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

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### **Competing interests**

The authors declare no competing interests.

## 1 **Abstract**

2 Acoustic data are invaluable information sources for characterizing the distribution and abundance of  
3 mid-trophic-level organisms (micronekton). These organisms play a pivotal role in the ecosystem as  
4 prey of top predators and as predators of low-trophic-level organisms. Although shipboard-ADCP  
5 (acoustic Doppler current profiler) acoustic backscatter signal intensity cannot provide an absolute  
6 biomass estimate, it may be a useful proxy to investigate variability in the distribution and relative  
7 density of micronekton. This study used acoustic recordings data spread across 19 years (1999–2017)  
8 from 54 ADCP cruises in New Caledonia’s subtropical EEZ (exclusive economic zone) to assess  
9 seasonal and interannual variabilities and spatial distribution of micronekton. The dataset was  
10 composed of two different ADCPs: 150 kHz for the first period, followed by 75 kHz for more recent  
11 years. We examined the 20–120 m averaged scattering layer. Using the few cruises with concurrent  
12 EK60 measurements, we proposed that the backscatter from the ADCPs and 70 kHz EK60 were  
13 sufficiently closely linked to allow the use of the backscatter signal from the ADCPs in a combined  
14 dataset over the full time series. We then designed a GAMM (generalized additive mixed model)  
15 model that takes into account the two ADCP devices as well as temporal variability. After accounting  
16 for the effect of the devices, we showed that the acoustic signal was mainly driven by diel vertical  
17 migration, season, year, and ENSO (El Niño-Southern Oscillation). In a second step, a consensus  
18 model between two statistical approaches (GAMM and SVM) (support vector machine) was  
19 constructed, linking the nighttime 20–120 m backscatter to the oceanographic and geographic  
20 environment. This model showed that sea surface temperature was the main factor driving backscatter  
21 variability in the EEZ, with intensified backscatter during the austral summer (December to May) in  
22 the northern part of the EEZ. We showed that acoustic density differed significantly, spatially and  
23 temporally from micronekton biomass predicted for the same period by the SEAPODYM-MTL (mid-  
24 trophic level) ecosystem model. The seasonal cycle given by ADCP data lagged behind the  
25 SEAPODYM-MTL seasonal cycle by around three months. Reasons to explain these differences and  
26 further needs in observation and modeling were explored in the discussion. In addition to providing  
27 new insights for micronekton dynamics in this EEZ (i.e., the science needed for ecosystem-based  
28 fisheries management), the data should help improve our ability to model this key trophic component.

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

30

31

## 32        **1. Introduction**

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

39    Tuna forage fauna is mostly composed of micronekton, which are mid-trophic-level  
40    organisms comprising crustaceans, molluscs, gelatinous organisms, and fish measuring  
41    between 1 and 20 cm (Bertrand et al., 2002; Young et al., 2015). Distributed in the upper  
42    1000 m of the water column (Gjøsaeter and Kawaguchi, 1980), micronekton are layer-  
43    distributed (Burgos and Horne, 2008). Vertical layer positions are influenced by physical-  
44    chemical properties of the water mass such as oxygen or temperature (Klevjer et al., 2016), or  
45    by the presence of predators (Benoit-Bird et al., 2017). Micronekton abundance is also  
46    influenced by environmental conditions such as primary production (Escobar-Flores et al.,  
47    2013; Irigoien et al., 2014) or the presence of eddies or fronts (Behagle et al., 2016; Sabarros  
48    et al., 2009). A large proportion of micronekton organisms undertakes diel vertical migrations  
49    (DVM), moving from the mesopelagic zone (200–1000 m), where they stay during the day, to  
50    the more productive surface layer (0–200 m) during the night (Pearre, 2003). DVM are  
51    observed across all oceans (Bianchi and Mislan, 2016; Klevjer et al., 2016) and are  
52    recognized today as the biggest biomass movement on earth (Hays, 2003). In addition to their  
53    pivotal role between low trophic-level organisms and top predators (Bedford et al., 2015;  
54    Giménez et al., 2018), micronekton actively contribute to the downward flux of nutrients and  
55    particulate organic matter by their DVM (Ariza et al., 2016, 2015; Drazen and Sutton, 2017;  
56    Kiko et al., 2017).

57    Understanding the dynamics of micronekton in the water column and their horizontal spatial  
58    distribution at different scales remains challenging. Net trawling is the traditional sampling  
59    approach (Potier et al., 2014). Trawl data, however, are size and/or species dependent due to  
60    the net avoidance behavior of organisms; therefore, obtaining an unbiased quantitative  
61    estimate with trawls is challenging (Heino et al., 2011; Kaartvedt et al., 2012). Further, trawls  
62    are temporally and spatially discrete data, which complicates their use in attempting to have  
63    large-scale micronekton estimates of the area considered. Therefore, net sampling is often

64 complemented by the use of echosounders to study the distribution and behavior of pelagic  
65 biota. Two types of echosounders exist: calibrated and un-calibrated. Calibrated  
66 echosounders, initially devoted for studying the behavior of pelagic organisms, are widely  
67 used to study the organism distribution throughout the water column (e.g., Cade and Benoit-  
68 Bird, 2015; Kloser et al., 2002).

69 The sampling coverage from the shipboard un-calibrated acoustic Doppler current profiler (S-  
70 ADCP, hereafter referred to “ADCP”) is potentially huge compared with the one available  
71 from calibrated echosounders. Indeed, given that the ADCP, initially devoted for measuring  
72 current velocities, has been used routinely for several decades to measure currents, ADCP  
73 records can provide much wider spatial and temporal coverage than scientific echosounders.  
74 Moreover, ADCPs have been successfully compared with calibrated echosounders (Brierley  
75 et al., 1998; Fiedler et al., 1998; Gostiaux and van Haren, 2010; Griffiths, 1996; Lee et al.,  
76 2004), suggesting that ADCPs can provide a proxy of relative density of combined  
77 zooplankton and micronekton (Lee et al., 2004; Menkes et al., 2015; Radenac et al., 2010).  
78 Several studies have used ADCP records to investigate the distribution and variability of  
79 scattering layers in the ocean (e.g., Chereskin and Tarling, 2007; Radenac et al., 2010; Smeti  
80 et al., 2015). These studies used the method developed by Flagg and Smith (1989), which  
81 allows the use of ADCP echo intensity as a proxy for abundance.

82 For both calibrated and un-calibrated echosounders, organism biomass estimation needs the  
83 knowledge of community species composition and their target strengths. To achieve a better  
84 discrimination between species or groups of species, a combination of methods such as net  
85 sampling (e.g., Nishikawa et al., 2001), optics measurements using videos (e.g., Kloser et al.,  
86 2016), eDNA (e.g., Bohmann et al., 2014), or recording several frequencies (e.g., Davison et  
87 al., 2015b) is recommended. Moreover, scattering of layers recorded by both types of  
88 echosounders could be dominated by some organisms’ resonance that hides weaker scatterers  
89 and, therefore, the echo intensity recorded is less representative of all micronektonic species  
90 that are present.

91 Net sampling and acoustic data also provide critical information to calibrate and validate  
92 ecosystem models, including a representation of mid-trophic functional groups (Handegard et  
93 al., 2013). Such models allow for estimating, at regional and global scales, the biomass of  
94 micronekton based on key biological processes and first ecological principles such as growth  
95 and mortality rates with temperature. SEAPODYM – Spatial Ecosystem and Population

96 Dynamics Model – is a model where both micronekton groups and predator fish (e.g., tuna)  
97 population dynamics are described (Lehodey et al., 2010, 2008). A method has been  
98 developed to assimilate biomass observations in this model for the estimation of energy  
99 transfer efficiency coefficients between micronekton groups (e.g., migrant and resident). It  
100 has been demonstrated, using acoustic data directly, that acoustic signal and biomass are  
101 directly proportional (Lehodey et al., 2015). To explore the interest in using existing abundant  
102 and archived ADCP data in a future data assimilation ecosystem modeling framework, we  
103 investigate a 19-year time series of ADCP data, collected through 54 oceanographic cruises in  
104 New Caledonia’s exclusive economic zone (EEZ).

105 New Caledonia is located in the Coral Sea at the southwestern edge of the Pacific Ocean. New  
106 Caledonia and the nearby Vanuatu Archipelago create an obstacle to the westward South  
107 Equatorial Current (SEC), the dominant feature of water circulation for surface, thermocline  
108 and intermediate waters. The SEC is divided into zonal jets when encountering New  
109 Caledonia’s islands, and finally, waters above the thermocline diverge into two branches  
110 around 15°S when reaching the Australian coast (Cravatte et al., 2015). In this region, general  
111 circulation models are prone to shear instabilities, and high eddy kinetic energy is observed  
112 (Qiu et al., 2009; Rousselet et al., 2016), which may influence the distribution of deep-sea  
113 organisms (Behagle et al., 2014; Tew Kai and Marsac, 2010). On the western barrier reef of  
114 New Caledonia’s main island, strong winds during the austral summer (December to May)  
115 also create upwelling conditions that cool the sea’s surface temperature and create the vertical  
116 movement of nutrients (Alory et al., 2006; Ganachaud et al., 2010; Marchesiello et al., 2010).  
117 Excluding very coastal areas, New Caledonia’s EEZ is regarded as oligotrophic, with a higher  
118 productivity zone south of 22°S (Ceccarelli et al., 2013; Dandonneau and Gohin, 1984).

