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Soutenu publiquement par
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Exploitation, biologie et structure de la population du denti,
***Dentex dentex*, en Corse (Méditerranée Nord Occidentale)**

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Chapitre I

Introduction Générale

I.1 Le contexte historique de la pêche

Au cours de l'histoire, les peuples du monde entier se sont installés le long des côtes pour faire usage des ressources marines vivantes (Lotze et al. 2011). Lorsque la rudesse des conditions venait à menacer les premières populations humaines, les ressources marines ont assuré leurs subsistances (Marean 2010). Mais depuis lors, l'humanité a prospéré et a fortement impacté les espèces et les écosystèmes côtiers, en particulier au cours de ces 150 dernières années (Jackson et al. 2001). Connaître l'ampleur des changements passés est essentiel pour juger de l'état actuel des écosystèmes marins, et comprendre ces phénomènes passés et leurs conséquences sont nécessaires pour atténuer les impacts humains actuels et futurs (Lotze et al. 2011). La pêche est une activité humaine millénaire qui contribue à la culture, l'économie, l'emploi et à l'approvisionnement alimentaire des communautés côtières (Gabriel et al. 2005). A la fin du XIX^{ème} siècle, la capacité de pêche a augmenté de façon exponentielle, et est devenue motorisée dans le début du XX^{ème} siècle (Vrgoc et al. 2004). Sans doute, la pêche industrielle a démarré dans les années 1880, avec le déploiement des premiers chalutiers à vapeur autour de l'Angleterre, qui a annoncé la première utilisation de combustible fossile (charbon) pour cette activité (Anticamara et al. 2011). L'évolution des flottes de pêche au cours du siècle dernier a montré une augmentation brusque de l'effort de pêche, en termes de puissance motrice et de tonnage total (Colloca et al. 2004). Des améliorations technologiques ont intensifié cet effort de pêche, ce qui a conduit à l'apparition de grands navires en capacité de sillonner les océans et pêcher à toutes les profondeurs et latitudes (Gabriel et al. 2005). En effet, alors que des conflits majeurs, tels que les deux guerres mondiales, ont conduit à la réduction temporaire de l'effort, elles ont également contribué à la mise au point de nouvelles technologies qui ont augmenté l'efficacité de l'effort de pêche (ex : radar, sondeur, sonar à balayage latéral et GPS) (Anticamara et al. 2011). Dans les premières décennies après la seconde Guerre mondiale, la croissance des activités de pêche de mer a été très rapide, pour atteindre un niveau maximal à la fin des années 1980 (Colloca et al. 2004). C'est durant cette période qu'a débuté l'industrialisation mondiale de la pêche (Pauly 2009). En effet, cette industrialisation massive a fait passer les captures de 5 millions de tonnes à la fin du XIX^{ème} siècle à 86 millions de tonnes à la fin des années 1980 (Revéret and Dancette 2010). Pendant de nombreuses années, les débarquements mondiaux déclarés se sont stabilisés à environ 80 millions de tonnes par an, avec près de 20 millions de tonnes de captures non déclarées et/ou illégales supplémentaires (Agnew et al. 2009). Cette stagnation s'est produite en dépit d'efforts de pêche accrus, et de l'expansion géographique et bathymétrique des activités de pêche (Swartz et al. 2010). Cependant il faut noter que les variations de production par pays, suivant les zones de pêche et espèces se compensent au niveau

mondial du fait d'évolutions inverses selon les pêches. Ainsi au cours de ces 20 dernières années, les captures de plusieurs stocks commerciaux ont fortement décliné (Morales-Nin et al. 2005).

