique, et l'influence de ce compartiment sur la distribution des prédateurs supérieurs qui s'en nourrissent.

## 7.1 Rappels des résultats principaux

Au cours du **chapitre 2**, nous utilisons les données d'un échosondeur non calibré (ADCP) largement répandu pour analyser 19 ans de données acoustiques et ainsi évaluer l'évolution de l'abondance relative du micronecton dans la ZEE Calédonienne. Deux fréquences distinctes (150kHz et 75kHz) sont utilisées conjointement pour obtenir une série temporelle continue entre 1999 et 2017 dans la couche 20-120m. En comparant le signal ADCP à des mesures simultanées d'un autre sondeur dédié et calibré pour les estimations de biomasse (EK60) à 70 kHz, nous montrons que les signaux d'ADCP à 150kHz et à 75kHz y sont étroitement liés. La variabilité du signal acoustique est majoritairement due aux migrations nyctémérales, puis à l'année (avec une diminution globale du micronecton de 1999 à 2007 puis une ré-augmentation jusqu'en 2017) et enfin au cycle d'ENSO (avec en moyenne plus de micronecton pendant les phases El Niño). Le lien avec les paramètres environnementaux met en évidence une distribution spatiale saisonnière variable : durant l'été, le micronecton se concentre autour des côtes, alors que pendant l'hiver il se concentre plutôt dans le nord de la zone économique exclusive et à l'ouest de la grande terre. Cette distribution spatiale du micronecton en surface de nuit, ainsi que son cycle saisonnier sont différents de ceux prédits par le modèle de dynamique de population SEAPODYM-MTL.

Nous nous sommes ensuite concentrés dans le **chapitre 3** sur la compréhension de la distribution verticale du micronecton à travers l'analyse de 6 campagnes d'enregistrement d'EK60 et encore une fois des facteurs océanographiques la contrôlant. Nous avons développé une méthodologie statistique originale qui a permis d'identifier trois zones homogènes en terme de distribution verticale : une zone au nord de 20°S, une zone au sud de cette limite et à l'est de 165°E (quart sud-est), et une dernière zone également au sud de 20°S et à l'ouest de 165°E (quart sud-ouest). La zone nord est caractérisée par des faibles densités de micronecton à la fois en surface et en profondeur, de jour et de nuit, et une plus faible proportion d'organismes migrants que dans le sud. Cette zone est majoritairement influencée par des faibles concentrations en oxygène et des fortes températures de surface. Dans les deux régions du sud, la distribution verticale de nuit est plus dense en micronecton en surface et en profondeur que dans le nord. Durant le jour, la distribution du micronecton du quart sud-ouest est plus dense en profondeur (vers 550 mètres) alors que dans le quart sud-est, la densité est plus forte entre 0 et 50 mètres. Ces deux régions du sud sont majoritairement influencées par de fortes concentrations en oxygène et une forte salinité. Dans le sud, la densité intégrée entre 0 et 600 mètres est globalement plus élevée que dans le nord avec une proportion de migrants plus importante.

Le **chapitre 4** nous a permis d'analyser des données de composition en espèces issues de 141 chaluts réalisés dans la zone entre 2011 et 2016. Cette étude a abouti à la description de sept assemblages dominants d'espèces de micronecton. La profondeur de chalutage ainsi que le moment de la journée sont les paramètres dominants dans la différenciation des assemblages. De jour, deux assemblages sont identifiés : un premier au-dessus de 350 mètres dominé par une espèce de crustacé et une espèce de mollusque, et un second en dessous de 350 mètres très diversifié avec une domination de plusieurs espèces de poissons. Quatre assemblages nocturnes se partagent la couche 0-250 mètres, avec deux changements de communauté à environ 80m et 250m. Les assemblages du nord sont dominés par des espèces de crustacés, tandis que les assemblages du sud sont dominés davantage par les espèces de céphalopodes et les espèces de poissons. Les prévisions spatiales de distribution des communautés de micronecton sont étroitement liées aux prévisions des distributions spatiales des écorégions acoustiques.

Dans le **chapitre 5**, nous avons exploré des scénarios d'évolution des distributions verticales et des abondances de micronecton issues du chapitre 3 dans un contexte de changement climatique. Pour cela, nous avons utilisé deux approches : la modélisation acoustique et le modèle SEAPODYM. Pour la couche épipélagique, les deux méthodes prédisent en moyenne pour toute la zone une diminution de l'abondance de micronecton. Cependant des différences spatiales sont présentes : une légère augmentation est prévue au nord de 20°S contre une plus forte diminution au sud. Pour les deux couches verticales inférieures (couches mésopélagiques haute et basse), les prévisions divergent fortement entre modélisation acoustique et SEAPODYM. Nous montrons au cours de ce chapitre que les divergences de prédictions sont encore trop grandes entre les deux moyens d'études du micronecton. Une validation plus fréquente des sorties de modèles écosystémiques avec comparaison aux données acoustiques d'observation est nécessaire pour améliorer la robustesse et notre confiance en ces projections.

Enfin, au cours du **chapitre 6**, nous nous sommes penchés sur la compréhension des facteurs, biotiques et abiotiques, contrôlant la dynamique spatiale de neuf prédateurs supérieurs (trois espèces de poissons pélagiques, trois groupes de cétacés et trois espèces d'oiseaux marins). L'influence de la distribution des proies sur les prédateurs est significative pour six prédateurs sur neuf et a donc permis d'améliorer significativement la modélisation de leurs distributions spatiales. Cependant, cette analyse a aussi montré que l'influence du micronecton dans les modèles de niche des prédateurs restait relativement faible en comparaison des autres variables abiotiques. Finalement, les prédictions spatiales de ces neuf prédateurs ont été combinées et ont permis de proposer des zones possiblement sensibles pour la conservation de ces espèces, zones qui pourront être utiles dans la planification spatiale des activités du parc naturel de la mer de Corail.

## 7.2 L'acoustique comme moyen d'étude

L'avantage de l'acoustique est sa large gamme d'échantillonnage temporelle (de la seconde à l'interannuel) et spatiale (du mètre à des milliers de kilomètres) pour peu que les supports d'observations (*e.g.* navires, mouillages) le permettent. Nous nous sommes concentrés au cours de cette thèse sur les gammes intermédiaires d'échelles spatio-temporelles : nous avons quantifié la distribution horizontale du micronecton à une résolution de l'ordre de 20km, la distribution verticale à une résolution de l'ordre de 5-10m, et la dynamique temporelle aux échelles journalière, saisonnière et inter annuelle (environ 20

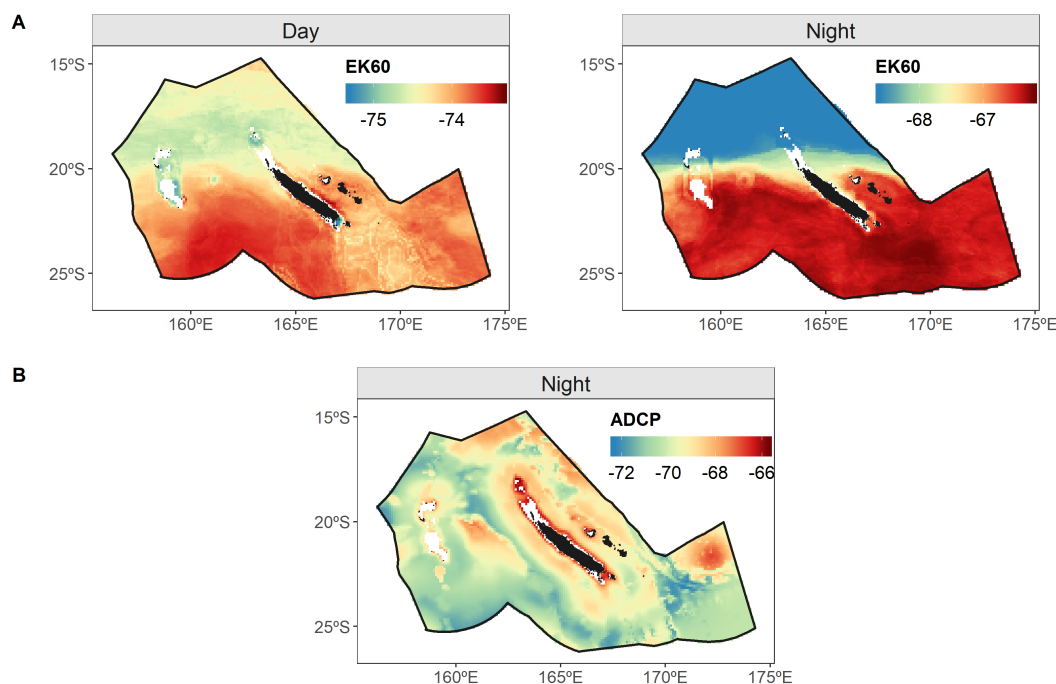


FIGURE 7.1 – Distributions spatiales de l'écho intensité acoustique ( $S_v$ ) prédites à partir des données d'EK60 (haut) et d'ADCP (bas) en moyenne sur la couche 20-120m.

ans). Dans une synthèse récente sur le potentiel de l'acoustique dans la compréhension des processus écologiques, [Benoit-Bird & Lawson \[2016\]](#) identifient neuf questions auxquelles l'acoustique peut apporter des éléments de réponse. Au cours de ce travail de thèse, nous avons confirmé l'utilité de l'acoustique pour apporter des éléments de réponse aux cinq questions suivantes :

- Biogéographie et distribution spatiale à grande échelle : où trouve t'on des animaux dans l'océan?
- Interactions biophysiques : comment l'environnement conditionne-t-il la répartition des animaux dans la mer?
- Dynamique temporelle : quand, pourquoi et comment les animaux se déplacent-ils?
- Sciences du climat : comment les écosystèmes réagissent-ils au changement climatique?
- Interactions prédateur-proies : comment les animaux trouvent-ils leur alimentation?

L'acoustique est donc un moyen d'étude puissant, non intrusif, qui mériterait d'être encore plus largement utilisé.

### 7.2.1 Comparaison EK60-ADCP

L'utilisation d'un engin non calibré a permis de réunir 54 campagnes couvrant 19 années et un cycle saisonnier complet (tous les mois ont été échantillonnés au moins deux fois). L'étude de l'influence du phénomène ENSO sur le micronecton par exemple nécessite de telle série temporelle car il faut échantillonner plusieurs fois chaque phase pour que les résultats soient robustes; son cycle étant compris entre 3 et 7 ans avec une moyenne à 3.5 ans. De même, l'étude de l'impact sur le micronecton du changement climatique nécessitera des séries temporelles de données les plus longues possibles.

Cependant, les différences de prédictions spatiales obtenues avec les données d'ADCP et d'EK60 posent question (Figure 7.1). Plusieurs hypothèses sont envisagées pour les expliquer.