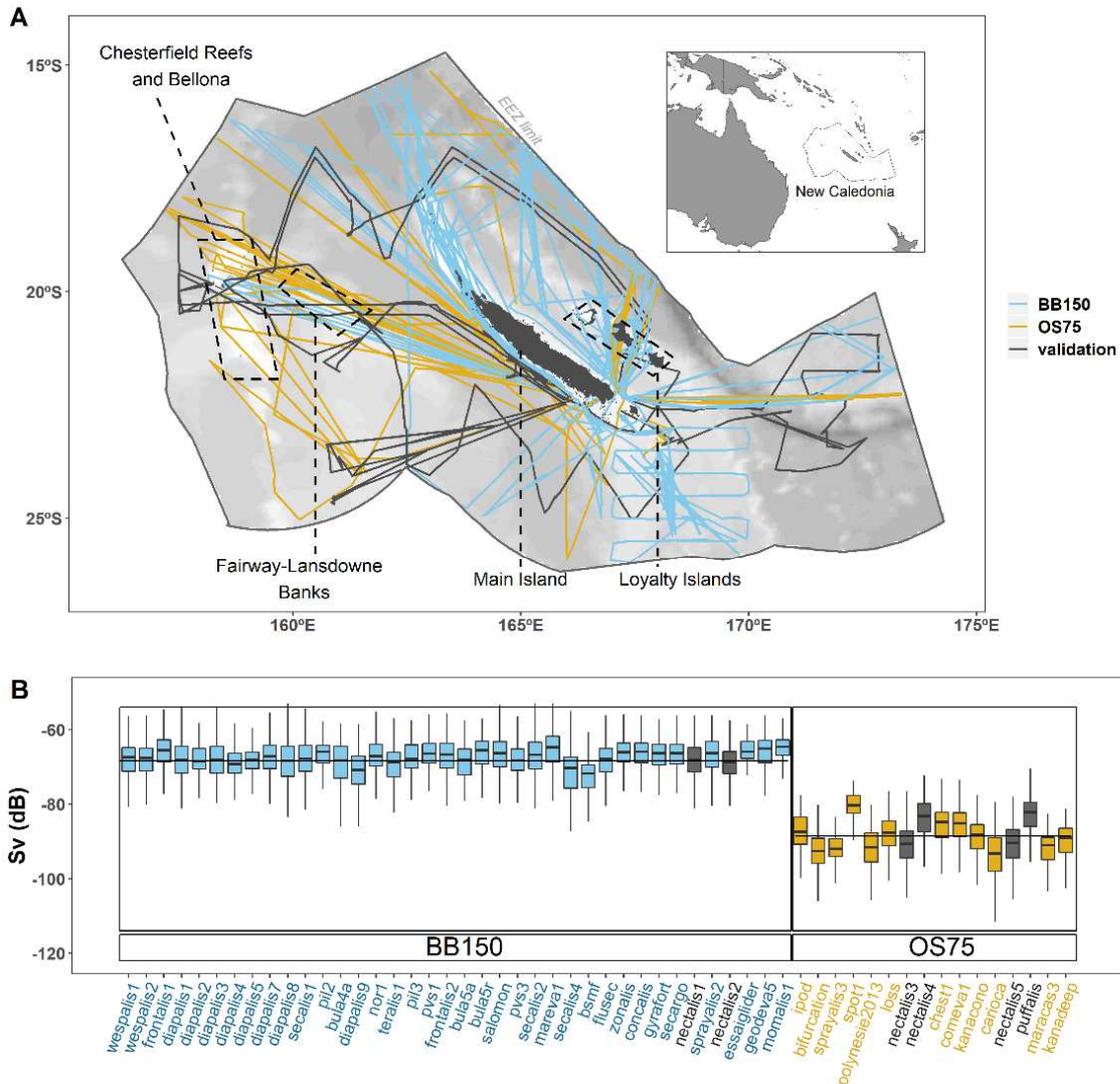
119 The active management of the recently created Coral Sea Natural Park (Decree 2014-  
120 1063/GNC) creates a need for robust information on the productivity and functioning of this  
121 remarkable ecosystem, including micronekton dynamics and the pivotal role of micronekton  
122 in food webs. Micronekton taxonomy, distribution and biomass are still poorly known in the  
123 Coral Sea (Ceccarelli et al., 2013) and in New Caledonia’s EEZ (Gardes et al., 2014). Top  
124 predator diet studies (Allain et al., 2012; Olson et al., 2014; Williams et al., 2014; Young et  
125 al., 2010) and trawl data analyses (Grandperrin et al., 1999; Menkes et al., 2015; Young et al.,  
126 2011) have emphasized a high level of diversity in macro-zooplankton and micronekton, with  
127 a dominance of Gonostomatidae, Sternoptychidae, Myctophidae, Scopelarchidae and

128 Phosichthyidae (Ceccarelli et al., 2013; Grandperrin, 1975; Sutton et al., 2017; Vourey et al.,  
129 2017).

130 Behind these studies focusing on species diversity, the amount of data collected specifically to  
131 study micronekton abundance, together with co-located oceanographic conditions, are still  
132 rare (Menkes et al., 2015; Smeti et al., 2015). In New Caledonia's EEZ, poor data coverage  
133 prohibits a comprehensive description of the pelagic ecosystem, including the main seasonal  
134 patterns of micronekton and their relationship with oceanographic drivers. In the present  
135 paper, we focused on analyzing the spatial and seasonal variability of acoustic backscatter  
136 collected around New Caledonia, and its relationship with oceanographic conditions,  
137 assuming that backscatter values are a proxy for the relative abundance of micronekton. First,  
138 we proposed a simple approach of inter-calibration between various instruments. We  
139 described DVM, seasonal cycles, and multi-year trends in backscatter data. Then, the effect of  
140 environmental variables (e.g., bathymetry, distance to the closest coast, sea surface  
141 temperature, chlorophyll-*a*, and thermocline depth) on backscatter values was investigated  
142 through statistical models, providing backscatter predictions at the scale of the EEZ. Finally,  
143 we compared acoustic data from the ADCP model to micronekton outputs of SEAPODYM  
144 simulations. In the discussion, pathways were proposed to progress on the observation,  
145 understanding and modeling of micronekton.

## 146 **2. Methods**

147 Micronekton dynamics are usually studied using calibrated echosounders such as SIMRAD  
148 EK60 systems. However, in the New Caledonian region, EK60 systems have been  
149 occasionally used to collect acoustic data (6 cruises) whereas un-calibrated ADCPs, usually  
150 switched-on for current measurements onboard oceanographic vessels, have been routinely  
151 used to collect data (54 cruises) between 1999 and 2017. Hence, despite the lack of  
152 calibration, ADCP offers a longer time series and wider spatial coverage than calibrated  
153 acoustic data for this region.



154

155 Figure 1: Map showing cruise tracks of the R/V *Alis* (solid lines) with S-ADCP device (blue line for  
 156 150 kHz, yellow line for 75 kHz, and grey line for cruises used for ADCP validation) in New  
 157 Caledonia's exclusive economic zone. Background grey colors represent seabed depth (lighter colors  
 158 indicate shallower depths). Important areas discussed in the paper are indicated by grey dashed line  
 159 (panel A). Panel B shows boxplots of ADCP backscatter values per cruise with the same color code  
 160 used for the map.

## 161 2.1 Acoustic data

162 We gathered historical ADCP data from 54 cruises on board the R/V *Alis* in New Caledonia's  
 163 EEZ (156°E–174°E and 14°S–27°S) from 1999 to 2017 (Fig. 1, Table 1 and Appendix A, Fig.  
 164 A1).

165 Table 1: Number of 10-km transects per season, warm season: DJF (December, January, February)  
 166 and MAM (March, April, May); and cold season: JJA (June, July, August) and SON (September,  
 167 October, November) and per year. Numbers in italics are for the 75 kHz ADCP, all other numbers are  
 168 for the 150 kHz ADCP.

	<b>DJF</b>	<b>MAM</b>	<b>JJA</b>	<b>SON</b>
<b>1999</b>	0	0	0	139
<b>2000</b>	0	115	0	0
<b>2001</b>	52	139	0	52
<b>2002</b>	12	89	0	0
<b>2003</b>	197	0	350	466
<b>2004</b>	503	140	123	202
<b>2005</b>	38	67	0	0
<b>2006</b>	0	0	0	94
<b>2007</b>	0	124	201	0
<b>2008</b>	0	512	182	0
<b>2009</b>	0	0	0	0
<b>2010</b>	0	233	0	0
<b>2011</b>	304	0	340	166
<b>2012</b>	0	174	100+106	323
<b>2013</b>	56	1	63	153
<b>2014</b>	154	0	0	207
<b>2015</b>	0	0	0	322
<b>2016</b>	127	233	85	327
<b>2017</b>	0	186	101	304

169

170 Two profilers were used: a 150 kHz broadband ADCP (BBADCP), from October 1999 to  
 171 May 2012, and an Ocean Surveyor 75 kHz narrowband ADCP (NBADCP) from October  
 172 2012 to August 2017.

173 All ADCP data were processed using the freely available CODAS software<sup>1</sup>, and by applying  
 174 the procedure described in Hummon and Firing (2003). The echo intensity in counts, recorded  
 175 by the ADCP was converted to the backscatter coefficient ( $S_v$  in dB.re.m<sup>2</sup>) using the standard  
 176 equation of sonar given by (RDI, 1998) for a NB-ADCP. Deines (1999) transformed this  
 177 equation for a BB-ADCP, subsequently rearranged by Gostiaux and van Haren (2010)  
 178 (Appendix B). The 150 kHz ADCP backscatter data also had to be corrected due to a  
 179 technical bias due to two technical interventions, where the mean level of backscatter values  
 180 changed abruptly twice. Cruises were grouped in order to have the constant mean  $S_v$  across  
 181 groups (i.e., Group1: Wespalis1 to Mareval1; Group2: Secalis4 to Secargo; and Group3:  
 182 Nectalis1 to Momalis) (Appendix B, Fig. B1). The maximum depth reached between these

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<sup>1</sup> <http://currents.soest.hawaii.edu>

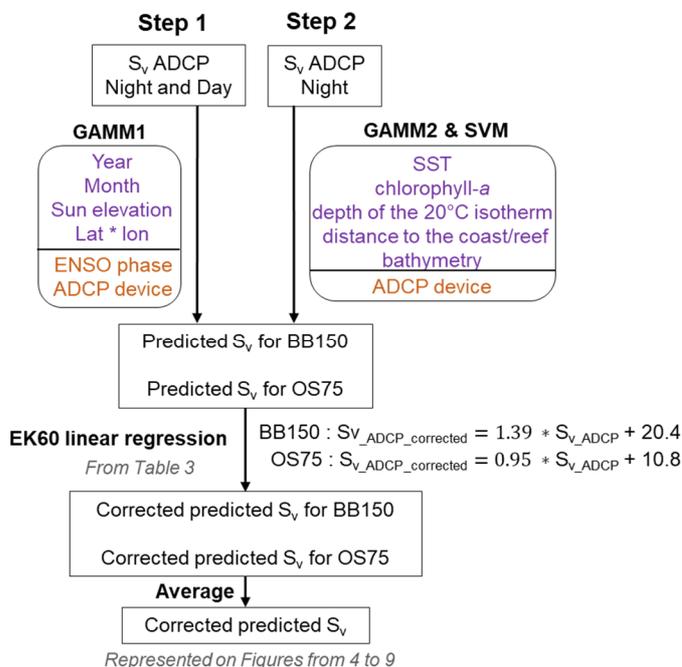
183 cruise groups was statistically different according to a Wilcoxon test (p-value < 0.05 for  
184 Group1-Group2, Group1-Group3 and Group2-Group3), which showed that changes in  
185 backscatter values were due to a technical bias and not to environmental changes. We  
186 adjusted backscatter values on a similar mean level across groups by adding offsets  
187 (Appendix B, Fig. B1). The final vertical resolution (bin) was 8 m for the 150 kHz ADCP and  
188 16 m for the 75 kHz ADCP, both starting at 16 m depth and ending at 300 m for the 150 kHz,  
189 and at 700 m for the 75 kHz, with a time resolution of 5 min.