I.2 La situation actuelle des ressources halieutiques au niveau mondial

Les ressources halieutiques mondiales sont soumises à d'intenses pressions (Pauly et al. 2002). Les stocks de poisson sont une source alimentaire riche en protéines importante pour l'humanité, pourtant ils sont exposés à de fortes pressions comme : la surpêche, le changement climatique mondial, la pollution et la dégradation d'habitat (Klemas 2012). De plus, la demande mondiale pour les produits de la mer est en hausse continue, aussi bien dans les pays développés, en raison de l'augmentation du niveau de vie, que dans les pays en voie de développement, dont la population ne cesse de croître rapidement (Pauly and Froese 2012). Au cours des dernières années, de nombreuses ressources halieutiques ont été surexploitées, ce qui soulève des doutes quant à la viabilité à long terme de certaines pêcheries (Castilla 2000). Ainsi les pêcheries mondiales sont en crise, et l'état d'exploitation des principaux stocks de poissons dans le monde montre une surexploitation ou la pleine exploitation de la plupart des stocks (Morales-Nin et al. 2010). Par définition, l'abondance des stocks pêchés à un niveau biologiquement non viable à long terme est inférieure au niveau requis pour assurer le rendement maximal durable, ce qui signifie que ces stocks sont surexploités. Le Rendement Maximal Durable (RMD) est une approche qui consiste à ajuster l'effort de pêche et les modalités de captures permettant l'exploitation des ressources halieutiques dans des conditions économiques, environnementales et sociales durables. Ainsi selon la FAO 2014, au niveau mondial 71.2 % des stocks de poissons étaient exploités à un niveau biologiquement viable à long terme en 2011. 61,3 % étaient exploités au maximum et 9,9 % étaient sous-exploités. Il a été estimé que 28,8 % des stocks de poissons étaient pêchés à un niveau biologiquement non viable à long terme et, donc, étaient surexploités. En 2011, les dix espèces les plus productives (l'anchois du Pérou¹, le colin d'Alaska², la bonite à ventre rayé³, le hareng de l'Atlantique⁴, le merlan bleu⁵, le maquereau blanc⁶, le chinchard du Chili⁷, l'anchois du Japon⁸, le poisson-sabre commun⁹ et le thon albacore¹⁰) ont fourni 24% de la production mondiale de la pêche en mer (FAO 2014). La plupart de leurs stocks sont exploités au maximum, et n'offrent donc aucune possibilité d'accroissement de la production. Les données finales indiquent qu'avec 93,7 millions de

¹ *Engraulis ringens* (Jenyns, 1842) ² *Theragra chalcogramma* (Pallas, 1814) ³ *Sarda sarda* (Bloch, 1793) ⁴ *Clupea harengus* (Linnaeus, 1758) ⁵ *Micromesistius poutassou* (A. Risso, 1827) ⁶ *Scomber japonicus* (Houttuyn, 1782) ⁷ *Trachurus murphyi* (Nichols, 1920) ⁸ *Engraulis japonicus* (Linnaeus, 1758) ⁹ *Trichiurus lepturus* (Linnaeus, 1758) ¹⁰ *Thunnus albacares* (Bonnaterre, 1788)

tonnes en 2011, la production mondiale totale de la pêche a enregistré son deuxième record historique, légèrement inférieur à celui de 1996 (93,8 millions de tonnes) (Fig. 1).

De plus, la production de l'année 2012 a encore été exceptionnelle (91,3 millions de tonnes). Ces résultats récents ne doivent pas pour autant nous faire espérer des augmentations importantes des captures. Ils témoignent plutôt du maintien de la situation globalement stable. Il faut noter aussi qu'à l'échelon mondial, l'aquaculture n'a cessé de prendre de l'importance dans l'offre totale de poisson avec une production totale estimée de 66.6 millions de tonnes en 2012 (FAO 2014).