- La différence entre les fréquences d'échantillonnages des deux engins : dans le cas de l'EK60, seul la fréquence 38kHz est utilisée dans cette thèse alors que le travail sur l'ADCP utilise les fréquences 75kHz et 150kHz, ramenées à un équivalent 70kHz. Cela pourrait expliquer une partie de la différence entre les prédictions spatiales car les fréquences ne détectent pas exactement les mêmes organismes. Cependant, les résultats du chapitre 1 montrent bien que les signaux des différentes fréquences sont corrélés entre eux et donc qu'une partie des organismes détectés est commune. Cette explication pourrait donc expliquer des légères différences, mais pas l'amplitude des différences que l'on observe sur la Figure 7.1.
- On peut également se demander si les données des six campagnes menées avec l'EK60 sont suffisantes pour mesurer la dynamique captées par les 54 campagnes d'ADCP.
- L'absence d'inter-calibration des campagnes ADCP questionne également. En effet, des différences de niveaux moyens apparaissent entre campagnes dans les valeurs d'ADCP qui ne reflètent pas les différences de niveau moyen des valeurs d'EK60 (Figure 2.3). Est-il possible d'analyser ensemble toutes les campagnes si elles ne sont pas calibrées? Le chapitre 2 montre qu'il est possible de construire un modèle mixant des campagnes d'ADCP et combinant jusqu'à deux fréquences différentes. De nombreux articles ont validé les valeurs de l'ADCP grâce à une comparaison aux données d'EK60 [Brierley *et al.*, 1998; Fiedler *et al.*, 1998; Griffiths, 1996; Lee *et al.*, 2004] ou par rapport aux données de chaluts [Fielding, 2004; Heywood *et al.*, 1991; Luo *et al.*, 2000; Ressler, 2002]. L'analyse conjointe de plusieurs campagnes a également déjà été faite par Bianchi *et al.* [2013a] et Bianchi & Mislán [2016] sur 389 campagnes effectuées à l'échelle mondiale avec des fréquences allant de 38 à 150 kHz, ou encore par Chereskin & Tarling [2007] qui ont analysés ensemble 127 campagnes. Nous avons-nous même utilisé la méthode proposée par Gostiaux & van Haren [2010] permettant d'utiliser des valeurs ADCP non calibrées lorsque l'intensité de l'écho est supérieure d'au moins 10 dB au niveau de bruit. Cependant, cela pourrait expliquer une partie des différences de prédiction entre EK60 et ADCP.
- Enfin, il est également possible qu'une partie de la différence s'explique par les méthodologies statistiques : pour l'ADCP (chapitre 2), les données sont moyennées entre 20 et 120 mètres et c'est cette valeur moyenne qui est expliquée en fonction de paramètres environnementaux. Dans l'étude avec l'EK60 (chapitre 3), c'est tout le profil vertical qui est analysé et lié à l'environnement. Ces profils sont d'abord classés en 10 classes et ce sont ces 10 classes qui sont modélisées en fonction de l'environnement. La valeur acoustique est ensuite reconstruite avec une moyenne des profils acoustiques de chaque classe, pondérée par la probabilité d'être dans cette classe. Le passage par les 10 classes réduit fortement la variance intrinsèque des données d'écho-intensité acoustique ( $S_v$ ). De nuit notamment, les profils verticaux ne sont groupés qu'en 4 classes. Les valeurs reconstruites sont dans la gamme maximale des combinaisons linéaires de ces 4 profils verticaux moyens, d'où la grande homogénéité spatiale de la Figure 7.1 de nuit. Finalement de nuit dans le nord de la zone, quasiment toutes les cellules spatiales sont prédites comme appartenant à une même classe acoustique, limitant fortement les potentielles différences de patterns spatiaux.

Pour améliorer la cohérence spatiale entre les deux prédictions, plusieurs pistes pourraient être envisagées. Premièrement, rendre disponible de manière plus systématique les données d'EK60, comme c'est le cas avec l'ADCP, permettrait de réaliser des comparaisons sur plus de campagnes et ainsi de

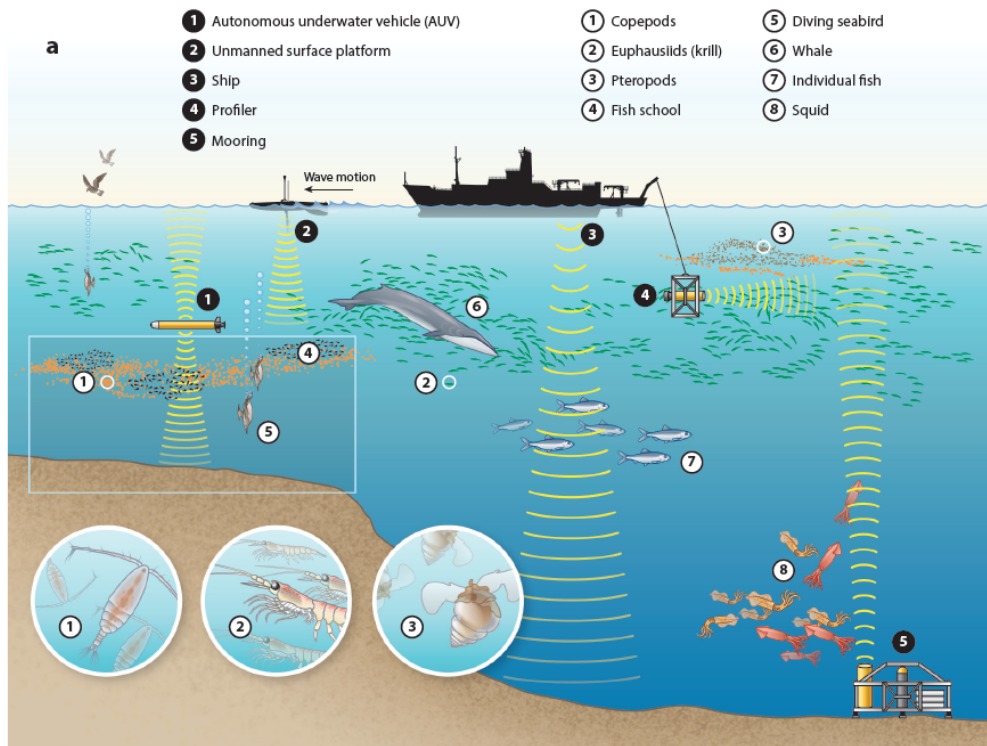


FIGURE 7.2 – Illustration des différents outils acoustiques existants. Figure extraite de Benoit-Bird & Lawson [2016].

valider ou invalider l'utilisation de l'ADCP. Les données ADCP, collectées d'une manière relativement routinière, sont en effet accessibles à la communauté scientifique grâce à un effort de coordination permettant le stockage national et international (voir notamment <https://data.ifremer.fr/SISMER> pour les données françaises et [https://currents.soest.hawaii.edu/docs/adcp\\_doc/adcp\\_data/index.html](https://currents.soest.hawaii.edu/docs/adcp_doc/adcp_data/index.html) pour des données internationales). Même si la transformation des données brutes en données acoustiquement analysables nécessite une transformation (cf chapitre 2), ces bases permettent d'envisager des études à grande échelle. Par exemple, une étude globale sur la variabilité des profondeurs de migration a notamment été possible grâce à ces bases globales de données d'ADCP [Bianchi & Mislán, 2016]. A notre connaissance, les bases similaires regroupant les données d'EK60 sont plus restreintes spatialement à certaines régions (<http://imos.org.au/facilities/shipsopportunity/bioacoustic/> par exemple pour l'Australie). Les analyses globales se basent souvent sur un faible nombre de campagnes [e.g. Irigoien *et al.*, 2014; Klevjer *et al.*, 2016].

Il serait donc utile de développer des bases similaires à l'ADCP pour encourager le partage de données et les analyses grandes échelles. Il serait également nécessaire de développer des méthodes de calibration adaptées à l'ADCP, en l'absence d'EK60. Enfin, augmenter le nombre de classes de la méthode de traitement des données EK60 permettrait d'incorporer plus de variabilité dans les valeurs d'écho-intensités acoustiques ( $S_v$ ) dans le modèle, et donc prédire une plus grande variabilité. Des contrastes spatiaux à plus fine échelle pourraient apparaître dans les prédictions du nord de la zone durant la nuit.

### 7.2.2 Compréhension des espèces associées au signal acoustique

La non-identification des espèces a également limité l'utilisation de l'acoustique seule pour comprendre la dynamique du micronecton, laissant toujours en suspens si les variations prédites d'écho intensité étaient dues à des changements d'abondance ou de communautés. En effet, à une fréquence donnée (cf Figure 1.23) un changement de  $S_v$  peut se traduire par un changement de densité des organismes (équation du  $S_v$ ) mais aussi par un changement des organismes présents. L'étude du chapitre 4 nous apporte des éléments de réponse montrant qu'effectivement les communautés varient dans la zone, même si ces variations sont relativement faibles (les 7 communautés identifiées se ressemblent). De jour par exemple, une seule communauté est prédite dans toute la ZEE alors que des variations apparaissent dans la densité acoustique, traduisant certainement des changements d'abondance de micronecton.

Une possibilité pour répondre plus pertinemment à ces questions serait de classer le signal acoustique en groupes d'organismes [De Robertis *et al.*, 2010; Kloser *et al.*, 2002; McQuinn *et al.*, 2013]. Cela est possible en utilisant seulement 2 fréquences, comme le proposent par exemple Behagle *et al.* [2017] avec l'utilisation du 38kHz et 120kHz pour différencier les 'fluid-like' (organismes composés en majorité d'eau) des 'gas-bearing' (organismes à vessie natatoire). Malgré tout, cette classification limiterait l'étude des distributions verticales aux 200 premiers mètres de la colonne d'eau, portée maximale du 120kHz. Cela fait apparaître une deuxième limite de ces études : l'utilisation de seulement deux engins acoustiques (EK60 et ADCP), placés tous deux sous la coque d'un navire océanographique. L'utilisation conjointe de plusieurs outils d'échantillonnage acoustique permettrait une meilleure couverture spatio-temporelle, notamment sur la verticale (Figure 7.2). L'objectif serait d'avoir plusieurs fréquences disponibles en profondeur. Pour cela, l'utilisation d'un mouillage serait appropriée pour avoir des mesures en un seul point ou bien des profileurs acoustiques pour avoir des données en station. Toutes les analyses de cette thèse ont débuté à 10m sous la surface car les sondeurs de coque sont sous la coque du bateau et qu'il faut y ajouter une zone aveugle. Positionner un mouillage qui 'regarde' vers la surface comme l'engin numéro 5 de la Figure 7.2 permettrait également d'intégrer la couche de subsurface (0-10m) dans les analyses. Enfin, le déploiement d'un véhicule autonome type glider permettrait d'acquérir des données continues spatialement et donc complémentaires de celles obtenues en station avec le profileur.

#### Aller plus loin pour comprendre le lien acoustique-chalut

Le chapitre 4 utilise une méthode d'analyse multivariées : un individu (un chalut en l'occurrence) est un vecteur (sa composition en espèces) au lieu d'être une valeur unique (analyse univariée). Une prochaine étude pourrait utiliser le même cadre statistique en analysant en parallèle la réponse acoustique moyenne de la couche échantillonnée et sa composition en espèces (Figure 7.3). Il faudrait extraire la réponse acoustique moyenne de chaque couche échantillonnée par chalut. Puis, il faudrait faire deux analyses RCP en parallèle : une avec la composition en groupes acoustiques (par exemple 'fluid like', 'no gaz' ..) (de manière similaire au travail du chapitre 3) et une autre avec la valeur moyenne de 2, 3 ou 4 fréquences par chalut. Cela permettrait de classer de manière indépendante l'acoustique et les espèces. Une comparaison des RCP obtenues permettrait alors de conclure si la réponse en fréquence moyenne d'une couche peut être utilisée pour caractériser sa composition en espèce. Cela permettrait également



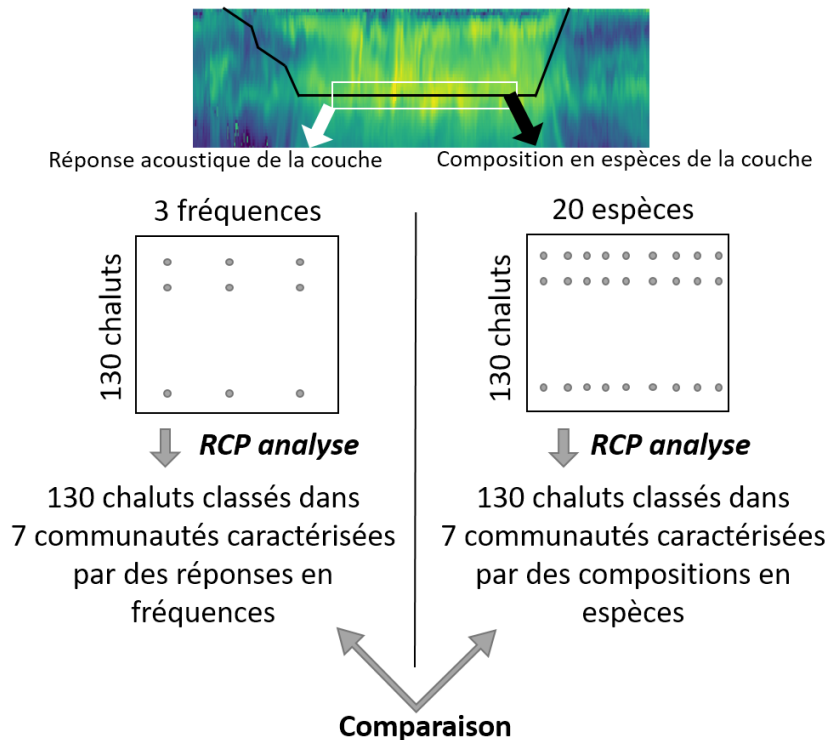


FIGURE 7.3 – Schéma explicatif de l'étude envisagée pour mieux comprendre le lien composition en espèces-acoustique.

de mieux comprendre une réponse acoustique en fonction d'une composition spécifique. Cela rejoindrait des études déjà existantes comme celle d' [Ariza et al. \[2016\]](#), en ajoutant un cadre de modélisation permettant d'aller plus loin dans la compréhension des phénomènes significatifs et dans l'extrapolation des résultats. Compte tenu de l'importance du gélatineux dans la rétrodiffusion acoustique, et en particulier des siphonophores [[Proud et al., 2018b](#)], il serait primordial d'inclure les gélatineux dans ce type d'étude.