190 We selected only the surface layer (20–120 m) because of the limited vertical range of the 150  
191 kHz ADCP: its initial vertical range was 300 m, but the depth actually reached after several  
192 years was limited to 120 m due to a decrease in the power of the device. Analyses were done  
193 on a thicker layer (20–200 m) with fewer cruises. The conclusions were similar, so the 20–  
194 120 m layer was kept and considered representative of the epipelagic zone (0–200 m).  $S_v$  data  
195 were transformed into a linear scattering measure ( $s_v = 10^{\frac{S_v}{10}}$ ) to be depth-averaged over 20–  
196 120 m. In order to remove phenomena happening at high spatiotemporal resolution (Escobar-  
197 Flores et al., 2018), the linear scattering measure was also averaged along survey traces every  
198 10 km, which corresponds approximately to 10 initial points with a vessel speed of 7 kt (~ 13  
199 km.h<sup>-1</sup>). Sensitivity analyses using linear backscatter averaged over different spatial  
200 resolutions (5, 10 and 20 km) and median values instead of the mean led to identical  
201 relationships to environmental variables and spatial predictions (not shown). Then, the  
202 logarithmic value ( $S_v = 10 * \log_{10}(s_v)$ ) was calculated and used for all following analyses  
203 ( $S_{v\_ADCP}$ , in dB.re.m<sup>2</sup>) (Appendix A, Fig. A2).

204 To analyze the complete time series (from 1999 to 2017), the two ADCP frequencies needed  
205 to be examined together in order to look for a potential long temporal trend. For that purpose,  
206 we offered a method to replace the two ADCP signals on a similar mean level by comparing  
207 them to EK60 data. Both instruments were used simultaneously during six cruises: Nectalis 1  
208 through 5 and Puffalis (cruise numbers 33, 35, 45, 46, 51, 52 in Appendix A, Table A1).  
209 During these cruises, the EK60 calibration was performed according to the method used by  
210 Foote et al. (1987) at the beginning of each cruise. As for ADCP, the mean value of the EK60  
211  $S_v$  of the 70 kHz frequency was calculated in the 20–120 m layer, with a 10-km resolution.  
212 Two linear regressions were fitted between the  $S_{v\_ADCP}$  values (one regression for each device:  
213 150 kHz and 75 kHz) and  $S_{v\_EK60}$  values (70 kHz). By comparing the two ADCP frequencies  
214 to the same EK60 frequency, we assumed that a part of each ADCP signal was correlated to

215 the EK60 signal. Based on the assumption that backscatter collected at 70 kHz in six different  
 216 cruises using calibrated EK60 echosounders could be compared, an “ADCP corrected value”  
 217 relative to the EK60 70 kHz value was calculated. For the rest of the text, the “corrected  
 218 backscatter” ( $S_{v\_ADCP\_corrected}$ ) corresponded to the  $S_{v\_ADCP}$  corrected with one of the two linear  
 219 regressions with EK60 values. These two regressions were used to adjust the same mean  
 220 backscatter reference level to the values of the two ADCP frequencies (Fig. 2).

221 The comparison with EK60 data made it possible to combine the two groups of cruises carried  
 222 out with the two ADCPs. The adjustment from  $S_{v\_ADCP}$  to  $S_{v\_EK60}$  was made globally for each  
 223 group, assuming that 38 cruises (150 kHz) on the one hand and 16 others (75 kHz) on the  
 224 other were comparable. Indeed, in a group, it is considered that variations in  $S_v$  values  
 225 between cruises are due solely to biological and environmental effects and not to a “device  
 226 effect” such as technical dependence on temperature. The influence of ambient temperature  
 227 on the backscatter calculation (Appendix B, Equation B1) was tested and found to be  
 228 negligible (not shown). Many previous studies have used a similar approach (e.g., Ashjian et  
 229 al., 2002; Bianchi and Mislan, 2016; Blanc et al., 2008; Chereskin and Tarling, 2007; Kaneda  
 230 et al., 2002; Liljebld and Thomasson, 2001; Radenac et al., 2010; Tarling et al., 2001).



231  
 232 Figure 2: Diagram explaining the different steps of the analysis. For models GAMM1, GAMM2 and  
 233 SVM, purple variables are numerical and orange variables are qualitative.  
 234

235 **2.2 Environmental data**

236 A suite of available environmental variables was selected to explore the physical drivers of  
 237 backscatter data. For each backscatter location, environmental variables were obtained at the  
 238 matching sampling position and date when data were available. Where real date data were not  
 239 available, climatologic data were used (Table 2).

240 Table 2: Environmental variable summary with unit, source, and resolutions detailed for each variable.  
 241 Variables with an asterisk (\*) were downloaded via the Copernicus portal, CMEMS (Copernicus  
 242 Marine Environment Monitoring Service) (<http://copernicus.eu/main/marine-monitoring>). Variables  
 243 with (C) are climatologic.

Variable name	Unit	Source	Temporal resolution	Spatial resolution
Bathymetry	km	ZoNéCo, 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 averaged on 30–100 m	cm/s	ARGO floats data and CSIRO Atlas of the Regional Sea (CARS2009)	Annual (C)	¼°
SADCP zonal and meridional currents in the 25–100 m layer	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 in the 20–110 m layer (*)	m/s	ARMOR3D	Week	¼°
Sea surface temperature (SST) (*)	°C	Advanced Very High Resolution Radiometer (AVHRR) infrared satellite	Day	¼°
Chlorophyll-a (*)	mg/m <sup>3</sup>	GlobColour-Processors versions: MODIS 2014.0.1/VIIRSN 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-degree isotherm (D20) (*)	m	ARMOR3D	Week	¼°

244

245 The bathymetry was extracted from a 500-m-resolution dataset (ZoNéCo, 2013), and the  
246 Euclidean distance to the closest coastline or shallow reef (0–30 m) was calculated from a  
247 coastline-reef shapefile (Andréfouët et al., 2008). Sun elevation was calculated for all points  
248 with an adapted version (Blanc and Wald, 2012) of the formula given by Michalsky (1988), a  
249 function of spatial position and date. Sun elevation negative values are for night (from  $-90^\circ$  to  
250  $0^\circ$ ) and positive values for day (from  $0^\circ$  to  $90^\circ$ ).

251 Several products were tested for zonal and meridional currents: a mean absolute geostrophic  
252 current climatology, based on 1000-m Argo floats combined with geostrophic currents  
253 computed from the CSIRO Atlas of the Regional Sea (CARS 2009) (Kessler and Cravatte,  
254 2013), seasonal ADCP current climatology (Cravatte et al., 2015), ARMOR3D gridded  
255 weekly velocities derived from satellite and *in situ* observations (Guinehut et al., 2012, 2004;  
256 Mulet et al., 2012), and the MERCATOR-OCEAN GLORYS ocean reanalysis. Other  
257 oceanographic physical parameters used were sea level anomaly (Pujol et al., 2016), sea  
258 surface temperature (Reynolds et al., 2007), and depth of the  $20^\circ\text{C}$  isotherm calculated from  
259 the ARMOR3D dataset. We used surface vector winds from the Cross-Calibrated Multi-  
260 Platform (CCMP-v2), produced using satellite, moored buoy, and model (Wentz et al., 2015).  
261 One biological parameter was extracted from the GlobColour project: surface chlorophyll-*a*  
262 (Saulquin et al., 2009). These geographic parameters and environmental datasets are detailed  
263 in Table 2 and spatial patterns by quarter are presented in Appendix C.

264 To assess the ENSO effect, the Oceanic Niño Index (ONI) – a three-month running mean of  
265 ERSST.v5 sea surface temperature (SST anomalies) in the El Niño 3.4 region ( $5^\circ\text{N}$ – $5^\circ\text{S}$ ,  
266  $120^\circ$ – $170^\circ\text{W}$ ) was used<sup>2</sup>. ENSO phases were defined with a 0.7 threshold; such that months  
267 with an ONI above 0.7 were classified as El Niño, and months with an ONI below -0.7 as La  
268 Niña.

### 269 **2.3 Statistical model and analysis**

270 GAM (generalized additive model) (Hastie and Tibshirani, 1995) and SVM (support vector  
271 machine) (Cortes and Vapnik, 1995) statistical models were used to investigate the variability  
272 of backscatter echo-intensities in New Caledonia’s EEZ. We studied the temporal variability  
273 (daily, monthly, multi-annually) as a first step, and the relationships between backscatter

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2 [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)

274 values and environmental variables as a second step to avoid collinearity problems (e.g.,  
275 between SST and month) (Fig. 2). Each model used has specific advantages. GAM allows  
276 variables to be ranked by relevance, and highlights the relationships between the response  
277 variables and predictors (explanatory variables), which is interesting from an ecological point  
278 of view. However, GAM is difficult to tune while respecting strong assumptions (e.g.,  
279 absence of autocorrelation in residuals, error distributed normally). SVM, as the state-of-the-  
280 art algorithm, has been applied in various scientific domains, especially in ecological niche  
281 modeling (Drake et al., 2006; Palialexis et al., 2011). For this method there is no requirement  
282 concerning predictors' distributions or autocorrelation (Hegel et al., 2010). Yet, it remains  
283 difficult to interpret SVM results, and there is no straightforward method for explaining the  
284 results and ranking the predictors by relevance. To interpret ecological phenomena, partial  
285 dependence plots were produced by environmental variables to visually explore the marginal  
286 effect of a given variable on the backscatter value, while other variables are fixed to their  
287 mean values (Friedman, 2001). SVM partial dependence plots are not presented, as strong  
288 interactions exist between predictors (Goldstein et al., 2015). Subsequent models were fitted  
289 with both GAMM and SVM models, excluding each of the remaining terms, one at a time, to  
290 assess the percentage of variation explained by predictor. We classified predictors according  
291 to their importance in the model.

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

304 To account for the potential difference between the two ADCP devices, we included an  
305 ADCP device effect in all models (GAMM and SVM); therefore, backscatter values were

306 predicted for each ADCP device, BB150 and OS75, respectively. We then corrected the  
307 predicted  $S_v$  using the corresponding EK60 linear regressions, and finally averaged the  
308 corrected predicted values from the two devices (Fig. 2). The effect of the ADCP device  
309 included in each model is different. For the GAMM, it is a “fixed effect”, meaning that  
310 relationships between backscatter and covariates have the same shape but with an offset  
311 function of the ADCP device. For the SVM approach, relationships linked to ADCP devices  
312 could have different shapes.

313 We explored visually the temporal dynamic over the entire time series (1999–2017) with  
314 GAMM outputs. In a first step, GAMM1 allowed us to investigate relationships between  
315  $S_{v\_ADCP}$  values and a set of temporal and spatial predictors. Six predictors were tested: the  
316 ADCP effect (BB150 or OS75) and the ENSO phase (Neutral, El Niño or La Niña) as  
317 categorical variables and sun elevation (a proxy for the moment of the day), year, month,  
318 latitude and longitude, as continuous variables (Fig. 2, step 1). The year variable was  
319 smoothed with a cubic spline, and the month variable with a cyclic cubic spline. Latitude and  
320 longitude were fitted inside the same isotropic spline (Wood et al., 2012) with a Gaussian  
321 process model smoothing basis (Golding and Purse, 2016; Miller et al., 2013). This spatial  
322 term was added to fit the mean spatial distribution pattern to account for differences in survey  
323 spatial localization across the years (Appendix A, Fig. A1).