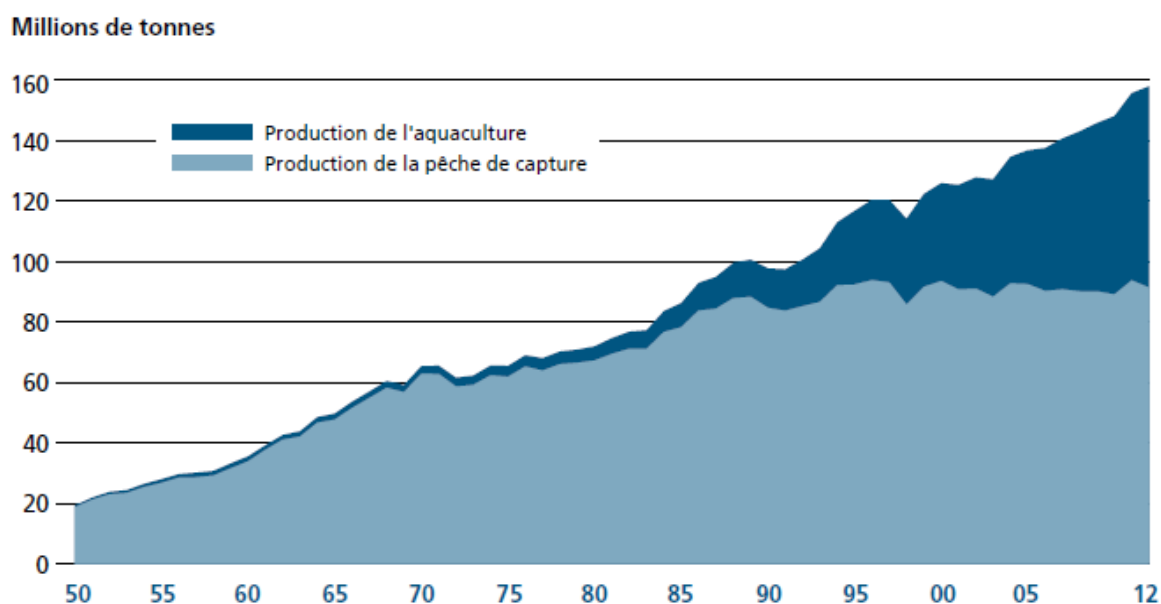


Fig. 1 : Evolution de la production mondiale de la pêche et de l'aquaculture de 1950 à 2012 (FAO 2014).

I.3 La mer Méditerranée : une biodiversité en danger

La mer Méditerranée est considérée comme un haut lieu de la biodiversité marine, étant donné la diversité exceptionnelle d'espèces dont elle regorge (Coll et al. 2010). Une évaluation estime à plus de 8500 le nombre d'espèces marines présentes en Méditerranée, correspondant à peu près entre 4% et 18% des espèces marines mondiales (Bianchi and Morri 2000). On y dénombre actuellement plus de 600 espèces de poissons marins (Abdul Malak et al. 2011). C'est un chiffre remarquable si l'on considère que la mer Méditerranée ne représente que 0,82% en superficie et 0,32% en volume par rapport à la superficie et au volume total de l'ensemble des océans (Bianchi and Morri 2000). Cette grande biodiversité peut s'expliquer notamment par des raisons historiques, paléogéographiques, et écologiques. Dans un même temps, c'est l'une des régions marines les plus menacées au

monde (Coll et al. 2010). La Méditerranée a été décrite comme un écosystème "assiégé" (Coll et al. 2012). Les impacts humains sont distribués de manière hétérogène le long de la mer Méditerranée et de nombreuses zones sont soumises à des impacts multiples simultanément (Coll et al. 2014). Ces menaces résultent d'une combinaison de plusieurs facteurs tels que la pollution, la dégradation d'habitat, l'introduction de nouvelles espèces, le changement climatique et l'exploitation (incluant la pêche industrielle, artisanale et récréative) (Coll et al. 2012). Ces impacts ont un effet sur la biodiversité et l'abondance de ressources marines mais aussi une influence sur la structure et le fonctionnement des écosystèmes marins (Worm et al. 2006). Beaucoup d'espèces marines de la Méditerranée sont menacées et certaines sont probablement enclines à l'extinction (Bianchi and Morri 2000). Ainsi en 2011, 52 pour cent des stocks halieutiques évalués de la Méditerranée étaient pêchés à des niveaux non viables, et 48 pour cent exploités au maximum ou sous-exploités (FAO 2014).