### 7.2.3 La fine échelle

L'acoustique permet également d'observer des comportements, surtout alimentaires, à très fine échelle [[Bertrand et al., 2014](#)] comme on peut l'observer sur les deux échogrammes de la Figure 7.4. Sur cette Figure, deux exemples d'enregistrements acoustiques montrent des comportements alimentaires de prédateurs supérieurs et une réaction immédiate des proies ciblées par le prédateur avec un changement de distribution verticale. La campagne PUFFALIS a été réalisée conjointement à une campagne à terre de marquage d'oiseaux marins, l'objectif était d'échantillonner les proies en même temps que les comportements d'alimentation des oiseaux autour de la colonie. Cependant les oiseaux s'alimentent sur des échelles temporelles trop courtes et rapides pour que le bateau puisse les suivre. La complexité des manipulations en station allongeait le temps de travail par station (environ 6 heures par station), et ne permettait donc pas la mobilité nécessaire pour suivre les oiseaux ou même atteindre des zones d'alimentation. Et enfin, la couche de surface 0-10m sur laquelle la plupart des oiseaux se nourrissent n'est pas bien échantillonnée par le sondeur qui se situe déjà à 3m de profondeur. Pourtant échantillonner acoustiquement et par chalut des couches où les oiseaux se nourrissent aurait été utile pour une meilleure

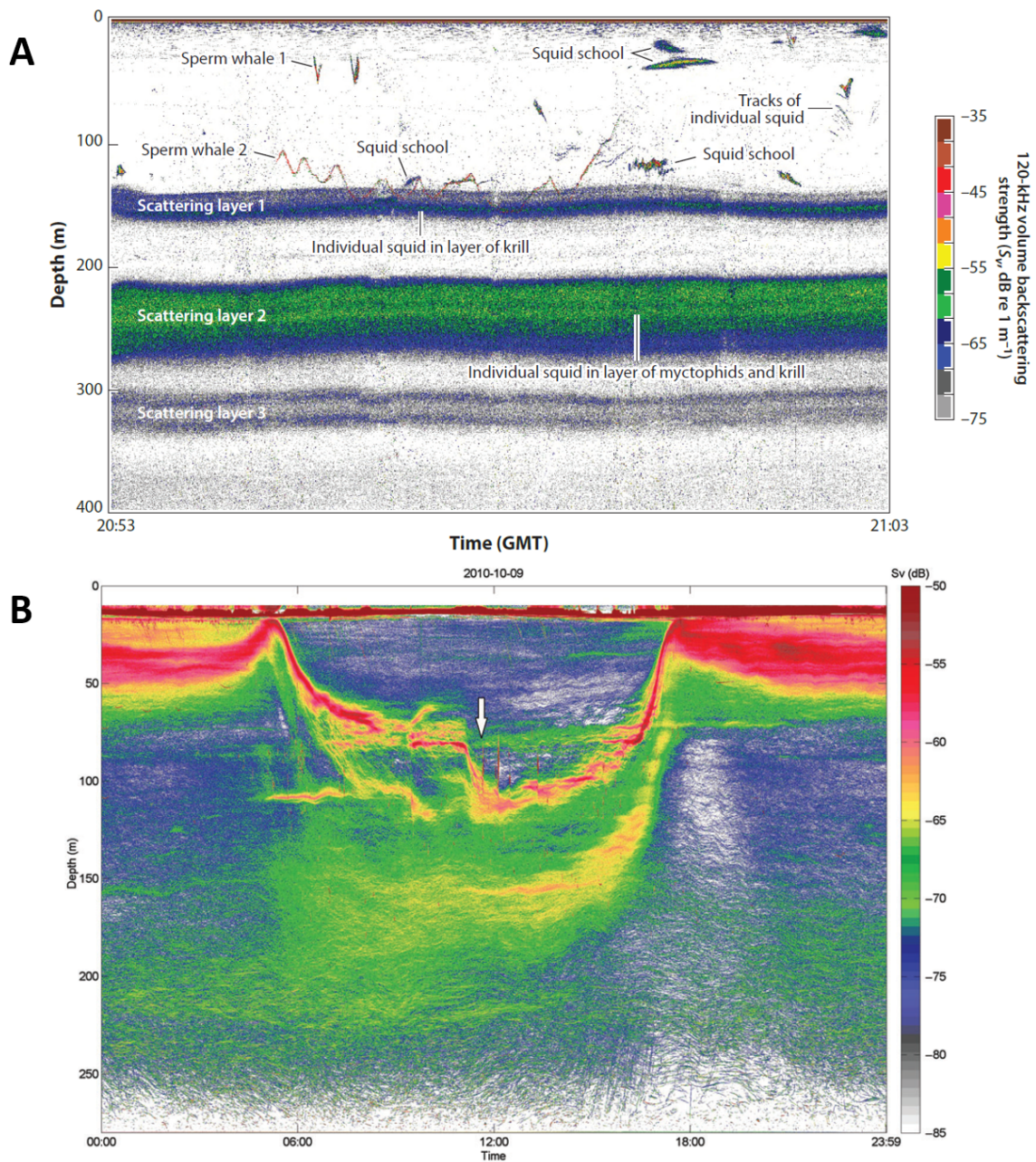


FIGURE 7.4 – Deux exemples d'échogrammes montrant une réponse rapide des couches de proies à une prédation par des baleines (A) et non précisée (B). Figures extraites de [Benoit-Bird & Lawson \[2016\]](#) (A) et de [Godo \*et al.\* \[2014\]](#) (B).

compréhension des proies recherchées par les oiseaux. Avec de telles données, des modèles liant le signal acoustique multifréquence et la composition des espèces pourraient également être mis en place pour prédire à plus large échelle les zones d'alimentation potentielle des oiseaux à partir de l'environnement et de l'acoustique.

### 7.3 La dynamique des proies mise en évidence dans le Pacifique sud-ouest

Dans les chapitres 2 et 3, nous avons étudié les facteurs influençant la distribution spatiale, verticale et temporelle du micronecton. On a notamment prédit plus de micronecton dans le sud de la ZEE que dans le nord (Chapitre 3) avec des variations à plus fine échelle comme une plus forte abondance de micronecton près des côtes (Chapitre 2).

La bathymétrie est un paramètre qui est revenu régulièrement comme facteur influençant le micronecton (chapitres 2, 3 et 4). Plusieurs raisons ont été avancées au cours des discussions, notamment un potentiel effet des monts sous-marins. Cependant, cette piste est toujours restée en suspens, faute de manque de données plus fines autour des monts. Un problème de définition des monts (surface, hauteur, forme) est également souvent revenu, compliquant leur caractérisation. D'après la littérature, l'influence d'un mont sous-marin sur les communautés de micronecton est complexe et dépend fortement de la hauteur du mont et de sa forme [Drazen *et al.*, 2011; Morato *et al.*, 2008, 2010]. De plus, les espèces ne sont pas toutes influencées de la même manière par un mont [Annasawmy *et al.*, 2019]. Les échelles spatiales de travail ne permettaient pas d'étudier un phénomène qui se produit à très fine échelle spatiale. Au cours de l'hiver austral 2019 (juin, juillet, août et septembre), sept campagnes sont conduites spécifiquement autour de monts sous-marins dans la ZEE Néo-Calédonienne avec un échantillonnage acoustique très serré (campagnes SEAMOUNTS et MARACAS). Au cours de quatre de ces campagnes, des chalutages ont été effectués autour des monts (Figure 7.5). Toutes les données récoltées en cours de traitement pourront certainement permettre de mieux comprendre la distribution des espèces autour des monts et des possibles changements d'abondance.

La concentration en oxygène est un autre paramètre qui est ressorti régulièrement dans nos résultats. Une analyse conjointe des données de CTD et d'acoustique (non présentée dans ce manuscrit) a mis en évidence une forte relation positive entre la valeur de rétrodiffusion de volume ( $S_v$ ) et la concentration en oxygène. Ces conclusions rejoignent celles de la littérature où la distribution verticale du micronecton a été liée à la structure verticale de l'oxygène à plusieurs reprises [e.g. Bertrand *et al.*, 2010; Bianchi *et al.*, 2013b]. La figure 5.3 montre une baisse de la concentration en oxygène liée au changement climatique dans tout le Pacifique sud-ouest, en accord avec la tendance prédite à l'échelle globale [Keeling *et al.*, 2010]. La concentration en oxygène reste un paramètre compliqué à mesurer sur de larges échelles spatiales (pas d'image satellite par exemple) et via des procédures à la mer assez lourdes. Sa modélisation n'est pas évidente non plus, avec de grandes variations dans les projections des conditions futures. Vu l'importance de cette variable pour la dynamique du micronecton, continuer l'effort de mesures et améliorer les modèles sont essentiels.

Enfin, la température apparaît à plusieurs reprises comme déterminante pour le micronecton. Comme pour l'oxygène, le profil vertical de la température est déterminant dans la distribution verticale du mi-

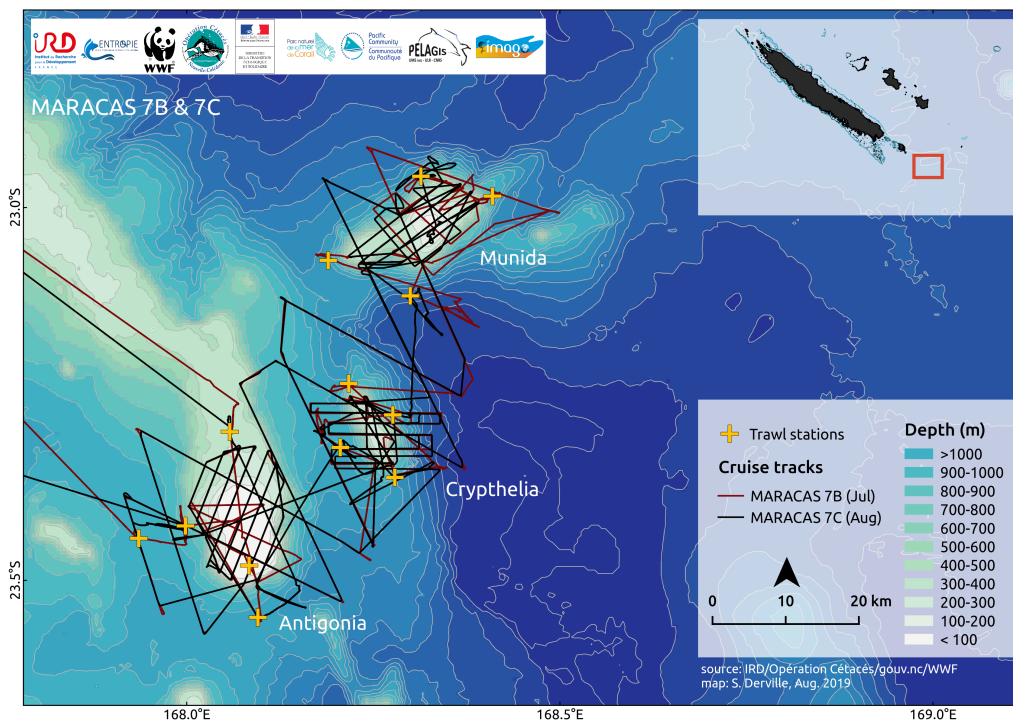


FIGURE 7.5 – Plan d’échantillonnage des campagnes MARACAS 7B et 7C et localisation de la zone d’étude dans le sud de la grande terre. Les transects et stations seront répétés encore 1 fois en septembre 2019 (MARACAS 7D).

cronection. La température semble aussi jouer un rôle dans la délimitation de larges zones homogènes dans la ZEE avec un front de température délimité vers 20°S. Au nord de cette limite on retrouve la masse d’eau, SPTWN (South Pacific Tropical Water North) qui est une masse d’eau chaude, salée et relativement peu oxygénée venant de la Polynésie. Au sud, on détecte plutôt la SPTWS (South Pacific Tropical Water South) qui est plus froide, moins salée et plus oxygénée. Cette masse d’eau semble plus favorable au micronecton.