324 In a second step, environmental variables described in Table 2 (i.e., bathymetry, distance to  
325 the coast or reef, sun elevation, currents (four different sources), SST, chlorophyll-*a*, sea level  
326 anomaly, winds and 20°C isotherm depth, and a fix effect of the ADCP device were included  
327 in GAMM2 and SVM (Fig. 2, step 2), independently of month or year variables. All variables  
328 were smoothed with cubic splines. Predictions were done on climatological environmental  
329 variables with a  $\frac{1}{4}^\circ$ -resolution grid and then averaged between models leading to a hybrid  
330 GAMM2-SVM prediction. A measure of the coherence between the two models was  
331 estimated through the coefficient of variation (i.e., standard deviation divided by mean),  
332 which ranged from 0 to 7%. We applied two different standard deviation thresholds (6%,  
333 2%): the lower the coefficient of variation threshold, the higher the confidence in the  
334 prediction, but the lower the number of cells predicted. We used two statistical models to  
335 compare large spatial predictions, combine common patterns (Oppel et al., 2012), and ensure  
336 that conclusions are robust to the underlying statistical assumptions. Before constructing  
337 models, we confirmed that collinearity was not apparent among the predictors using variance

338 inflation factors (VIFs) (O'Brien, 2007) and Spearman correlations between each pair of  
339 covariates. We considered covariates to be non-collinear when both Spearman correlations  
340 were inferior to 0.5 and VIFs were inferior to 3.0.

341 GAMM1 assesses the seasonal cycle by fitting a month variable as a continuous variable.  
342 GAMM2-SVM does not include a month variable but uses relationships with environmental  
343 variables (such as SST) in which seasonality is inherent to predict backscatter values at each  
344 point; finally, the seasonal cycle is assessed by averaging all EEZ-predicted values by month.

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

#### 348 **2.4 SEAPODYM simulation**

349 The submodel of SEAPODYM for mid-trophic levels (MTL) simulates several functional  
350 groups of micronekton for the oceanic epi- and mesopelagic layers (Lehodey et al., 2010,  
351 2015). The spatial and temporal dynamics of production and biomass are modeled with a  
352 system of advection-diffusion-reaction equations driven by ocean temperature, horizontal  
353 currents, primary production, and euphotic depth. Currently, there are six groups of  
354 micronekton defined according to the DVM patterns of mesopelagic organisms between three  
355 broad epipelagic, upper and lower mesopelagic vertical layers. The euphotic depth  $Z_{eu}$  is used  
356 to define the depth boundaries of the vertical layers (i.e.,  $0-1.5*Z_{eu}$  for the epipelagic layer,  
357  $1.5-4.5*Z_{eu}$  for the mesopelagic layer, and  $4.5-10.5*Z_{eu}$  for the bathypelagic layer). In New  
358 Caledonia,  $Z_{eu}$  is around 70–75 m, hence the epipelagic layer in the model occupies the top  
359 ~110 m. During the day, only the epipelagic group inhabits the epipelagic layer, but during  
360 the night, it also includes the migrant upper-mesopelagic and highly migrant lower  
361 mesopelagic groups.

362 We compared the predicted backscatter to SEAPODYM-MTL-modeled micronekton  
363 biomass, and used a SEAPODYM-MTL micronekton simulation for the 1999–2017 period.  
364 The biomass of micronekton groups inhabiting the epipelagic layer at night was extracted at  
365 the date and place of the ADCP data. Values were centered (the mean was subtracted) and  
366 scaled (divided by the standard deviation) for both SEAPODYM and acoustic models.

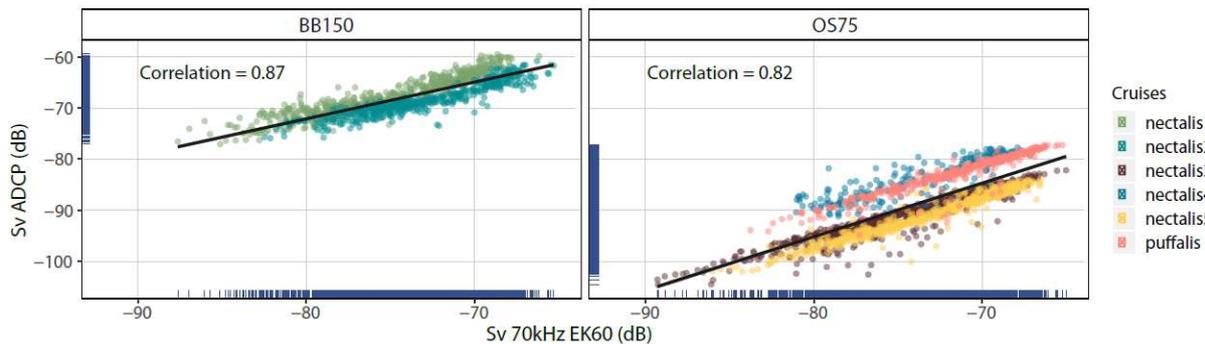
367 Biomass values were compared along the tracks by calculating correlations, and distribution  
368 patterns compared over the whole of the EEZ.

### 369 3. Results

370 In total, 89,530 km of survey track across 435 days (288 days for the 150 kHz ADCP and 147  
371 for the 75 kHz ADCP) over 19 years were analyzed in this study. All quarters were sampled  
372 at least nine times during the study period (Table 1), and the whole EEZ was surveyed at least  
373 once except for a small area in the southeast corner of the EEZ, and an area in the southwest  
374 below the Chesterfield Reefs (Fig. 1).

#### 375 3.1 Comparison to EK60 values

376 We compared the un-calibrated ADCP acoustic data to the calibrated EK60 echosounder data.  
377 Two cruises were available with concomitant 150 kHz  $S_{v\_ADCP}$  and  $S_{v\_EK60}$  records (1110  
378 paired values) and four cruises with 75 kHz  $S_{v\_ADCP}$  and  $S_{v\_EK60}$  (1955 paired values). For both  
379 ADCP frequencies, correlations between mean 20–120m  $S_{v\_ADCP}$  and  $S_{v\_EK60}$  were significant  
380 and higher than 0.8 (Fig. 3). The two regressions were significant (p-values <0.01) and had  
381 different slopes: 1.05 (standard error 0.017) for the 75 kHz ADCP, and 0.72 (standard error  
382 0.012) for the 150 kHz ADCP (Table 3). For the 75 kHz ADCP, the data scatterplot from  
383 Nectalis 4 and Puffalis on one side, and from Nectalis 3 and Nectalis 5 on the other side,  
384 could warrant the estimation of different intercepts (Fig. 3).



385  
386 Figure 3: ADCP backscatter ( $S_v$ ) as a function of the 70 kHz EK60 echosounder  $S_v$  and the associated  
387 linear regressions (black line) for the 150 kHz SADCPC device (BB150, Nectalis 1 and 2) (left) and the  
388 75 kHz SADCPC (OS75, Nectalis 3, 4, 5 and Puffalis) (right). Blue ticks on both axes show the  
389 distribution of the observations.

390

391

392 Table 3 Linear regression analysis outputs, including the intercept, slope, slope standard error, p-value,  
393 and deviation explained (or  $R^2$ ), and the number of observations for each ADCP device.

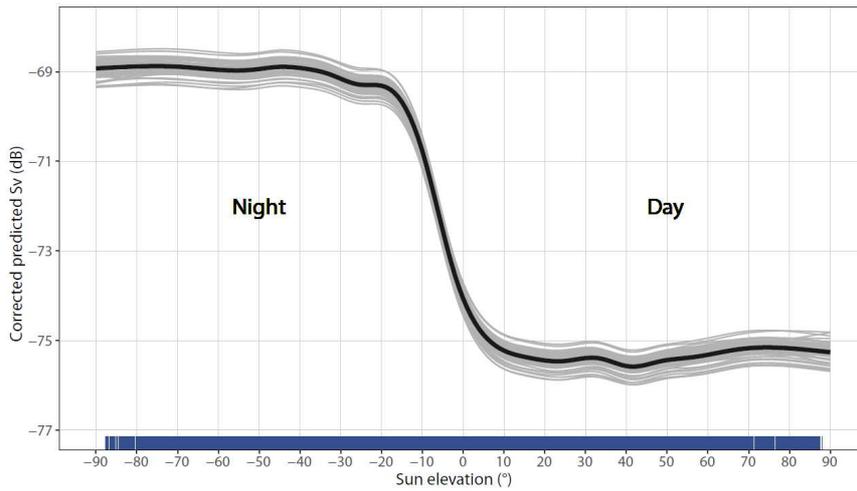
ADCP device	Intercept	Slope	Slope standard error	Slope p-value	Deviation explained	n
OS75	-11.32	1.05	0.017	<2e-16	67	1955
BB150	-14.64	0.72	0.012	<2e-16	76	1110

394

### 395 3.2 Temporal variability of backscatter

396 Temporal variability of backscatter micronekton was analyzed at three scales: daily, monthly  
397 and yearly using a GAMM, including all  $S_{v\_ADCP}$  values (night and day) as a function of  
398 ADCP device, sun elevation, year, ENSO phase, month and location (latitude and longitude)  
399 with a nested auto-correlative model (Fig. 2, left part). In this model, the largest part of the  
400 variance was explained by sun elevation (Table 4).  $S_{v\_ADCP}$  in the 20–120m layer was higher  
401 during the night than during the day (respectively, -69 dB and -75 dB) (Fig. 4), a difference of  
402 6 dB. The usual value used as a density proxy is the linear value ( $s_v$ ), so a 6 dB difference  
403 meant that the micronekton density was about four times higher during the night than during  
404 the day in the 20–120m layer.  $S_{v\_ADCP}$  values were constant during the night, but started to  
405 decrease at dawn when sun elevation exceeded  $-20^\circ$ . The variance explained by sun elevation  
406 demonstrated the important impact of the DVM in the 20–120m layer. The second most  
407 important variable was the effect of the ADCP device (Table 4).

408



409

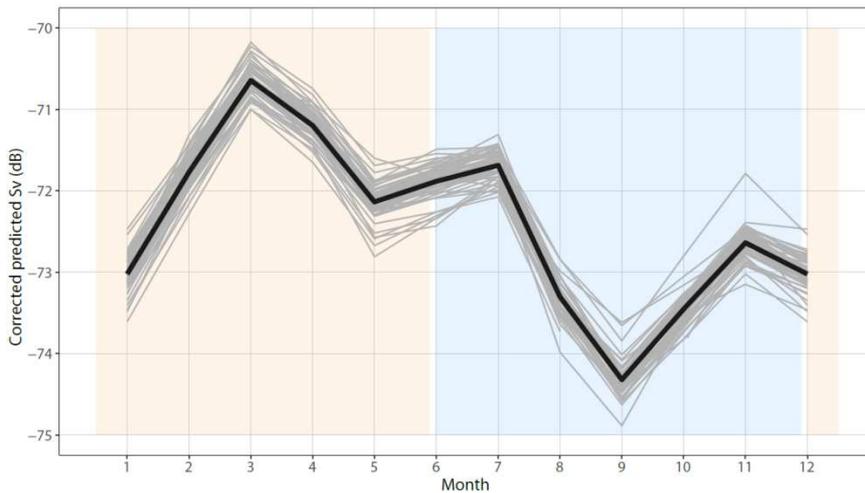
410 Figure 4: GAMM1 partial dependence plot showing the effect of sun elevation on corrected  
 411 backscatter values ( $S_v$ ). Solid grey lines are estimates of the smooths for the 54 simulations from  
 412 cross-validation, and the black line is the average smooth. Blue ticks on the inner X-axis show the  
 413 distribution of the observations .