I.4 La gestion des pêches

Trouver un équilibre entre la sécurité alimentaire, la santé économique, la durabilité de la pêche, la conservation de la biodiversité et le fonctionnement des écosystèmes marins est un défi (Hobday et al. 2015). La gestion des pêches fait face à la tâche difficile de développer dans un même temps des scénarios pour une exploitation durable, protéger la biodiversité marine et les moyens de subsistance des communautés de pêcheurs (Forcada et al. 2009). Traditionnellement, la gestion des pêches a surtout privilégié l'optimisation de la productivité au niveau de l'espèce et/ou du stock en négligeant la complexité des interactions au sein des écosystèmes marins (Avadí and Fréon 2013). En général, la gestion des pêches applique une combinaison de mesures telles que la réduction de la capacité de pêche par des mesures «traditionnelles» (ex : quotas de débarquement, réduction de l'effort de pêche, réglementation des engins, mise en place d'une taille minimale de débarquement). Une vision plus globale de la gestion des écosystèmes s'est récemment imposée avec l'Approche Ecosystémique des Pêches (AEP): celle d'une exploitation viable des ressources, et respectueuse des écosystèmes marins (FAO 2003). L'AEP intègre les dynamiques spatiales des espèces mais aussi les interactions entre les espèces en tant qu'enjeu pour la gestion des pêcheries (Cury 2013). Plus spécifiquement, plusieurs engagements en relation avec l'AEP ont été pris par l'Union européenne comme : (i) l'application du code de conduite pour une pêche responsable (ii) la réduction significative du taux de perte de la biodiversité, (iii) la restauration des pêcheries à leur niveau de production maximale soutenable (Rendement maximal durable : RMD), (iv) ou encore la création d'un réseau d'aires marines protégées. Aujourd'hui, les aires marines protégées (AMP) sont mises en œuvre dans le

monde entier comme l'un des outils majeurs pour une approche écosystémique des pêches (Garcia et al. 2003). Dans ce contexte, les AMP sont de plus en plus considérées comme un outil de gestion important pour réduire, prévenir et/ou inverser le déclin constant de la biodiversité marine (Roberts et al. 2005). Le pourcentage de la surface protégée en mer Méditerranée est de 3,8 % (Abdul Malak et al. 2011). Les AMP facilitent potentiellement la durabilité à long terme de beaucoup de pêcheries (Gell and Roberts 2003). Elles peuvent être décrites comme un outil visant à atteindre des objectifs multiples de conservation et de promotion du développement durable (en tenant compte des aspects sociaux et économiques) (Di Franco et al. 2014a). La gestion de ces zones nécessite des informations spatiales précises sur la distribution des espèces, les habitats, l'exploitation et d'autres caractéristiques écologiques (Costello et al. 2010). Cependant ces informations ne sont que rarement disponibles. Les effets directs et/ou indirects de la pêche menacent beaucoup d'organismes marins (Worm et al. 2006). En Méditerranée, l'exploitation accrue a modifié et simplifié la structure du réseau trophique au fil du temps, notamment en réduisant les proportions de grands prédateurs et poissons de grande taille (Colloca et al. 2013). Dans ce contexte, la reconstruction de la structure de la population est un objectif important pour les stocks méditerranéens tant de nombreuses espèces commerciales ont montré une troncature de leur structure de taille et d'âge résultant d'une surpêche historique (Colloca et al. 2013). Cette reconstruction de la structure de la population combine à la fois des objectifs de gestion monospécifique comme le RMD avec des objectifs spécifiques d'une AEP, tels que le maintien d'une configuration trophique saine et le rôle écologique des différentes espèces (Froese et al. 2008). Il est urgent, par conséquent, d'évaluer l'impact potentiel que les différents types d'activités de pêche peuvent avoir sur la durabilité des ressources côtières et sur le fonctionnement général des écosystèmes côtiers (Albouy et al. 2010). La connaissance de ces impacts est non seulement importante pour une meilleure compréhension des réponses de l'écosystème à ces pressions, mais peut aussi favoriser l'instauration des mesures de gestion efficaces (Batista et al. 2014).