## 7.4 L’impact potentiel du changement climatique

L’étude de l’impact potentiel du changement climatique sur les proies a été menée à partir de deux approches (Chapitre 5). Nous avons prédit en moyenne une baisse d’abondance des proies entre 0 et 1000m, résultat en accord avec les études globales d’impact du changement climatique sur les écosystèmes [Kwiatkowski *et al.*, 2019; Lotze *et al.*, 2019] et les études par bassin [Bryndum-Buchholz *et al.*, 2019; Lefort *et al.*, 2015]. Cette diminution moyenne est comprise entre -4% (acoustique) et -22% (SEAPODYM) mais avec une forte variabilité selon la couche verticale (-7%, -6% et +2% respectivement pour les couches épipélagique, mésopélagique haute et mésopélagique basse pour l’acoustique et -2%, +3% et -69% respectivement pour les mêmes couches dans SEAPODYM).

Il apparait notamment que la diminution de la couche mésopélagique basse (ou bathypélagique, d’environ 500 à 1000m) contrôle la diminution moyenne dans SEAPODYM et que cette diminution d’abondance de la couche mésopélagique basse est en forte contradiction avec les prédictions des valeurs acoustiques. A notre connaissance, peu d’études prennent en compte la distribution verticale du mi-

cronecton dans les études d'impact du changement climatique. [Lefort et al. \[2015\]](#), à partir des sorties du modèle écosystémique APECOSM, séparent les organismes en trois groupes : la communauté épipélagique, la communauté mésopélagique et la communauté migrante. Cependant, tous les organismes de plus de 2cm sont analysés ensemble : on ne peut donc pas différencier le micronecton des prédateurs supérieurs. Les auteurs montrent une diminution de la biomasse du groupe migrant en 2100 (environ -15%) et des biomasses des groupes épipélagique et mésopélagique (environ -30%) par rapport aux années 2000. Ils lient les différences entre groupes aux changements de taille moyenne : une diminution de 1.3cm des tailles moyennes de la communauté migrante contre une diminution de 2.1 cm et 5cm pour les deux autres communautés. La communauté migrante verrait également sa production d'œufs augmenter (+4.5%). La baisse de taille moyenne est liée à la baisse de production primaire : quand la disponibilité en nourriture baisse, les organismes réduisent l'énergie allouée à leur croissance et conservent cette énergie pour le maintien des fonctions vitales de base [\[Maury et al., 2007\]](#). Toutes ces conclusions font apparaître la complexité des changements potentiels pour chaque espèce. La modélisation déterministe (comme SEAPODYM ou APECOSM) se base sur la mise en équation de ces processus. Certains processus peuvent être mal pris en compte, voire absents, et biaiser les résultats des prédictions de micronecton. Il apparaît donc essentiel de valider d'une manière ou d'une autre ces prédictions.

Les paramètres de ces modèles sont optimisés et les prédictions validées en comparant les sorties à des observations de terrain pour quasiment tous les niveaux trophiques : la télédétection par satellite et les mesures directes en mer fournissent des informations sur les niveaux trophiques inférieurs, et les données de pêches fournissent des informations sur les espèces exploitées. L'efficacité de ces comparaisons a été montrée pour modéliser correctement les prédateurs supérieurs [\[Anderson et al., 2017; Tittensor et al., 2018\]](#). Cependant, ces modèles souffrent d'un manque d'observations pour les niveaux dits intermédiaires, qui sont mal échantillonnés par les méthodes conventionnelles. Les données acoustiques semblent bien adaptées pour valider les sorties de modèles déterministes grâce notamment à leur large couverture spatiotemporelle. Mais d'une part un travail d'homogénéisation entre les données prédites par les modèles et les données observées est nécessaire pour une bonne comparaison et d'autre part il sera nécessaire de mieux comprendre les relations entre signal acoustique et biomasse réelle.

### **Le développement d'un modèle d'observation**

Plusieurs pistes ont été proposées pour améliorer l'incorporation des données acoustiques dans les modèles écosystémiques [\[Handegard et al., 2013\]](#). Pour ce faire, il est nécessaire de définir des normes de métadonnées et ainsi faciliter la mutualisation des données acoustiques comme proposé récemment par exemple, avec un format standard Netcdf [e.g. [Haris et al., 2018](#)]. Il est également important de mettre en place systématiquement des capteurs acoustiques dans les programmes d'observation à grande échelle. L'acquisition croissante de données permettrait le développement d'un "acoustic-based coupled observation and modeling system" que l'on pourrait traduire par un système couplé observation-modélisation basé sur l'acoustique (Figure 7.6).

Les intensités acoustiques peuvent être transformées en biomasse à deux conditions : connaître la réponse acoustique par espèce et être capable de donner la proportion d'espèces ou de taxons présent dans la couche échantillonnée. Pour ce deuxième objectif, on peut échantillonner directement la couche avec un autre engin d'échantillonnage (un chalut par exemple), ou utiliser l'acoustique multi-

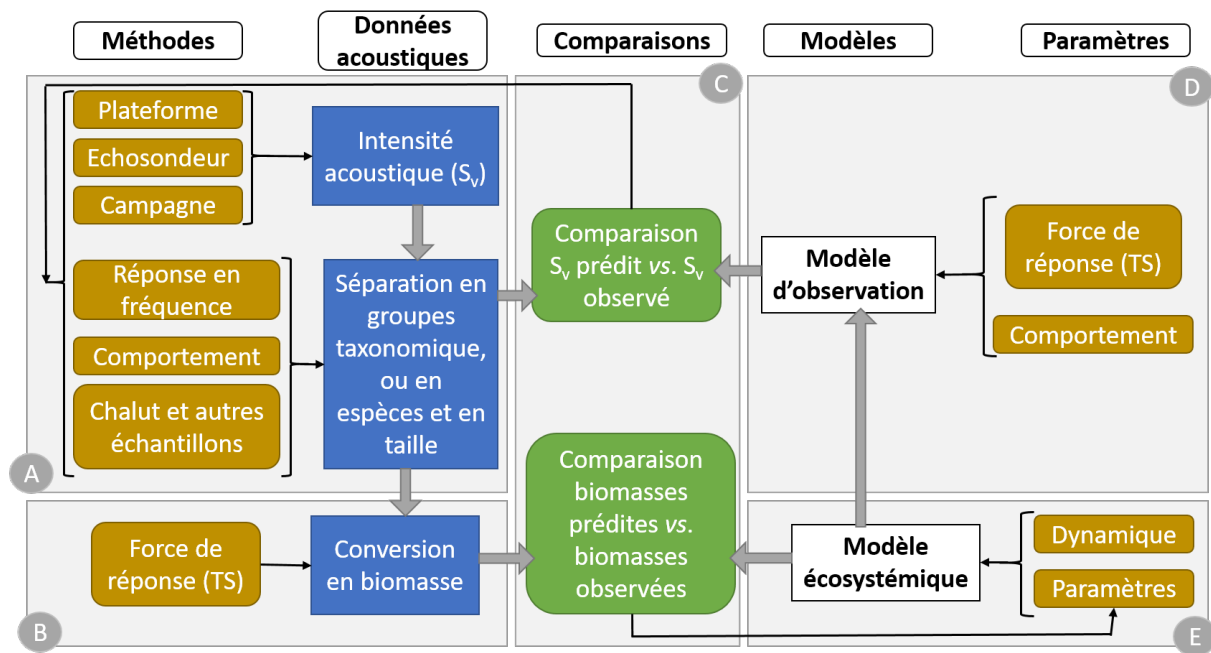


FIGURE 7.6 – Schéma conceptuel du flux d'informations dans un système couplé observation-modélisation. Les flèches épaisses indiquent les sorties des modèles et des observations, et les flèches minces représentent les paramètres des modèles, les éléments du plan d'échantillonnage et de son interprétation. (a) L'intensité acoustique mesurée sur diverses plates-formes est répartie en groupes taxonomiques, fonctionnels ou en espèces. (b) Les méthodes établies dans le domaine des pêcheries sont utilisées pour obtenir des indices d'abondance relative. (c) Comparaison des données modélisées et d'observations en terme de valeurs acoustiques ou de biomasses. La comparaison peut aider au choix des plates-formes d'observation et du plan d'échantillonnage. (d) Le modèle d'observation. (e) les modèles écosystémiques, avec l'étape d'optimisation des paramètres (assimilation des données). Figure adaptée de [Handegard et al. \[2013\]](#).

fréquences, ou encore identifier un comportement spécifique à une espèce (forme du banc et caractère migratoire par exemple) (Figure 7.6, cadre A). Ensuite, l'intensité acoustique peut être transformée en biomasse, notamment grâce aux connaissances des index de réflexion individuels (TS) des espèces exploitées dont la gestion se fait grâce aux campagnes acoustiques (Figure 7.6, cadre B). Cette biomasse peut alors être comparée aux biomasses prédites par les modèles (Figure 7.6, bas du cadre C). Cependant, malgré toutes les avancées technologiques récentes (véhicules autonomes, acquisition en large bande...), la transformation de l'intensité acoustique en biomasse reste délicate notamment à cause du manque d'identification taxonomique précise des espèces présentes et du manque de connaissances des TS de chaque type d'organisme et encore plus compliquée dans une région telle que la Nouvelle-Calédonie où la diversité d'espèces est très forte.

Une autre possibilité pour valider les prédictions issues des modèles écosystémiques serait de transformer les biomasses prédites par les modèles en intensité acoustique, et ensuite de comparer ces intensités acoustiques prédites aux intensités acoustiques mesurées, qualifiée de comparaison dans l'espace des observations (Figure 7.6, haut du cadre C). Contrairement à la méthode de comparaison des biomasses, cette méthode n'exige pas que l'intensité acoustique soit répartie par espèce ou par taxon avant la comparaison. Cependant, les réponses acoustiques de chaque groupe modélisé doivent être connues, ce qui n'est pas simple dans le cas de la Nouvelle-Calédonie où on observe une grande diversité d'organismes aux propriétés rétro-diffusantes différentes [Fielding, 2004; Godo *et al.*, 2009]. Néanmoins, la transformation de biomasse en intensité acoustique reste plus simple que l'inverse [Handegard *et al.*, 2013]. On suppose initialement des relations linéaires entre biomasse et intensité acoustique, et de manière itérative on optimise la composition en taxons pour obtenir une intensité acoustique totale proche de celle mesurée.

Pour initialiser cette optimisation à partir de composition en taxons observées, Handegard *et al.* [2013] proposent l'identification de zones d'intérêt : le délimitation de zones spatiales réduites où concentrer les efforts d'échantillonnage pour caractériser au mieux les populations de micronecton présentes. Le nombre de points d'intérêt serait à définir en fonction de la complexité de l'écosystème. Au vu des résultats de la thèse, au moins 5 points d'échantillonnages seraient nécessaires dans la zone économique exclusive de Nouvelle-Calédonie (Figure 7.7).

L'utilisation d'un tel cadre permettrait de mieux lier les prédictions issues des modèles comme SEA-PODYM aux observations de terrain et donc de réduire l'incertitude qui existe dans les prédictions futures de micronecton dans un contexte de changement climatique.

Lehodey *et al.* [2015] propose une autre approche : la redistribution entre les différents compartiments de micronecton de l'énergie totale venant de la production primaire est optimisée sur la base des proportions des valeurs de NASC moyens entre les groupes (Figure 1.26). Cependant, la valeur absolue de l'énergie totale venant de la production primaire n'est pas optimisée, il faudrait pour cela calculer une valeur absolue de biomasse à partir des données d'acoustique, ce qui n'est pas encore possible en l'état.

## 7.5 La gestion de l'écosystème et le parc naturel de la mer de Corail

L'acoustique est régulièrement mise en avant comme outil de gestion efficace pour la gestion écosystémique des pêches [Koslow, 2009; Melvin *et al.*, 2016; Trenkel *et al.*, 2011]. Son efficacité a notamment été démontrée pour le suivi des stocks de poissons d'intérêt commercial (le hareng, la sardine, l'anchois, le lieu sont quelques exemples), et pour comprendre les relations proies-prédateurs. Le cas de la Nouvelle-Calédonie sort largement de ce cadre : aucun stock de poisson n'y est géré par acoustique. Nos campagnes scientifiques avaient pour objectif de comprendre la dynamique du micronecton, proies des prédateurs, dans leur environnement. Nous avons aussi confirmé que l'échantillonnage acoustique pouvait aider à comprendre les relations prédateurs-proies. Néanmoins, la compréhension des processus régissant la dynamique de l'écosystème pélagique dans son ensemble pourrait être largement améliorée avec des campagnes écosystémiques. Dans ce cadre-là, des mesures sont menées en même temps sur un maximum de compartiments biologiques (producteurs primaires, secondaires, proies et prédateurs), comme c'est le cas durant les campagnes PELGAS conduites dans le golfe de Gascogne [Certain *et al.*, 2011] et dans sa partie Espagnole [Louzao *et al.*, 2019a,b].