414 Table 4: Model summary with the model name, response variable, explicative variables, total  
 415 deviation explained (or  $R^2$ ), and the rank of importance by variable. All predictors were significant in  
 416 the GAMMs output ( $p$ -values < 0.05). An asterisk (\*) indicates that an auto-correlative model is  
 417 nested into the GAMM.

Model	Response variable	Explicative variables	Deviation explained	Rank of importance by variable
GAMM1 (*)	SV_ADCP	Sun elevation	83.9	1
		year		5
		month		3
		Lat * lon		4
		ENSO_phase		6
		ADCP_device		2
GAMM2 (*)	SV_ADCP_NIGHT	SST	78.1	2
		D20		4
		Log_chloro		3
		Bathy		5
		Dist_coast		6
		ADCP_device		1
SVM	SV_ADCP_NIGHT	SST	87.9	2
		D20		3
		Log_chloro		6
		Bathy		4
		Dist_coast		5
		ADCP_device		1

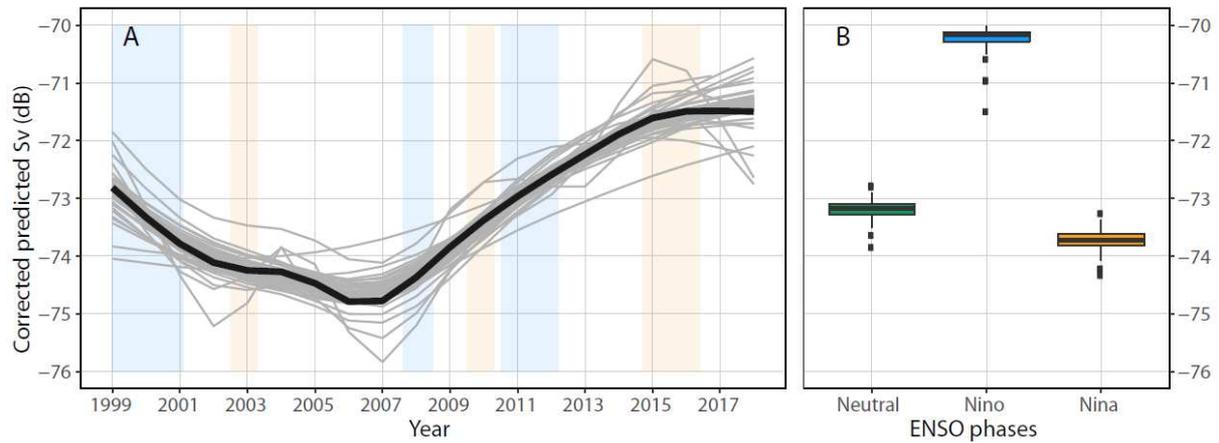
418

419 Month was the third variable explaining the variance of  $S_{v\_ADCP}$  (Table 4). The seasonal cycle  
 420 displayed a maximum in March (-70.8 dB), and a minimum in September (-74.3 dB), with  
 421 two superimposed relative maxima in July and November (-71.8 dB and -72.8 dB,  
 422 respectively) (Fig. 5). The difference between extreme values was about 3.5 dB, meaning  
 423 there was, on average, 2.0 times more biomass during March than during September, 1.6 more  
 424 in July, and 1.4 more in November compared to September. The 54 cross-validation  
 425 simulations (Fig. 5) confirmed the robustness of the seasonal cycle.



426  
 427 Figure 5: GAMM1 partial dependence plot showing the effect of the month on corrected backscatter  
 428 values ( $S_v$ ). Solid grey lines are estimates of the smooths for the 54 simulations from cross validation,  
 429 and the black line is the average smooth. Cold season is indicated in blue, and warm season in orange .

430 The variance explained placed the year variable at the 5<sup>th</sup> rank and ENSO at the 6<sup>th</sup> rank  
 431 (Table 4). The relationship between the  $S_{v\_ADCP}$  and the year was non-linear, with a minimum  
 432 and a maximum (Fig. 6A). Predicted  $S_{v\_ADCP}$  were about -73 dB in 1999, decreasing to a  
 433 minimum of -75 dB in 2007, and reaching a maximum of -71.5 dB in 2017. So, on average,  
 434 the acoustic density decreased by 1.6% between 1999 and 2007 and then increased by 2.2%  
 435 between 2007 and 2017. The ENSO phase effect was significant in the GAMM1:  $S_{v\_ADCP}$  was  
 436 twice as high during an El Niño phase than during a neutral phase (Fig. 6B), and the  $S_{v\_ADCP}$   
 437 during a La Niña phase was not significantly different from the value during a neutral phase.



438

439 Figure 6: GAMM1 partial dependent plot terms showing the effect of year (A) and ENSO phases (B)  
 440 variables on corrected backscatter values ( $S_v$ ). Solid grey lines are estimates of the smooths for the 54  
 441 simulations from cross validation, and the black line is the average smooth. El Niño events are  
 442 indicated in blue on panel A, and in orange for La Niña events.

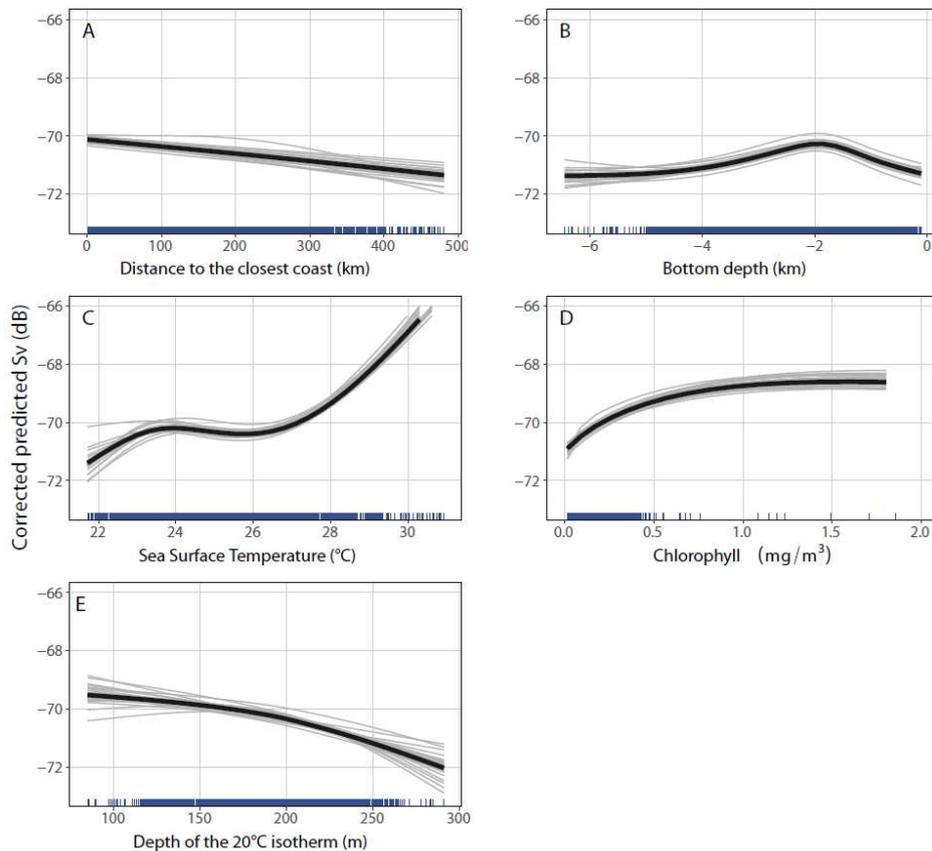
### 443 3.3 Estimating ecological relationships

444 To investigate the impact of environmental variables on  $S_{v\_ADCP}$  values during the night, only  
 445  $S_{v\_ADCP\_night}$  were fitted through both a GAMM2 (with a nested auto-correlative model) and an  
 446 SVM with environmental variables and an effect on ADCP device (150 kHz or 75 kHz) (Fig.  
 447 2, right part). We focused this part of the study on nighttime values to reveal the potential  
 448 influence of environmental parameters that could have been masked by the strong impact of  
 449 sun elevation on backscatter. The night signal was preferred over the day signal because in the  
 450 20–120 m layer it better represents the micronekton community by accumulating both  
 451 permanent epipelagic organisms and migrating organisms coming from deeper layers.

452 Based on Spearman correlation tests and VIF, depth of the 20°C isotherm (d20) and SLA  
 453 were correlated, which required selecting only one of those variables to be included in the  
 454 model. As SLA was not significant for the GAMM2 model, we kept d20 in the final model.  
 455 The zonal and meridional currents and wind data were un-significant in the GAMM2 model;  
 456 thus they were not considered further in models GAMM2 and SVM. The final models  
 457 included SST, chlorophyll-*a*, depth of the 20°C isotherm, distance to the coast or reef,  
 458 bathymetry, and the effect of the ADCP device for both the SVM and GAMM2 models.

459 After considering the effect of the ADCP device, the two statistical methods mostly agreed on  
 460 the relative contribution of variables (Table 4), with SST demonstrating the main effect

461 among oceanographic variables. The contribution rank of chlorophyll-*a* was different between  
 462 the GAMM2 and SVM models: chlorophyll-*a* was the second most important variable for  
 463 GAMM2, and the last (6<sup>th</sup>) for SVM. Then, in descending order of importance, the 20°C  
 464 isotherm depth, the bathymetry and the distance to the closest coast or reef were found to be  
 465 important.



466

467 Figure 7: GAMM2 partial dependent plot terms showing the effect of various continuous variables on  
 468 corrected backscatter values ( $S_v$ ). Solid grey lines are estimates of the smooths for the 54 cross-  
 469 validation simulations, and the black line is the average smooth. Blue ticks on the X-axis show the  
 470 distribution of observations .

471 The relationship between backscatter values and distance to the closest reef or coast linearly  
 472 decreased, with higher values closer to the coast (Fig. 7A). The influence of bathymetry was  
 473 not linear, but an optimum of the 20–120 m backscatter value was observed over the sea floor  
 474 at a depth of 1800 m (Fig. 7B). The SST relationship increased non-linearly, with a first  
 475 optimum at around 24°C and a rise from 26 to 31°C (Fig. 7C). The chlorophyll-*a*  
 476 concentration relationship also increased, and the backscatter value was higher with higher  
 477 chlorophyll-*a* concentrations (Fig. 7D). The relationship with the 20°C isotherm decreased:

478 the mean backscatter value was higher when the isotherm was shallower (Fig. 7E). All  
479 relationships were significant according to GAMM outputs, and the variability through cross  
480 validation was small over almost all the variable ranges, showing the robustness of the model  
481 (Fig. 7).

### 482 **3.4 Predicted spatial distribution**

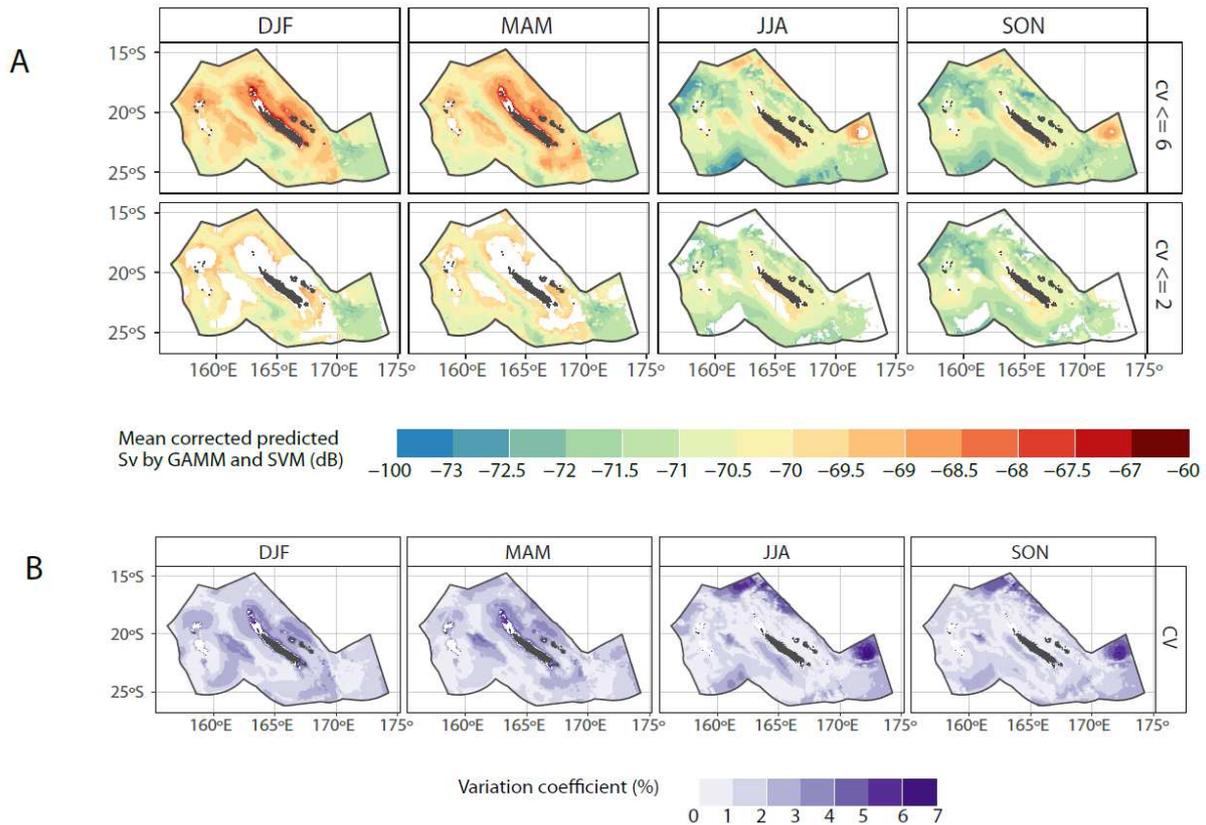
483 We defined the austral summer or warm season as the months of December, January and  
484 February (DJF) and March, April and May (MAM) quarter periods, and the austral winter or  
485 cold season as June, July and August (JJA) and September, October and November (SON)  
486 quarters. This definition was chosen relative to the common knowledge of these seasons in  
487 New Caledonia (Cravatte et al., 2015). Spatial predictions of the GAMM2-SVM hybrid-  
488 model were highly homogenous across one season: DJF was very similar to MAM, and  
489 identically for JJA and SON (Fig. 8A).

490 Generally, values were higher during the warm season, during which the distributions showed  
491 aggregations of high values in the central part of the EEZ in a wide strip area with a southeast  
492 to northwest orientation encompassing the main island and the Loyalty islands where there  
493 was a high confidence in the predictions (see Fig. 1 for island and reef names). The values  
494 were particularly high north of 22°S (Fig. 8A, DJF and MAM) and around the Chesterfield  
495 Reefs. Values were lower in the southeastern corner of the EEZ. The channel between the  
496 group – made up of the Chesterfield and Bellona reefs, and the Fairway-Lansdowne Bank,  
497 and the main island – was also predicted to have lower values.

498 During the cold season, values were lower in the north, close to the coast of the main island,  
499 and in the south along the edges of the EEZ (Fig. 8A, JJA and SON). Highest values during  
500 the cold season were located south of 20°S, south of the main island and the Chesterfield  
501 Reefs, and north of the southeast corner of the EEZ where there was a higher prediction  
502 divergence between the models GAMM2 and SVM and, thus, less confidence was given to  
503 the results in this area. Along the southwest coast of the main island, values were higher  
504 farther towards the coast than during the warm season.

505 There was good agreement between the predictions of the two models (coefficient of variation  
506 ranges from 0 to 7%) for most of the EEZ (Fig. 8B). However, discrepancies between the  
507 GAMM2 and SVM models were observed in some areas, with relatively high model

508 coefficients of variation in the north of the EEZ, in the north of the southeastern corner of the  
 509 EEZ, and the Fairway-Lansdowne Bank for the cold season, and north of the main island for  
 510 the warm season. Using a 6% threshold for the coefficient of variation removed only 0.17% of  
 511 the cells (0.084% for DJF, 0.034% for MAM, 0.53% for JJA and 0.042% for SON), whereas  
 512 28% of the cells were removed for a 2% threshold for the coefficient of variation (31% for  
 513 DJF, 30% for MAM, 27% for JJA and 22% for SON).



514  
 515 Figure 8: Corrected backscatter values at night predicted on average by GAMM2 and SVM1 in the  
 516 exclusive economic zone of New Caledonia by quarter, with two different thresholds applied to  
 517 coefficient of variation (panel A, top row: 6%, bottom row: 2%), and the associated coefficient of  
 518 variation (panel B). Warm season: DJF (December, January, February) and MAM (March, April,  
 519 May) and cold season: JJA (June, July, August) and SON (September, October, November).

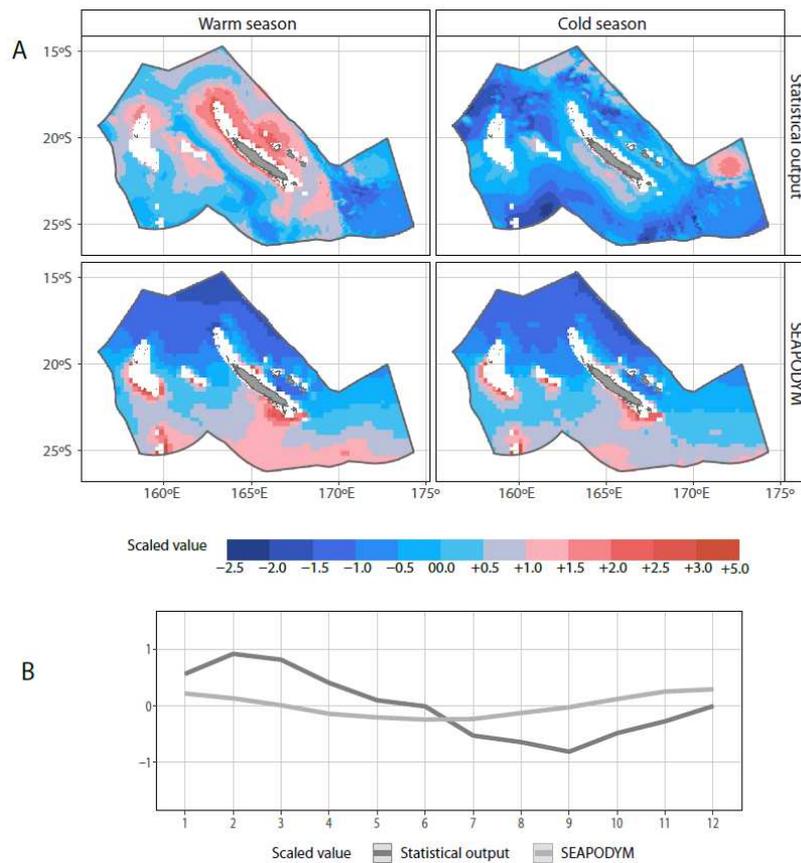
### 520 3.5 Comparison with SEAPODYM-MTL

521 The correlation between the observed 20–120 m backscatter and SEAPODYM-MTL values,  
 522 extracted for the dates and locations of the cruise tracks was close to zero and non-significant,  
 523 suggesting an absence of direct coherence between the two sources. We then compared the  
 524 seasonal patterns of the output of the GAMM2-SVM gridded predicted model of backscatter  
 525 to seasonal SEAPODYM-MTL outputs. The warm and cold seasons were calculated as the

526 averages of the two quarters composing each season. Within each season, we kept the data  
527 with CV  $\leq 6\%$  to keep the largest dataset in the hybrid model.

528 During the cold season (June to November) the GAMM2-SVM and the SEAPODYM-MTL  
529 models showed different spatial patterns (Fig. 9A). In SEAPODYM-MTL simulations, high  
530 values were located in the southern part of the EEZ in oceanic waters close to the EEZ  
531 boundary, while in the GAMM2-SVM model, this area was characterized by low values,  
532 while high values occurred close to the south coast of the main island. However, in the two  
533 cases, values were low in the northern part of the EEZ. During the warm season (December to  
534 May), the SEAPODYM-MTL spatial distribution pattern was similar to the SEAPODYM-  
535 MTL austral winter pattern with enhanced values. The difference between SEAPODYM-  
536 MTL and GAMM2-SVM predictions based on observed acoustic data was stronger during the  
537 warm season than during the cold season, with higher values found around islands and reefs  
538 in the GAMM2-SVM predictions. For the two seasons, the SEAPODYM-MTL spatial  
539 distribution showed a north–south gradient that the acoustic data did not show. The spatial  
540 structures provided by the GAMM2-SVM predictions were spatially more detailed than in the  
541 SEAPODYM-MTL predictions. For the two seasons, the Spearman correlations were very  
542 low ( $< 0.2$ ). In SEAPODYM-MTL, the predicted biomass level changed but the spatial  
543 distribution stayed similar over seasons, whereas in the GAMM2-SVM predictions, a spatial  
544 distribution change over the seasonal cycle was observed as was a change in the mean level.

545 The seasonal cycle coming from the GAMM2-SVM hybrid model showed increased acoustic  
546 density during the austral summer, and decreased density during the austral winter (Fig. 9B).  
547 The seasonal cycle showed an approximate three-month lag between the GAMM2-SVM  
548 predictions, and the SEAPODYM-MTL and seasonal variability was much weaker in  
549 SEAPODYM-MTL than in the GAMM2-SVM predictions. The peak was in December for  
550 SEAPODYM-MTL (averaged scaled values over the EEZ), while the highest peak was, on  
551 average, in February for GAMM2-SVM outputs (Fig. 9B). The seasonal cycle from acoustic  
552 data was mainly driven by change in the north of the EEZ, while the SEAPODYM seasonal  
553 cycle seemed to be due to change in the biomass level in both the north and the south (Fig.  
554 9A).