Malgré l'ambition et le fort potentiel de l'acoustique pour aider à caractériser un écosystème et pour gérer les pêcheries de manière écosystémique, son utilisation dans le calcul d'indicateurs de la santé des écosystèmes est compliquée [Trenkel *et al.*, 2011]. Dans une région comme la ZEE de Nouvelle-Calédonie, il semble actuellement quasiment impossible d'utiliser des indicateurs acoustiques. La première limite vient de la définition de niveaux de références : pour que l'indicateur soit utile, il faut pouvoir le comparer à une valeur de base (souvent mesurée à un autre endroit ou à un autre moment de référence) qui est souvent méconnue [Rochet & Trenkel, 2003]. La première campagne réalisée avec un sondeur EK60 dans la zone date de 2011, ce qui est loin d'être une période "historique". Par ailleurs, les indicateurs sont surtout adaptés à des régions avec un petit nombre d'espèces et/ou à des régions où la gestion des stocks se fait par campagne acoustique [Trenkel *et al.*, 2011]. Le signal acoustique nécessite d'être discrétisé un minimum en taxon, ce qui n'est pas le cas.

L'analyse conjointe des données de deux engins acoustiques, associée à (i) l'analyse des données de chalutage, (ii) les sorties d'un modèle écosystémique, et (iii) l'étude des distributions de neuf prédateurs supérieurs, nous ont permis de proposer cinq zones dont la dynamique semble relativement homogène. Les limites de ces zones se déplacent au cours des saisons, et nous présentons ici une situation moyenne (Figure 7.7).

Globalement le nord de la ZEE est influencé par une masse d'eau chaude venant de l'équateur, pauvre en production primaire. Cette zone est relativement pauvre en micronecton avec une majorité d'espèces de poisson. En 2100, le micronecton serait légèrement favorisé. Elle est enfin la zone privilégiée d'alimentation des oiseaux marins et on y retrouve du thon blanc en grande quantité dans l'ouest.

Le sud de la ZEE est caractérisé par une plus grande proportion d'organismes migrants et se sépare en deux zones : le sud-est et le sud-ouest. Le sud-est est influencé par une masse d'eau froide et oxygénée venant d'Antarctique. On y retrouve une forte densité de micronecton entre 400 et 600mètres, caractérisée par une grande richesse spécifique. Ce sont les poissons et les crustacés qui y sont majoritaires et on y retrouve surtout des dauphins et les deux espèces de thon (thon germon et thon jaune). Le micronecton de cette zone aurait tendance à voir son abondance diminuer en 2100.



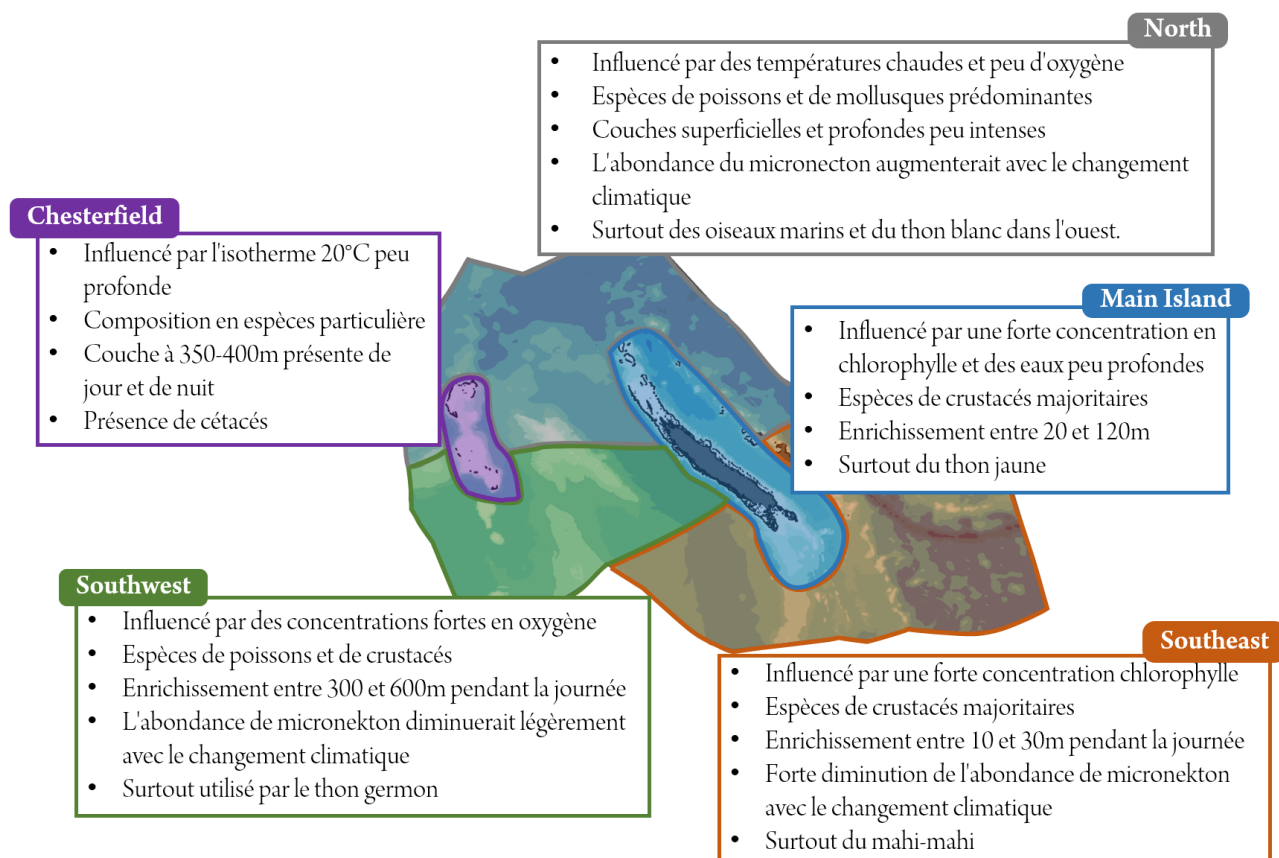


FIGURE 7.7 – Schéma représentant les 5 zones identifiées au cours de la thèse.

Au sud-est, c'est la couche de sub-surface (10-30m) qui est enrichie pendant le jour, notamment due à de fortes concentrations en chlorophylle. Le micronecton de cette région aurait une tendance négative face au changement climatique. Ce sont les mollusques qui semblent dominés, et le mahi-mahi (dorade coryphène), les globicéphales et les baleines à bec chez les prédateurs supérieurs.

La région autour des Chesterfield se démarque du reste de la zone : on y retrouve des couches de micronecton qu'on ne trouve pas ailleurs comme celle entre 350 et 400m de jour. Une nouvelle espèce de *Polyipnus* sp. (poisson hache d'argent de la famille des Sternoptychidae) y a été découverte au cours des missions Nectalis (Elodie Vourey, *Pers. Comm.* description en cours). La faible profondeur de l'isotherme 20°C y est un paramètre environnemental important, indicateur de beaucoup de mélange de la colonne d'eau, et est également certainement lié à la faible bathymétrie. Les cétacés semblent y être très présents, ce qui a déjà été observé dans le cas des baleines à bosses [Derville, 2018].

Enfin, nous avons identifié une enveloppe autour de la grande terre, s'arrêtant au niveau des îles Loyautés. Comme pour les récifs des Chesterfield, la composition en espèces de micronecton y est différente des eaux qui l'entourent, et le chapitre 2 montre un potentiel enrichissement d'espèces de micronecton résonnant à 75 et 150kHz. Cette zone est influencée par des apports lagonaires et donc riche en chlorophylle. On y retrouve des thons jaunes et du mahi-mahi en grande quantité. Cette zone englobe les récifs Pétrie et Entrecasteaux que nous avons identifiés comme zone potentielle de concentration en prédateurs supérieurs et donc potentiellement en zone d'intérêt pour la conservation.

Cette délimitation a été rendue possible grâce notamment à l'utilisation conjointe d'outils statis-

tiques. Toutes les données disponibles étaient dispersées et il aurait été compliqué d'arriver à une compréhension intégrative du milieu en se basant uniquement sur les données brutes éparses dans le temps et l'espace. Ces outils d'analyses ont des limites et peuvent introduire des biais qu'il faut garder à l'esprit lors de l'interprétation des résultats. Cependant, ils sont nécessaires à la compréhension et à la synthèse des dynamiques. Les résultats issus des extrapolations statistiques que nous avons menées ont notamment permis de travailler à l'échelle de toute la ZEE de Nouvelle-Calédonie et de recouper les informations sur l'abondance des proies, la composition en espèces et, avec plus de difficulté, sur la distribution des prédateurs supérieurs.

## 7.6 Conclusion

En conclusion, ce travail de thèse a permis de mieux comprendre la dynamique spatiotemporelle des espèces composant le micronecton dans le Pacifique sud-ouest et les processus physiques le contrôlant. Ces travaux ont également apporté une première pierre dans la caractérisation de l'écosystème pélagique dans son ensemble. Nous avons proposé des méthodes pour replacer le micronecton dans un contexte de changement climatique et comme proies des prédateurs supérieurs. Ces deux dernières études méritent de nouveaux développements pour confirmer les résultats obtenus. Tout le travail de thèse s'est concentré sur la zone économique exclusive de Nouvelle-Calédonie. En 2020, 2021 et 2022 des campagnes similaires seront réalisées dans tout le Pacifique ouest (Figure 7.8). Les méthodes développées au cours de cette thèse pourraient servir à plus large échelle, pour identifier des bio-régions.

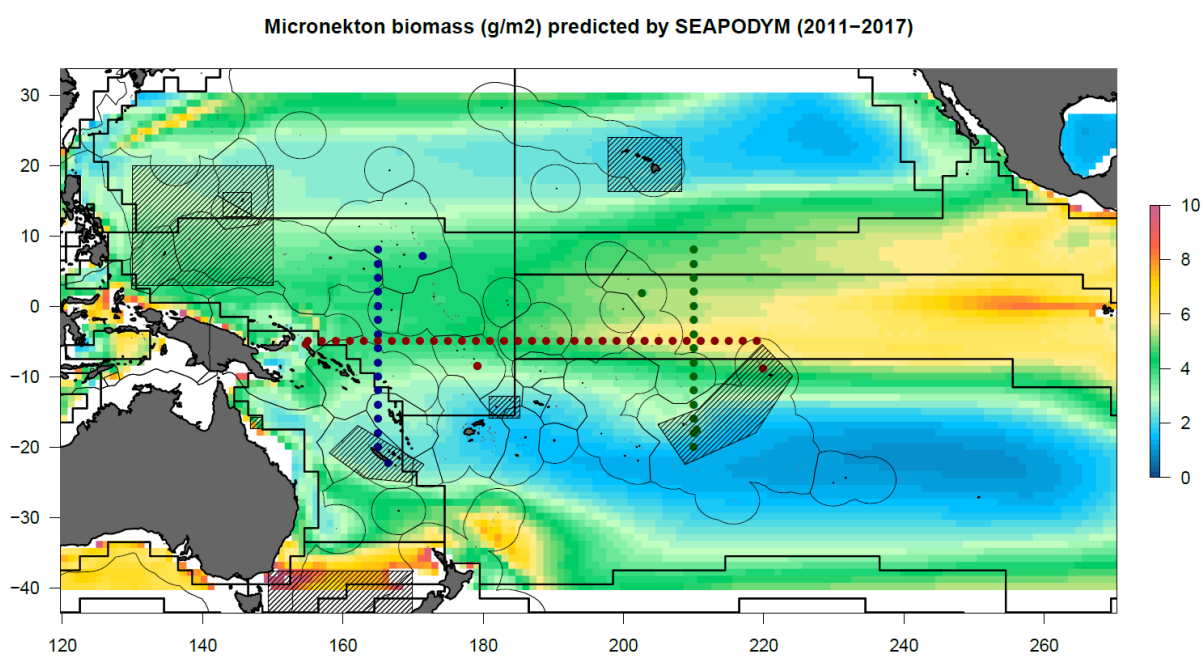


FIGURE 7.8 – Carte du Pacifique montrant les points prévisionnels d'échantillonnage des campagnes WARMALIS. Les couleurs du fond de carte représentent la biomasse de micronekton (g/m<sup>2</sup>) prédite par SEAPODYM en moyenne entre 2011 et 2017. Les polygones hachurés montrent les zones où des études sur le micronekton ont déjà été publiées récemment.

## Chapitre 8

# Annexe : Sensibilisation du jeune public au milieu pélagique et à son étude

Un objectif du projet BIOPELAGOS était la vulgarisation des résultats et la sensibilisation du jeune public au milieu marin. Comme c'est par ailleurs un sujet qui me tient à cœur, j'y ai investi du temps et de l'énergie, complétant ainsi mon travail de transmission des connaissances issues de la recherche. Cette annexe a pour objectif de présenter rapidement le public accueilli, les outils pédagogiques mis en place au cours du projet et enfin de donner quelques remarques personnelles. Cela permettra également d'avoir un document de référence pour remettre en place ce genre d'activités.

### 8.1 Les classes rencontrées

J'ai participé au cours de ces trois dernières années à 12 interventions (Table 8.1). Chaque intervention dure en moyenne 4 heures, mais il y a, au préalable, au moins le même temps de préparation. Par ailleurs, chaque nouvel outil pédagogique a demandé bien plus de temps pour son développement, afin de proposer une activité de qualité et accessible à ce genre de public. Les élèves venaient majoritairement du collège de Tuband (collège de Nouméa avec une population culturellement très mixée), mais nous avons également accueilli des élèves de Kindy School (maternelle privée bilingue) ou encore d'une école primaire (école publique Charles Bichon). Au cours de la mission embarquée dans la ZEE de Wallis et Futuna, nous avons également pu intervenir dans le collège de Futuna et faire venir sur le bateau des lycéens de Wallis. En novembre 2018, j'ai également participé à un forum/atelier des femmes au sein du collège de Tuband. Nous étions 12 femmes à témoigner des difficultés rencontrées dans nos différents milieux en tant que femme et nous étions surtout présentes pour répondre aux questions des élèves. Ce panel de classes et de lieux a permis de rencontrer et de discuter avec des jeunes de cultures et de milieux très variés et ainsi de se faire une idée assez représentative de la perception qu'ont les jeunes de leur environnement marin et de la science.

TABLEAU 8.1 – Tableau récapitulant les accueils de classe auxquels j’ai participé.

| Date       | Etablissement            | Niveau   | Age des élèves | Nombre d’élèves | Lieu d’intervention |
|------------|--------------------------|--|----------------|-----------------|---------------------|
| 05/08/2016 | Kindy school             | Moyenne section                                  | 4-5 ans        | 14              | CPS                 |
| 12/05/2017 | Collège portes de fer    | 3 <sup>ème</sup>                                 | 14-15 ans      | 16              | CPS                 |
| 23/06/2017 | Ecole charles bichon     | CE2  | 7-8 ans        | 24              | CPS                 |
| 07/06/2018 | Lycée grand Nouméa       | 6 <sup>ème</sup> à la 3 <sup>ème</sup>           | 11-15 ans      | + - 30          | Lycée               |
| 10/07/2018 | Collège de Futuna        | 3 <sup>ème</sup>                                 | 15 ans         | 20              | Collège             |
| 10/07/2018 | Lycée de Wallis          | 2 <sup>nde</sup> , 1 <sup>ère</sup> et terminale | 16-18ans       | + - 40          | Alis                |
| 29/11/2018 | Collège Tuband           | 6 <sup>ème</sup> à la 3 <sup>ème</sup>           | 11-15 ans      | + - 30          | Collège             |
| 06/03/2019 | Conseil municipal junior | 4 <sup>ème</sup>                                 | 13-14 ans      | + - 50          | CPS                 |
| 19/03/2019 | Collège Tuband           | 6 <sup>ème</sup>                                 | 11-12 ans      | 21              | CPS                 |
| 03/06/2019 | Collège Tuband           | 5 <sup>ème</sup>                                 | 12-13 ans      | 22              | CPS                 |
| 25/06/2019 | Collège Tuband           | 4 <sup>ème</sup>                                 | 13-14 ans      | 18              | CPS                 |
| 11/07/2019 | Collège Tuband           | 3 <sup>ème</sup>                                 | 14-15 ans      | 22              | CPS                 |

## 8.2 Déroulement des interventions

L’objectif de ces interventions était double : apporter des connaissances sur le milieu pélagique qu’ils ont pu l’occasion de découvrir et leur faire découvrir les métiers de la recherche. Les ateliers et outils mis en place avaient donc ce double objectif : dans chacun des cas, nous nous demandions "quelles informations sur le milieu pélagique nous voulons leurs apporter" et "quel(le) métier/tâche scientifique nous voulons leur montrer". La section qui suit présente les outils.

### 8.2.1 Les outils pédagogiques développés

#### Le poster de l’écosystème

Alors qu’une partie des jeunes naviguent sur le lagon régulièrement, ils côtoient nettement moins souvent le milieu pélagique. Un des premiers objectifs a donc été de faire un bilan non exhaustif des organismes vivant en milieu pélagique, au moins pendant une partie de leur cycle de vie. Comme pour tous les outils, nous voulions construire un support facilement déplaçable pour pouvoir l’utiliser en dehors de la CPS. La manière la plus parlante de présenter les espèces de cet écosystème étant de les montrer, nous nous sommes tournés vers un poster. Ce poster ne présente bien sûr qu’une petite partie des espèces, mais a le grand avantage de balayer tous les échelons trophiques et positionne verticalement les espèces en fonction de leurs habitats (Figure 8.1). Par ailleurs ce poster est interactif : au début l’océan est vide, seules les silhouettes des animaux sont présentes (Figure 8.1A). L’océan se remplit au cours de la discussion avec les jeunes, les animaux sont placés au fur et à mesure (Figure 8.1B). Cela permet de discuter de la biologie, de l’écologie et de la distribution spatiale de chaque espèce au fur et à mesure. Les silhouettes blanches peuvent également aider pendant le déroulement de l’activité comme nous le verrons plus bas.

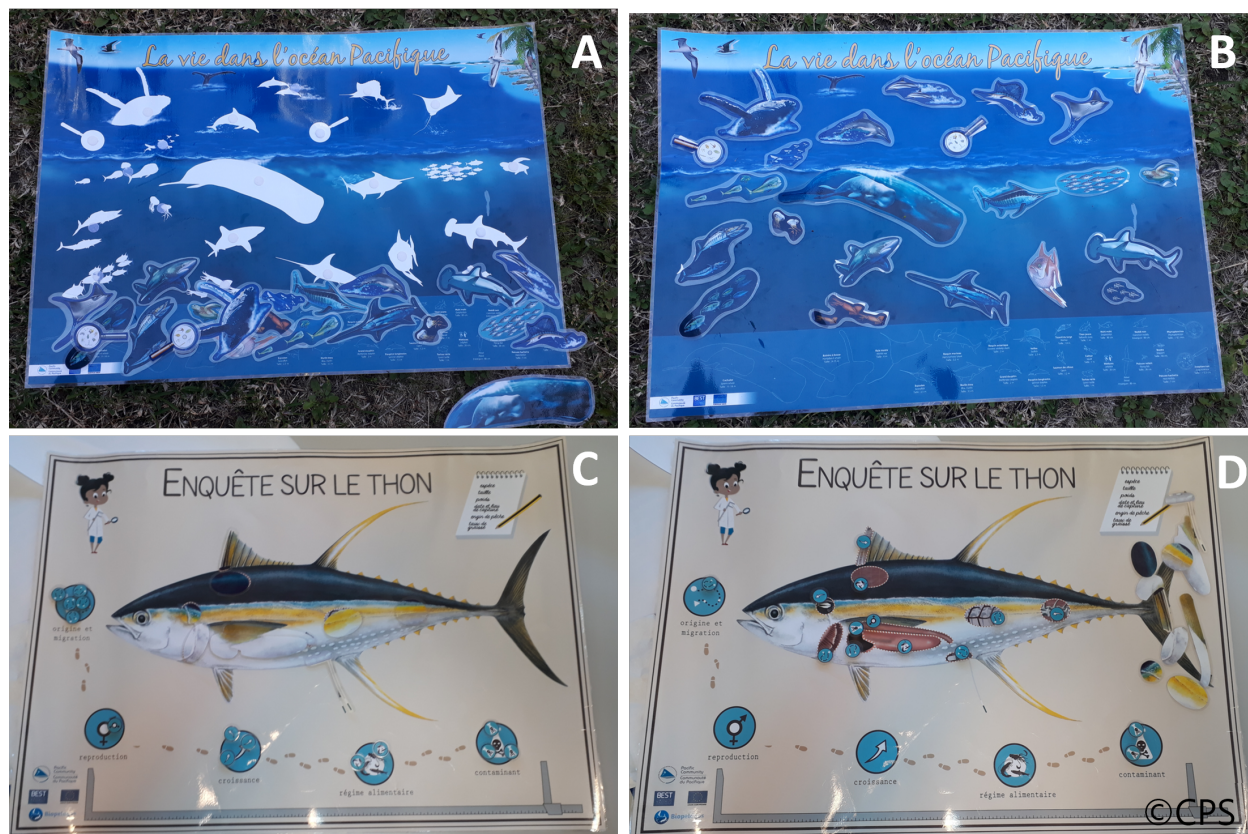


FIGURE 8.1 – Poster de l'écosystème pélagique (avant positionnement des animaux (A) puis une fois complété (B)) et poster de l'échantillonnage biologique (poisson entier sans les pictogramme (C) puis avec pictogrammes (D)).

### Le poster de l'échantillonnage biologique

Après avoir abordé la diversité des espèces présentes dans ce vaste milieu, nous voulions abordé les moyens d'étude. Contrairement aux espèces lagunaires, il est complexe d'observer les espèces pélagiques dans leur milieu naturel. L'échantillonnage biologique est une des sources essentielles d'informations concernant la biologie des organismes pélagiques et constituent par ailleurs un part non négligeable du métier de technicien. Cette fois lors de la conception du poster, nous avons voulu illustrer ce qui se passe réellement au port lors de l'échantillonnage : le poisson est initialement entier (Figure 8.1C), et on doit l'ouvrir au fur et à mesure pour y découvrir des organes/parties d'intérêt (Figure 8.1D). Souvent les jeunes n'ont aucune idée de ce qui peut être prélevé, la peau du thon jaune peut être enlevée du poster, partie par partie, et le dessin de l'organe qui apparait en dessous les aide à deviner de quel organe/partie il s'agit. On y retrouve : un muscle, un otolithe, une branchie, l'épine dorsale, le foie, une gonade, l'estomac, du sang, une vertèbre et même une marque électronique. Autour du thon, on retrouve les étapes de la vie du thon pour lesquelles on cherche des indices : son origine et ses migrations, sa reproduction, sa croissance, son régime alimentaire et la présence potentielle de contaminants. Quand une partie de peau est enlevée et l'organe/partie découvert, on vient associer le ou les pictogrammes correspondant aux informations que l'on peut en tirer. Par exemple, la gonade nous renseigne sur la reproduction (stade de maturité, sexe), l'estomac sur le régime alimentaire, ou encore le sang sur les migrations et les contaminants.

Concrètement, tous les éléments sont aimantés : un aimant plat très fin est collé sous le poster,

des petits bouts d'aimant plats sont collés sous les parties de peau qui peuvent s'enlever, et les pictogrammes sont collés sur des aimants plus épais qui les mettent en relief. Lorsque le poster est entièrement construit, on voit à la fois les organes/parties qui peuvent être échantillonnés et aussi à quoi ils peuvent servir. Bien sur, des explications sont nécessaires en parallèle pour que les jeunes comprennent bien.

Ce poster est en téléchargement libre à cette adresse [https://www.spc.int/DigitalLibrary/Doc/FAME/Posters/Anon\\_19\\_enquete\\_thon\\_A4.pdf](https://www.spc.int/DigitalLibrary/Doc/FAME/Posters/Anon_19_enquete_thon_A4.pdf) avec une plaquette explicative à cette adresse [https://www.spc.int/DigitalLibrary/Doc/FAME/Posters/Anon\\_19\\_enquete\\_thon.pdf](https://www.spc.int/DigitalLibrary/Doc/FAME/Posters/Anon_19_enquete_thon.pdf).