555

556 Figure 9: Corrected backscatter values predicted, on average, for the hybrid GAMM2-SVM model  
 557 with a coefficient of variation inferior to 6% (statistical output, panel A, top row), and SEAPODYM-  
 558 MTL model (panel A, bottom) averaged by season. Only cells predicted by SEAPODYM-MTL are  
 559 shown in both rows of panel A. The same data are averaged by month (panel B). Values on the three  
 560 panels are scaled and centered for comparison.

#### 561 4. Discussion

562 Backscatter values from 54 ADCP surveys at 75 kHz and 150 kHz over 19 years (1999–2017)  
 563 were used to examine micronekton dynamics in the upper 120 m of the ocean in New  
 564 Caledonia’s EEZ (southwest Pacific), assuming that micronekton density was proportional to  
 565 backscatter values. A strong diel signal was found as well as a clear seasonal cycle, an impact  
 566 of El Niño, and a sign of a longer-term temporal trend. The link to environmental variables  
 567 such as SST, surface chlorophyll-*a*, depth of the 20°C isotherm, bathymetry, and distance to  
 568 the coast were studied. A hybrid model constructed with two statistical models (GAMM2 and  
 569 SVM) was used for predictive statistical modelling of backscatter values. A large variability  
 570 in spatial distribution was found over the seasons. Those spatial distributions were quite  
 571 different from separate SEAPODYM-MTL model simulations.

#### 572 **4.1 ADCP-EK60 comparison**

573 The lag between mean ADCP levels was relatively large, about 20 dB. Due to the absence of  
574 a similar offset among EK60 Nectalis data (Fig. 3), this lag was linked to the reported ADCP  
575 device and not to a biological effect. High positive correlations between the 70 kHz  $S_{v\_EK60}$   
576 and the 150 kHz and 75 kHz  $S_{v\_ADCP}$  have been previously observed in other regions (e.g.,  
577 Brierley et al., 1998; Griffiths, 1996). Based on the positive correlations, data from both  
578 ADCP devices could be combined and analyzed as one dataset when adjusted to a common  
579 EK60 reference. With this methodology, we studied data from the ADCP at different  
580 frequencies to obtain a long time series for the present region (19 years by aggregating data  
581 from the two devices, including 12 years for the 150 kHz ADCP and 7 years for the 75 kHz  
582 ADCP).

583 Although the relationships with the EK60 reference signal allowed us to combine data from  
584 the two ADCP devices, uncertainty remained among cruises using the same ADCP device. By  
585 analyzing the 54 cruises together, the methodology assumed that cruises performed with each  
586 ADCP device (38 cruises for the 150 kHz device and 16 cruises for the 75 kHz device) were  
587 comparable (i.e., the relationships found between  $S_v$  and environmental variables or across  
588 time were due to biological changes and were not linked to a device's temperature  
589 dependence for example). We based this hypothesis on previous studies where several ADCP  
590 cruises were aggregated to analyze them together (e.g., Ashjian et al., 2002; Bianchi and  
591 Mislán, 2016; Blanc et al., 2008; Chereskin and Tarling, 2007; Kaneda et al., 2002; Liljebladh  
592 and Thomasson, 2001; Radenac et al., 2010; Tarling et al., 2001). Moreover, regression  
593 curves for the EK60 signal for one cruise (one color on Fig. 3) were linear, whereas the  
594 cruises covered areas including large variations of temperature, particularly between the north  
595 and south of the EEZ (Fig. 1). This analysis indicated a constant survey-dependent shift rather  
596 than an environmental effect such as a device dependence to temperature. Finally, we had no  
597 other choice than to use a unique set of estimated regression parameters for all the cruises as  
598 only six cruises with EK60 data were available. For future studies using S-ADCPs, we  
599 recommend recording EK60 reference transects at least once a year for calibration.

600 While the size-range of organisms detected by ADCP was not defined precisely, both ADCP  
601 devices were thought to detect a broad range of organisms from macrozooplankton to  
602 micronekton in the 20–120 m layer. Smeti et al. (2015), using data from zooplankton nets and  
603 TAPS (Tracor Acoustic Profiling System), concluded that a 150 kHz ADCP is appropriate for  
26

604 detecting organisms such as macrozooplankton. The very high correlations of the ADCP  
605 signal with the EK60 at various frequencies as presented in Menkes et al. (2015) and in the  
606 present study, confirm the contribution of the micronekton to the 70 and 75 kHz ADCP  
607 backscatter.

## 608 **4.2 Environmental predictors**

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

611 The relationship between SST and  $S_v$  was non-linearly increasing, reaching a first maximum  
612 at 23.5°C and a second above 26°C. Fewer SST values were sampled above 28°C, and so the  
613 relationship above 28°C was assumed with caution. This type of relationship with two  
614 temperature optima may express contrasted situations either spatially (e.g., as in Boersch-  
615 Supan et al., 2015) or by season as observed in the Gulf of Maine (Hazen et al., 2009). In the  
616 present study, it seemed due to a clear difference between warm and cold seasons but also  
617 between north and south regions.

618 The relationship between backscatter and chlorophyll-*a* (a proxy for primary production)  
619 showed an increase, with a plateau at higher values. Escobar-Flores et al. (2013) found a  
620 strong correlation with chlorophyll-*a* and the acoustic backscatter at the scale of the entire  
621 South Pacific. However, they obtained a bell-shaped relationship instead of the plateau  
622 predicted in the present study. Their maximum backscatter was obtained for a  $\sim 0.5 \text{ mg}\cdot\text{mm}^{-3}$   
623 chlorophyll-*a* concentration, very similar to the present asymptotic chlorophyll-*a*  
624 concentration value. At the global scale, a similar strong positive link was found between the  
625 38 kHz acoustic backscatter (EK60 echosounder) in the mesopelagic layer and satellite-  
626 derived primary production (Irigoiien et al., 2014). However, Boersch-Supan et al. (2015) in  
627 the Indian Ocean, and Hazen and Johnston (2010) in the central equatorial Pacific, did not  
628 find such significant relationships, suggesting that relationships may be ecosystem- or region-  
629 dependent. In any case, understanding the mechanisms linking chlorophyll-*a* or primary  
630 productivity and micronekton requires the understanding of the intermediate zooplankton  
631 compartment; accordingly, measuring phytoplankton, zooplankton and micronekton  
632 simultaneously is required to better understand interactions in the lower trophic levels.

633 Backscatter values decreased gradually with increasing distance from the coast, and during  
634 the warm season (DJF and MAM), backscatter values increased with increasing proximity to  
635 the reef. This pattern was observed both for the main island and for the Chesterfield Reefs,  
636 and could be linked to an intensification of primary productivity close to the coast, and  
637 conversely more patchiness offshore (Escobar-Flores et al., 2013). Shallow waters offer a  
638 reduced habitat for mesopelagic organisms and induces a densification of the different  
639 functional groups that they constitute (Escobar-Flores et al., 2018; Lehodey et al., 2010). Low  
640 backscatter values far from the reef could also be due to changes in species composition, with  
641 species responding differently to acoustic frequencies. For example, in the Southern Ocean, a  
642 clear change in species composition was observed between the neritic zone and oceanic zone  
643 (Duhamel et al., 2000; Koubbi et al., 2011). In the Southern California Bight, Davison et al.  
644 (2015a) observed what they called a “seasonal basin effect”, which they found to be  
645 consistent with blooms of the siphonophore *Nanomia bijuga*. In the Southern Ocean between  
646 New Zealand and the Ross Sea, Escobar-Flores et al. (2018) found that while the backscatter  
647 (38 kHz) consistently and significantly decreased from north to south, a higher biomass of  
648 mesopelagic fish was estimated from net sampling in the central region. Clearly, in absence of  
649 *in situ* sampling, the acoustic data alone may be misleading.

650 Bathymetry and distance from the coast were not correlated because of the complexity of the  
651 sea bed within New Caledonia’s EEZ (Appendix C). The relationship between backscatter  
652 and bottom depth showed an optimum of around 2000 m depth. The areas with a bottom  
653 depth between 1500 m and 2500 m were located between the main island and the Loyalty  
654 Islands, south of the main island, around the Chesterfield and Bellona reefs, and the Fairway–  
655 Lansdowne Bank, and included seamounts (Appendix C, Fig. C2). Seamounts may aggregate  
656 micronekton as demonstrated by other studies, but highly depending on the type of seamount  
657 (e.g., shape and depth, presence of upwelling) and the type of organisms as not all species  
658 aggregate around seamounts (Annasawmy et al., 2019; Drazen et al., 2011; Morato et al.,  
659 2010, 2008). From our study, a direct seamount aggregation effect was not highlighted. To  
660 understand the effect of seamounts on micronekton aggregation, a better characterization of  
661 seamounts would be necessary, including considering variables such as distance to the  
662 seamount and typology (e.g., depth of the summit, shallow or deep, sharp or flat morphology).

663 Higher backscatter values were found when the 20°C isotherm was closer to the surface, but  
664 with a larger confidence interval before 150-m depth and after 250 m where sampled values

665 were more scattered. The depth of the 20°C isotherm is a proxy for the thermocline location.  
666 A deep 20°C isotherm (and thus thermocline) likely limits possible nutrients inputs in the  
667 euphotic surface layer (Kessler and Cravatte, 2013). On the contrary, the closer the 20°C  
668 isotherm is to the surface, the higher the vertical mixing is in the surface layers, bringing more  
669 nutrients to the photic layer, thus making the surface layer more productive. This productivity  
670 increase propagates through the food web as potentially detected here and in other studies  
671 (Benoit-Bird and McManus, 2012; Lebourges-Dhaussy et al., 2014). Therefore, together with  
672 biogeochemical variables and sea surface temperature, the 20°C isotherm appears to be a  
673 useful proxy for the thermocline in the context of climate change to understand and monitor  
674 the impacts of increased temperature and vertical stratification of the water column on prey  
675 availability for top predators (Ceccarelli et al., 2013; Choy et al., 2016).

676 The 20°C isotherm is also used to characterize mesoscale activity with deeper closed-contours  
677 of the 20°C isotherm characterizing anticyclonic “downwelling-type” eddies, and shallower  
678 20°C closed-contours isotherms characterizing cyclonic “upwelling-type” eddies. Eddy  
679 activity is relatively important around New Caledonia. Previous studies have demonstrated a  
680 positive impact of eddies on primary production (Chelton et al., 2011; Gaube and  
681 McGillicuddy, 2017; McGillicuddy et al., 2007) and some impacts on zooplankton  
682 (Goldthwait and Steinberg, 2008; Hauss et al., 2016; Lebourges-Dhaussy et al., 2014). The  
683 relationship with micronekton is less clear and sometimes contradictory or specifically related  
684 to observed eddies (Behagle et al., 2014; Brandt, 1983; Griffiths and Wadley, 1986; Sabarros  
685 et al., 2009). Further studies to determine how eddies affect backscatter and micronekton  
686 should include specific metrics to eventually propose a typology.