### Les masses d'eau

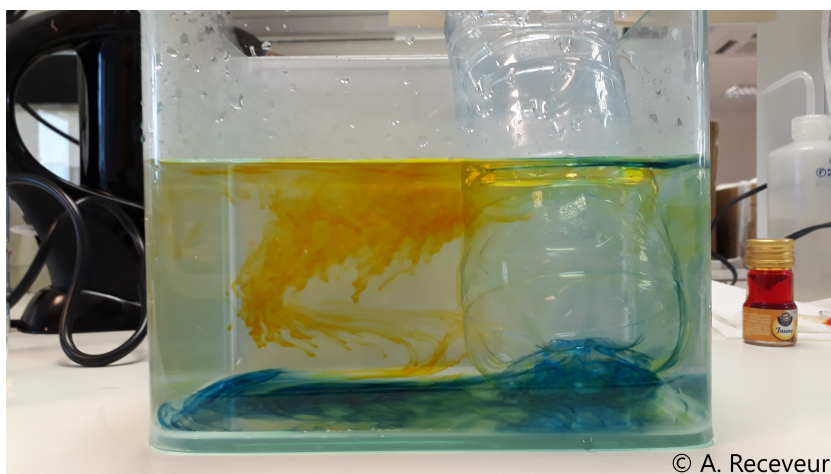
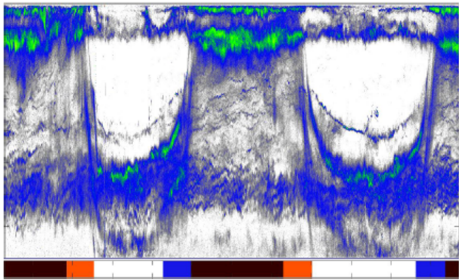


FIGURE 8.2 – Bac avec les colorants montrant le déplacement des masses d'eau.

L'étude de l'écosystème pélagique commence avec la compréhension des processus océanographiques. La circulation globale et ses moteurs m'ont toujours fascinés. C'est donc cette connaissance du mouvement des masses d'eau que j'ai voulu transmettre à travers cet atelier. Pour cela, avec l'aide de nombreux tutoriels sur internet et après de nombreux essais infructueux, j'ai mis en place une petite expérience pour visualiser le mouvement de deux masses d'eau (Figure 8.2). Dans ce petit bac transparent (l'expérience serait plus visible avec un bac plus grand), l'eau est initialement homogène et à température ambiante. Sur la droite du bac, une bouteille glacée est positionnée pour refroidir l'eau de cette partie du bac. Puis des gouttes de colorant alimentaire sont directement incorporés dans le bac : du colorant jaune sur la gauche et du colorant bleu le long de la bouteille glacée. En quelques minutes, le colorant bleu se retrouve tout au fond du bac, montrant que l'eau froide est plus dense (donc plus lourde) et se retrouve au fond et le colorant jaune reste dans la partie haute du bac. Avant d'arriver à l'état d'équilibre comme sur la photo, on observe le 'glissement' de la masse d'eau chaude sur la masse d'eau froide et l'absence de mélange : le colorant jaune qui tombe ne pénètre pas dans la couche froide, mais reste à la surface de la couche profonde.

10. Que représente cette image : les axes ? les couleurs ? est-ce le jour, la nuit, les deux ?




11. Certains poissons effectuent des migrations nyctémérales, qu'est-ce que c'est:

- des migrations de la côte vers le large
- des migrations verticales le matin et le soir entre la surface et la profondeur
- des migrations de la mer vers les rivières
- des migrations liées aux regroupements de reproduction

12. Citez le nom de deux techniques de pêche ciblant les thons.

13. Qui est qui ? A replacer : thon blanc, thon jaune, thon obèse, bonite




14. Citez deux informations obtenues à partir des données de marquage.

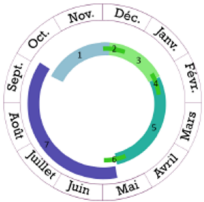
15. Cherchez les intrus. Quels sont les oiseaux marins ?

|                                   |                                   |  |
|-----------------------------------|-----------------------------------|--|
| <input type="checkbox"/> albatros | <input type="checkbox"/> aigrette | <input type="checkbox"/> notou           |
| <input type="checkbox"/> manchot  | <input type="checkbox"/> sterne   | <input type="checkbox"/> poule           |
| <input type="checkbox"/> lunette  | <input type="checkbox"/> puffin   | <input type="checkbox"/> noddi           |
| <input type="checkbox"/> frégate  | <input type="checkbox"/> pétrel   | <input type="checkbox"/> paille-en-queue |
| <input type="checkbox"/> fou      | <input type="checkbox"/> mouette  | <input type="checkbox"/> cagou           |

16. Redonnez son nom à chacun des Procellariiformes nichant en Nouvelle-Calédonie (Pétrel à ailes noires, Puffin fouquet, Pétrel de Tahiti, Pétrel de Gould).



17. Remplacez les différents stades du cycle reproducteur des puffins fouquet en leur donnant le bon numéro.



- Ecllosion
- Exode inter-nuptial
- Ponte
- Envol du jeune
- Incubation (couvaision)
- Période pré-positale
- Elevage du poussin

18. Pourquoi les oiseaux marins sont-ils marqués ? Plusieurs réponses possibles.

- pour pouvoir les identifier
- pour mieux comprendre leurs comportements d'alimentation
- pour qu'ils soient plus jolis
- pour identifier les zones marines très productives, riches en proies et en biodiversité
- pour analyser la structure des réseaux trophiques marins
- pour savoir où ils nichent

19. Pouvez-vous donner un âge à ce poisson ? (Aidez-vous de la zone entourée) ©CPS

FIGURE 8.3 – Deux exemples de pages du quizz mis en place pour les élèves de troisième.

### Le quizz des troisièmes

Lors de la venue de la première classe de troisième (12 mai 2017), nous avons choisi de séparer la matinée en deux temps : deux premières heures de présentation pour leur apporter des connaissances avant de faire deux heures d'ateliers pour replacer ses connaissances dans leurs contextes de manière interactive. Pour garder leur attention durant les présentations, nous avons mis en place un quizz dont les réponses étaient données au cours des présentations (Figure 8.3). Les présentations portaient sur divers sujets : la CPS et le projet BIOPELAGOS, la physique, le micronecton, les thons et les oiseaux marins. Le quizz enchainait donc les questions sur ces différentes thématiques. Il y avait des questions très ciblées avec des réponses à choix multiples mais aussi des questions très ouvertes pour les faire réfléchir (par exemple, "Qu'est-ce-que le mot phénomène El Niño évoque pour vous?" ou encore "Quelle est la source d'énergie qui permet aux vents de souffler, aux océans de bouger, à la vie de se développer dans l'océan et sur terre?"). Un accent était mis sur les outils d'analyses, avec des questions sur une CTD (sonde pour *Conductivity Temperature Depth*), un échogramme acoustique, les données de marquage, les otolithes.

Cependant, les présentations proposées étaient sûrement trop longues et il n'est pas simple de garder l'attention de ce jeune public, en particulier lorsqu'ils sont en dehors de leur salle de classe. Malgré le mot 'quizz', les élèves m'ont demandé si cela allait être noté et leur investissement est largement retombé lorsque j'ai répondu par la négative. Nous n'avons pas réitéré cette expérience même avec les classes suivantes de troisième, et nous avons ensuite privilégié tous les ateliers interactifs où les jeunes pouvaient être acteurs des connaissances.



### 8.2.2 Les méthodes/ateliers mis en place

Nous avons donc choisi de mener uniquement des ateliers interactifs plutôt que des présentations plus formelles. Nous avons construit une demi-journée type où la classe est séparée en quatre groupes et chaque groupe tourne entre quatre ateliers. Au total, nous avons construit cinq ateliers et nous en choisissons quatre parmi eux en fonction du public accueilli et des collègues présents pouvant animer ses ateliers. Globalement, le déroulement est toujours le même : il y a un atelier pour poser le cadre de l'écosystème pélagique et ses moyens d'études, et trois autres ateliers plus vivants avec des jeux/manipulations que les élèves mettent en œuvre eux mêmes.

#### L'écosystème pélagique

Cet atelier a pour objectif de poser un cadre, de faire du lien avec les trois autres. Le plan de cet atelier reprend le plan de l'introduction générale de cette thèse, ou plutôt, j'ai repris le plan de cet atelier dans mon introduction de thèse. Nous abordons dans un premier temps les habitants de l'écosystème pélagique, puis les menaces et enfin nous tentons de déterminer quelles solutions pourraient être apportées. L'animation débute avec un *brainstorming* des espèces vivant en haute mer qu'on ne retrouve pas dans le lagon. Les silhouettes blanches du poster sont évidemment une grande aide pour deviner les espèces. A partir de la classe de 6<sup>ème</sup>, je cache le poster pour ne pas que les silhouettes empêchent les élèves de réfléchir par eux mêmes. Une fois toutes les espèces du poster à leurs places (comme sur la Figure 8.1B), j'introduis la notion de réseau trophique et le principe du 'qui mange qui', et je ré-enlève chacune des espèces au fur et à mesure que l'on monte dans la pyramide trophique.

Nous commençons tout naturellement avec le phytoplancton et la production primaire. Nous discutons ensuite du zooplancton puis du micronecton. Une manière de leur montrer l'importance de ce dernier groupe, est d'enlever le phytoplancton, le zooplancton, les méduses, les calmars, les poissons volants et les poissons hache et de leurs montrer que toutes les espèces restantes sur le poster (presque toutes) dépendent de ce micronecton. Et donc que même si l'homme ne les consomme pas directement, toutes les espèces que nous mangeons ou que nous aimons observer (baleines ou dauphins) dépendent fortement et directement de la présence de ces petites espèces.

Le thème des oiseaux marins amène beaucoup de questionnement. Les élèves ont l'air de savoir que certains oiseaux sont marins et d'autres non, mais peu d'élèves peuvent expliquer ce qui différencie vraiment ces deux groupes. Lorsque nous cherchions ensemble quelles espèces d'oiseaux marins pouvaient être présent sur le poster, le pigeon est souvent arrivé en première position jusqu'en classe de quatrième (et pourtant nous ne vivons pas à Paris).

Une fois que les espèces pélagiques et le réseau trophique sont compris, nous passons aux menaces (Figure 8.4). Je rajoute alors simplement trois grandes cartes A4 sur le mur à côté du poster où le nom de chacune des menaces est inscrit (pollution, sur-pêche et changement climatique) une fois la menace identifiée par les élèves. Nous discutons ensuite sans support, des leviers d'action possible à notre échelle contre la pollution et le changement climatique. Finalement, j'aborde les différentes mesures de gestion des pêcheries en commençant toujours par un *brainstorming*. Les mesures de limite de taille (minimale et maximale) arrivent souvent en première position, sûrement car cette mesure est très uti-



FIGURE 8.4 – Atelier sur l'écosystème pélagique.

lisée pour les espèces récifales en Nouvelle Calédonie. La notion de quotas et de limite de nombres de bateaux par licences arrive souvent en deuxième position. Par contre, la délimitation d'aires marines protégées n'est que peu proposée par les élèves.

Je leur explique alors que toutes ces mesures nécessitent des connaissances solides sur la biologie et l'écologie de chaque espèce, et que pour en apprendre d'avantage, l'échantillonnage biologique est une source inestimable d'informations. La connaissance des migrations est par exemple nécessaire pour délimiter des zones protégées, la quantité de mâles et de femelles, le taux de reproduction, la vitesse de croissance pour la mise en place des quotas, ou encore que les analyses chimiques permettent de s'assurer que le poisson est sain à la consommation.

Cet atelier brosse donc un tableau du fonctionnement de l'écosystème pélagique, des menaces et des solutions et chacun des trois autres ateliers de la matinée est replacé dans son contexte. L'avantage d'avoir un atelier dédié à l'explication du contexte est de laisser plus de temps aux autres ateliers pour expérimenter, jouer, manipuler. En donnant tout le raisonnement en une fois aux élèves, cela clarifie également le message et leur permet de mieux suivre, de le comprendre et donc de le retenir.

### La taxonomie

Au cours de cet atelier, les élèves sont sensibilisés au travail de laboratoire et à la taxonomie du micronecton. L'atelier commence avec une identification de requin à l'aide d'une clé d'identification simplifiée (Figure 8.1). Cette démarche permet de faire manipuler aux élèves les critères morphologiques du requin dont une représentation simplifiée accompagne la clé d'identification. S'en suit une discussion sur le rôle de la taxonomie : pourquoi est-ce important de pouvoir nommer ce qui nous entoure. Pour finir, les élèves observent des spécimens de micronecton à la loupe et au microscope. Cela leur per-



FIGURE 8.5 – Atelier taxonomie.

met de mettre en œuvre les apprentissages qu'ils ont suivi sur les manipulations en laboratoire pendant leurs cours de SVT. Des poissons hachés sont notamment observés pour faire le lien avec le poster de l'écosystème pélagique où ils apparaissent.

### Les otolithes

L'extraction d'otolithes a toujours beaucoup de succès. L'animation débute avec des images A4 de coupe transversale de tronc d'arbres, les élèves reconnaissent rapidement la coupe d'arbre et savent que l'on peut connaître l'âge de l'arbre en comptant les cernes. On leur montre ensuite des images A4 de coupes d'otolithes bien choisies où l'otolithe ressemble fortement à la coupe d'arbre, pour leur faire comprendre que l'on peut connaître l'âge du poisson avec une coupe d'otolithe. Pour les plus âgés (à partir de la 5<sup>ème</sup>), l'animation continue avec l'exécution d'un petit logiciel développé par l'IUEM qui permet de lire plusieurs lames d'otolithes d'une espèce à la suite (téléchargeable sur ce lien <https://www-iuem.univ-brest.fr/intranet/communication/ressources-danimations-et-mediations/animation-sclerochronologie>). Le logiciel affiche une photo de lame d'otolithe, et les élèves doivent entrer l'âge qu'ils estiment donner au poisson. Ensuite, le logiciel donne la réponse de l'âge du poisson ainsi que sa taille. Les élèves peuvent alors placer sur une grille qu'on leur distribue une vingtaine de couples (age du poisson-taille du poisson) et ainsi construire une courbe taille-âge. Cette étape leur permet de comprendre explicitement l'intérêt de l'analyse d'otolithes.

La dernière partie de l'atelier est celle qui connaît généralement le plus grand succès : chaque binôme a une tête de poisson (souvent des mullets dont les otolithes sont gros) et doit retrouver les deux otolithes dans la tête du poisson. L'animateur leur montre au préalable un exemple pour savoir où chercher (Figure 8.6). Passé un petit moment de dégoût, notamment chez les adolescents, les élèves mettent toute leur énergie pour trouver ces précieux otolithes qu'ils peuvent ramener avec eux.



FIGURE 8.6 – Démonstration au cours de l'atelier otolith.

### **Le jeu de rôle du tagging**

Le dernier atelier porte sur la mise en place du marquage des thons. Il commence avec une courte vidéo (4 min) où toutes les étapes d'une campagne de marquage de la CPS sont montrées. La vidéo n'a ni paroles ni musique, et la personne qui anime doit donc d'écrire les étapes successives. Le bateau est d'abord filmé, avec les différents postes de travail. On y voit le capitaine qui commande le bateau, les marins qui observent l'océan pour détecter les bancs et qui agitent une cloche lorsqu'ils en détectent un. On voit ensuite le maître des appâts qui les lance à la mer pour attirer les thons, et le coup de pêche peut commencer. Les pêcheurs à la canne remontent le poisson sur le pont; puis le scientifique le mesure, le marque et le remet à l'eau.

Une fois que la vidéo est terminée, le jeu de rôle peut commencer. Tout d'abord, les rôles sont distribués entre les élèves. Pour les plus jeunes, une couronne avec leur rôle est distribuée (comme sur la photo 8.7). Ensuite, avec plus ou moins d'aide en fonction de l'âge des élèves, ils doivent reproduire un coup de pêche. Un élève pilote donc le bateau, un autre tient des jumelles et doit sonner une cloche lorsqu'il repère un banc, un maître des appâts lance des petites poissons en caoutchouc. Puis les pêcheurs entrent en action et doivent attraper des poissons posés sur un support; qu'ils passent au scientifique. Le scientifique identifie l'espèce, le mesure, le marque et le rejette à l'eau. Un assistant scientifique doit écrire ces informations sur une feuille.

Il est possible pour les plus grands d'ajouter une partie réflexion : un certain nombre de poissons sont cachés sous un drap, nous leur donnons le nombre de poissons marqués qui ont été recapturés et ils peuvent alors calculer le nombre de poissons total qu'il y a sous le drap. Les 4<sup>èmes</sup> et les 3<sup>èmes</sup> pouvaient deviner la formule, mais nous la donnions aux plus jeunes.

Cet atelier a été animé pour des élèves de la moyenne section de maternelle à la troisièmes. Comme pour les autres ateliers, la manière d'apporter les connaissances et d'animer l'atelier changent en fonction de l'âge des élèves mais l'outil reste identique.



FIGURE 8.7 – Atelier marquage des thons.

### La physique

Cet atelier n'a été mis en place que pour des troisièmes car il aborde des notions plus compliquées à appréhender. L'atelier commence avec l'animation présentée plus haut où les élèves observent simplement le mouvement des colorants simulant les masses d'eau chaude et froide. S'ensuit une discussion pour les amener à la notion de densité et des paramètres pouvant faire varier cette densité (Figure 8.8). Ensuite, l'animateur leur explique que grâce à ces différences de densité, les masses d'eau plongent à certains endroits du globe et remontent à d'autres. Les élèves dessinent alors la circulation thermo-haline globale (le 'tapis roulant' de l'océan). Le changement climatique et ses processus physiques sont aussi abordés au cours de cet atelier par la visualisation de cartes de SST dans le présent et dans le futur.

Finalement, des cartes (de la taille de cartes à jouer) avec différents engins d'observations leurs sont montrées (un mouillage ancré, un satellite, un filet à plancton, une CTD, un éléphant de mer avec une sonde accorchée à la tête, une bouée dérivante et un glider). Ces cartes doivent être replacées sur une grille temps-espace en fonction des échelles spatiotemporelles que ces engins peuvent mesurer.



FIGURE 8.8 – Atelier physique.

### 8.3 Quelques résultats

Pour conclure cette partie, je mets quelques constats personnels fait au cours de ces ateliers afin de proposer une sorte d'évaluation-bilan de cette approche de vulgarisation que nous avons mis en place. J'ai spécialement organisé les quatre dernières interventions : un accueil de classes de la sixième à la troisième en deux mois. Je voulais essayer de comprendre l'évolution des connaissances et du comportement de l'enfant qui grandit et pouvoir proposer des pistes d'adaptation des outils et des messages au public rencontré. La partie qui suit a donc pour objectif de donner quelques résultats qui pourraient aider à la mise en place d'interventions plus systématiques. Tous ces résultats se basent sur des observations faites sur un nombre restreint d'élèves et n'engagent que moi. J'ai essayé de dégager des faits qui me semblaient représentatifs de tous les élèves rencontrés.

#### 8.3.1 Sur les développement de l'enfant

J'ai noté un net changement dans le comportement et dans les capacités de réflexion des élèves entre les 6<sup>èmes</sup>, 5<sup>èmes</sup> d'un côté et les 4<sup>èmes</sup>, 3<sup>èmes</sup> de l'autre. Jusqu'en 5<sup>ème</sup> les élèves sont très spontanés et donnent à peu près toutes idées qui leurs passent par la tête. A partir de la 4<sup>ème</sup>, les élèves donnent moins de réponses mais ces dernières sont plus réfléchies. Les 3<sup>èmes</sup> sont encore moins spontanés, et réfléchissent à chacune de leurs réponses. J'ai eu le sentiment que la peur de la moquerie des autres les bloquait. Ils ne veulent plus se démarquer des autres et ne cherchent donc plus à donner de réponse. Par conséquent, l'intérêt de ce genre d'intervention est limité car les élèves ne cherchent plus vraiment à comprendre. A mon sens, la classe idéale pour faire ce genre d'intervention est donc la 4<sup>ème</sup> où l'on retrouve une alliance parfaite entre la curiosité, la spontanéité et les capacités de réflexion.

Des différences de comportement entre fille et garçon apparaissent. Un exemple qui m'a marqué s'est passé avec la classe de CE2 (environ 8 ans). Lors du jeu de rôle sur le marquage, un scientifique a

pour mission de mesurer, marquer et remettre le poisson à l'eau. Un assistant scientifique doit noter les informations sur une fiche. Parmi tous les rôles (dont capitaine, pêcheur et scientifique par exemple), la majorité des filles voulaient être assistante. Elles aimaient remplir les fiches proprement et que ces dernières soient belles. J'ai pourtant essayé de les encourager à faire pêcheur, capitaine, ou scientifique en leurs expliquant les tâches très intéressantes que ces métiers impliquaient, mais elles insistaient pour être assistante et se battaient pour ce poste. Je constate une auto-censure des filles sur des métiers à tort attribués aux hommes et je me demande quelles actions nous pourrions mettre en place pour palier à ce constat.

Un peu plus tard, une bonne majorité des collégiennes étaient capable de citer les baleines et les dauphins comme habitants de l'écosystème alors que les garçons parlaient de Mahi-mahi (le nom local de la dorade coryphène), de thons et de coup de pêche. De la même manière, comment réussir à désaxifier certaines activités comme la pêche reste une question importante.

### 8.3.2 Sur leurs connaissances

Le principe général de la photosynthèse est abordé en classe de sixième pour la première fois et est revu en cinquième. Il semble effectivement important de rappeler ces notions au cours de tous les niveaux car le terme photosynthèse (lors des discussions sur le phytoplancton) n'est apparu qu'avec les quatrièmes et une bonne explication de la photosynthèse n'a été donné que par des élèves de troisième. C'est finalement la répétition au fil des années de collège qui permet aux élèves de maîtriser cette notion et d'être capable de la ré-investir en dehors du contexte de leur classe de SVT.

De la même manière, j'étais assez étonnée que des élèves de cinquième ne puissent pas vraiment différencier les mammifères marins des autres espèces. Un élève a par exemple parlé de baleine à écailles en cinquième. De manière générale, et jusqu'à la troisième les élèves ne semblent pas très familiers au milieu marin. La source principale de connaissances est l'alimentation, les élèves connaissaient souvent les poissons consommés régulièrement en Nouvelle-Calédonie. Jusqu'à la troisième, ils avaient du mal à différencier les espèces du lagon des espèces pélagiques. Comme citée plus tôt dans cette annexe, la différence fondamentale entre un pigeon et une mouette ou un puffin n'était pas toujours pas maîtrisée.

J'étais également surprise de la méconnaissance du changement climatique en sixième et en cinquième. Parmi tous les élèves de ces deux niveaux, un seul a été capable de me parler du changement climatique (un deuxième a cité le "sur-chauffage" de la terre et n'était donc pas bien loin de l'idée). Les quatrièmes et les troisièmes étaient plus conscients de cette problématique. Lorsque finalement je leurs donnais la réponse et que nous discussions des choses que nous pourrions faire à notre échelle pour limiter cette menace, là encore ce n'était pas simple. Le lien entre l'énergie (essence, électricité) et le changement climatique n'est pas du tout compris en sixième et cinquième et n'est pas facilement explicité par les quatrièmes et troisièmes.

Au contraire, la pollution, et notamment le plastique, est connue par tous. Connaissez-vous l'histoire de la tortue qui mange un sac plastique en la confondant avec une méduse? Et bien absolument tous les élèves que j'ai rencontré connaissent cette histoire et me l'ont cité dans les deux premières minutes de la discussion sur les menaces. Je pense que c'est dû à plusieurs facteurs : la tortue est un animal relativement emblématique, facilement identifiable et très présent en NC, le cas est concret et met en

scène un objet du quotidien, le sac. Contrairement au changement climatique, cette image parle aux élèves. Je pense qu'il serait intéressant de mener une étude sur la manière dont cette publicité/image a été diffusée ces dernières années, et de s'en inspirer pour faire passer d'autres messages cruciaux.

Au niveau de la surpêche, les élèves avaient des idées assez claires. Encore une fois, le contexte local aide. Dans tous les niveaux, ils étaient capable de citer de nombreuses mesures pour préserver la ressource, avec même parfois quelques réflexions enfantines naïves mais criantes de vérités comme cet élève de sixième "si on pêche presque tous les adultes trop vite, on ne les laisse pas assez longtemps dans l'eau pour qu'ils grandissent et aient des bébés, et alors ils disparaissent et on ne peut plus en manger".

Pour conclure, je pense qu'il serait intéressant d'ajouter quelques connaissances sur le milieu marin et sur le changement climatique au programme du collège, d'autant plus dans une île comme la Nouvelle Calédonie où la population dépend fortement de l'océan (voir description du projet BIOPELAGOS au début de ce manuscrit). Je pense que des évènements comme la fête de la science sont également des évènements parfaitement adaptés pour faire passer ces messages. J'ai personnellement beaucoup aimé mener ces différentes activités, et côtoyer ces jeunes de tout horizon culturel qui font la richesse de la Nouvelle-Calédonie. J'espère que la description des ateliers pourra inspirer d'autres équipes à les mettre en place.



FIGURE 8.9 – Photo de groupe avec les élèves de 3<sup>ème</sup> du collège de Tuband.





## Chapitre 9

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