687 Finally, we did not test a possible effect associated with the dissolved oxygen concentration  
688 because oxygen is not limiting in this subtropical zone. Further, although oxygen is especially  
689 important for the maximum depth of migration (Bertrand et al., 2010; Bianchi et al., 2013;  
690 Maas et al., 2014), that was not a parameter considered in this study as we limited our  
691 analyses to nighttime abundance within the 20–120m layer.

## 692 **4.3 Variability of acoustic backscatters in the EEZ**

### 693 **4.3.1 Mean spatial distribution**

694 Without an independent dataset to validate our predicted distributions, the use of two different  
695 modeling approaches offered an alternative to assess prediction robustness. GAMMs have

696 been largely used to explain backscatter value variability with environmental data (Bertrand et  
697 al., 2004; Boersch-Supan et al., 2015; Escobar-Flores et al., 2018; Hazen and Johnston, 2010).  
698 Machine-learning algorithms such as SVM have been used for species distribution modeling  
699 (Drake et al., 2006) but not yet applied to acoustic data. One major difference between models  
700 was how they dealt with interaction terms: GAMM relationships between  $S_v$  and  
701 environmental variables had the same shape for the two ADCP devices, whereas SVM  
702 relationships had different shapes. The underlying assumption was that depending on the  
703 ADCP frequency, organisms respond differently and thus show different responses to  
704 oceanographic variables. As the reality was unknown and as quadratic errors for the two  
705 models were very close, assuming common patterns seemed to be reasonable: the use of two  
706 methods concurrently increased the predictions confidence. Predicted spatial patterns were  
707 coherent with the model based on GAMM1, which included latitude and longitude instead of  
708 environmental predictive variables (Appendix D, Fig. D1). However, acoustic data remained  
709 relatively complicated to analyze due to the high collinearity, and difficult to interpret due to a  
710 persistent uncertainty about which organisms were being measured.

711 The two approaches, GAM and SVM, generally agreed with one another with some  
712 exceptions. Both models predicted higher backscatter close to reefs during the warm season,  
713 and in the southern part of the EEZ during the cold season. These areas were characterized by  
714 high chlorophyll-*a* concentration, warm water, close to the coast, and optimum bathymetry.  
715 The main island's western coast seemed to be a favorable habitat year round. On the contrary,  
716 low predicted backscatter values in the EEZ's south during the austral winter (Fig. 8A) were  
717 in waters with the highest chlorophyll-*a* concentration (Appendix C). SST may be too low,  
718 despite high chlorophyll-*a* concentrations, to be favorable to backscatter values. The  
719 combination of all intertwined environmental parameters determined the backscatter value at  
720 a specific location and time, defining micronekton habitat.

721 The areas where the two models diverged the most were the northern part of the southeast  
722 corner of the EEZ, the Fairway-Lansdowne Bank, and the northern part of the EEZ. Those  
723 areas had all been sampled several times (Fig. 1). The high variability predicted by models  
724 could be linked to the large variability in oceanographic variables used as predictors or could  
725 be linked to large variability in observed scattering values in a region with shallow bottom  
726 depths.

727

728

### 729 **4.3.2 Temporal variability**

730 Not surprisingly, the largest variability in abundance of micronekton (20–120 m) was  
731 associated with the DVM, a well-known ubiquitous phenomenon (Bianchi and Mislan, 2016).  
732 Sun elevation was found to explain the largest part of  $S_{v\_ADCP}$  variability, with higher values  
733 during the night than during the day.  $S_{v\_ADCP}$  became constant across a 24-hour cycle when  
734 sun elevation was lower than  $-20^\circ$  at night and higher than  $10^\circ$  during the day. Sun elevation  
735 threshold values were close to the values used in SEAPODYM-MTL to define a “night  
736 period” and a “day period” (Lehodey et al., 2015). The difference in the mean backscatter  
737 value between night and day was in agreement with previous results (Domokos, 2009).

738 Backscatter echo intensity was globally higher during the warm season (February–March) and  
739 lower during the cold season (July–August) with a clear seasonal cycle both by the GAMM1  
740 results (Fig. 5) and the second hybrid GAMM2/SVM. Secondary peaks in the seasonal cycle  
741 could be explained by different rates of recruitment and mortality according to the species,  
742 and thus different optima induce different peaks in species abundance over the year. This  
743 hypothesis was reinforced by the fact that areas predicted as having favorable habitat changed  
744 across the year (Fig. 8A), and may be due to favorable habitat for different species. Such  
745 variability could be expected given the high diversity of micronekton observed in the region,  
746 where more than 480 species of fishes, crustaceans, squids and gelatinous organisms have  
747 been recorded (Payri, 2018).

748 A significant influence of ENSO on acoustic densities was detected in the EEZ, with higher  
749 values during El Niño than La Niña or neutral years. We showed that micronekton density  
750 increased with both increasing surface chlorophyll-*a* and SST (Fig. 7). In the EEZ, El Niño is  
751 characterized by colder SSTs (Delcroix and Lenormand, 1997) but more productive waters  
752 (Dandonneau and Gohin, 1984; Radenac et al., 2012). Therefore, we suggested that the  
753 chlorophyll-*a* effect (positive anomaly) associated with El Niño was stronger than the effect  
754 of SST (negative anomaly), explaining the higher backscatter during El Niño. Additionally,  
755 we knew that ENSO could have an impact on micronekton species, especially on their  
756 recruitment (Hewitt et al., 2003; Quetin and Ross, 2003). Such mechanisms also likely  
757 occurred in New Caledonia’s waters.

758 An interesting long-term temporal trend was finally observed over the 1999–2017 time  
759 period, with eight years of acoustic density decrease from 1999 to 2007, followed by eight  
760 years of increase from 2007 to 2015 (Fig. 6). This trend could be related to the IPO/PDO  
761 cycle (Interdecadal Pacific Oscillation/Pacific Decadal Oscillation). PDO fluctuations have  
762 basin-wide effects on SST and thermocline slope that are similar to El Niño (warm phase) and  
763 La Niña (cold phase) but on an approximately 10-year cycle (Mantua and Hare, 2002). A  
764 PDO warm period started in 2008 and coincided with the increasing trend of backscatter  
765 values. However, we did not identify any related long-term anomaly in the oceanographic  
766 variables used as predictors in this study, and the shift in backscatter after 2007 remained  
767 unexplained.

#### 768 **4.5 Interest for ecosystem modeling**

769 The predicted backscatter was compared to micronekton biomass from the ecosystem model  
770 SEAPODYM for the functional groups inhabiting the epipelagic layer during the nighttime. If  
771 we assume that backscatter was directly proportional to the biomass of all micronekton  
772 organisms included in these functional groups, a good match between the two products would  
773 provide confidence in the results of both the ecosystem model and the statistical approach  
774 used to inter-calibrate and merge a large volume of acoustic data collected with ADCP. This  
775 was not the case, however. Micronekton SEAPODYM biomass distribution in the epipelagic  
776 layer at night was close to the average distribution of chlorophyll-*a*, with higher productivity  
777 in the southern region (Fig. 9 and Appendix C4), but a delayed seasonal peak (November–  
778 December) of five months relative to the peak of chlorophyll-*a* that occurs around July–  
779 August (Condie and Dunn, 2006; Smeti et al., 2015). The predicted average backscatter had a  
780 seasonal peak in the warmest months (February–March), and higher values, on average, in the  
781 northern warmer region.

782 For a better understanding of these results, it seems essential to characterize the community of  
783 mesozooplankton and micronekton species in these different regions and seasons, the target  
784 strengths of dominant species at different frequencies and their cycles of abundances. It is  
785 possible for instance that the observed discrepancy between model outputs was due to  
786 seasonal blooms of gas-bearing siphonophores (Davison et al., 2015b; Proud et al., 2018) or  
787 similar organisms that have strong acoustic resonance but low energy (carbon) content.  
788 Conversely a large biomass of mesopelagic fish without gas-filled swim bladders may be  
789 present but transparent to the acoustic signal (Foote, 1980).

790 Continuing to validate ecosystem models is another essential task. The SEAPODYM-MTL  
791 advection model may appear too simple to take into account the spatial variation of observed  
792 micronekton distribution across seasons, based on acoustic estimates. Implementing a  
793 zooplankton compartment in SEAPODYM-MTL may improve that model by giving more  
794 flexibility to the model to better fit with observed backscatter values.

795 Comparing ecosystem model outputs with equivalent observations such as acoustic data was  
796 challenging. The biomass of taxonomic groups defined in ecosystem models needs to be  
797 converted into measures suitable for comparison, in this case target strength, by making simple  
798 approximations of target shape and assumptions regarding density and sound speed contrasts  
799 (Lavery et al., 2007; Scouling et al., 2015). This approach still requires collecting *in situ* data to  
800 attribute which part of the ecosystem model biomass is observable, or not, with a given acoustic  
801 frequency. A multi-platform approach to observation, combining nets, acoustics, imagery  
802 techniques and eDNA, appears necessary to achieve this goal (Handegard et al., 2013;  
803 Lehodey et al., 2015).

#### 804 **4.6 Conclusions and perspectives**

805 Our results bring additional evidence that ADCP echosounders are a valuable source of data  
806 for studying the variability top predator prey through time and space, particularly  
807 macrozooplankton and micronekton. The access to a large historical ADCP acoustic database  
808 was of primary interest, especially in the context of climate change, to explore past variability.  
809 We provided an approach to merge two un-calibrated acoustic datasets using a reference  
810 calibrated dataset. Key environmental predictors such as SST, chlorophyll-*a*, thermocline  
811 depth, bathymetry and distance from coast seemed sufficient to statistically predict the  
812 backscattering intensity recorded from ADCP in New Caledonia's EEZ. The temporal and  
813 spatial variability of the signal were analyzed and provide interesting results at seasonal, inter-  
814 annual (ENSO) and long-term scales. Finally, we showed that a state-of-the-art model  
815 (SEAPODYM-MTL) did not always reproduce acoustic estimates. To be fully comparable  
816 with ecosystem model outputs, a research effort on the development of acoustic observation  
817 models is needed. Acoustic data need to be complemented with multiple observation  
818 platforms to reduce overall bias in estimates of micronekton biomass. The resulting estimates  
819 can be used to assess, initiate and assimilate into ecosystem models.

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

823 The case of New Caledonia and the implementation of the Coral Sea Natural Park  
824 (<https://mer-de-corail.gouv.nc/>) provides a good example of a close link between science and  
825 management. Observed and predicted distributions of micronekton along with the knowledge  
826 of top predator distributions are central to refining management and conservation measures in  
827 such a vast oceanic region. Cooperation and coordination at a larger international scale is also  
828 highly desirable, such as through the Global Ocean Observing System (GOOS), to model and  
829 forecast the impact of the climate change on the functioning of the ecosystems and to support  
830 development of long term mitigation and conservation measures (Bax et al., 2018; Muller-  
831 Karger et al., 2018).

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833

834

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