I.5 Présentation de l'espèce

Le denté commun, plus couramment appelé denti, *Dentex dentex* (Linnaeus, 1758), est un poisson marin côtier (0-200m) emblématique et patrimonial de la Méditerranée. Ce sparidé est communément distribué en Méditerranée et signalé en Mer Noire. En Atlantique on le retrouve depuis les Iles Britanniques, en passant par le Golfe de Gascogne, les Iles Canaries jusqu'au sud du Sénégal (Bauchot and Hureau 1986; Morales-Nin and Moranta 1997; Marengo et al. 2014a). Le denti est un poisson de relativement grande taille (jusqu'à 1m et plus de 10 kg) dont la longévité est importante (supérieure à 20 ans) (Fig. 2) (Morales-

Nin and Moranta 1997; Chemmam-Abdelkader et al. 2004). Il a une haute valeur commerciale et représente un intérêt économique important pour la pêche artisanale. Le denti est aussi particulièrement ciblé par la pêche récréative. Du fait de sa grande taille, de la qualité de sa chair et de sa combativité, Il est considéré comme une espèce trophée par cette activité. Il est également considéré comme un candidat potentiel pour l'aquaculture, en raison de sa facilité de reproduction en captivité et de taux de croissance élevés au cours de ses premières années de vie (Rueda and Martinez 2001). Par ailleurs en tant que prédateur supérieur, le denti occupe une position clé au sommet de la pyramide trophique et constitue donc potentiellement une espèce indicatrice de la structure et du fonctionnement des écosystèmes côtiers dont il dépend. Enfin, il présente un statut de conservation en étant classé comme « Vulnérable » par l'Union Internationale pour la Conservation de la Nature (IUCN) dans la liste rouge des espèces menacées (Carpenter and Russell 2014). Malgré son importance écologique et économique, les informations sur cette espèce sont encore limitées. Le denti focalise ainsi des intérêts environnementaux, sociétaux et économiques certains en Méditerranée et en particulier en Corse.



Fig. 2 : Photo (i) d'un juvénile de denti capturé par la pêche artisanale en Corse (à gauche; Nicolas Tomasi, STELLA MARE) ; (ii) d'un spécimen adulte dans l'herbier de posidonies (*Posidonia oceanica*, L.Delile) (à droite; Christophe Quintin).

I.6 La Corse: Une montagne dans la mer

La Corse se situe dans le bassin nord occidental de la Méditerranée. Elle a une superficie de 8 722 km², c'est la troisième plus grande île méditerranéenne derrière la Sicile et la Sardaigne. Elle a une altitude moyenne de 568 mètres et compte plus de 20 sommets dépassant 2000 m, dont le plus important est le Monte Cinto qui culmine à 2710 m.

Le rivage de la Corse s'étire sur une longueur de 1047 km, ce qui représente plus de la moitié du littoral français de Méditerranée, et 14% des cotes hexagonales. La spécificité du rivage insulaire est due à la forte proportion de côtes rocheuses (71%). Le littoral sableux se

concentre essentiellement sur la façade maritime orientale de l'île (Pluquet 2006). Autour de la Corse, la largeur du plateau continental est en général très faible : l'isobathe 200 mètres est à 7 milles du rivage sur la côte orientale, à 5 milles sur la côte nord ouest et à moins de 1 mille de certains points de la côte ouest.

Le nombre de poissons marins recensés en Corse dépasse aujourd'hui les 400 espèces. On note que les deux tiers de ces espèces peuvent être considérées comme rares et le tiers restant comme communes. Les espèces commercialisées sont au nombre de 150.

I.7 Contexte de l'étude

La pêche corse est composée d'une flottille artisanale de 195 unités réparties sur 4 Prud'homies (Ajaccio, Bonifacio, Bastia-Cap Corse et Balagne). L'effort de pêche s'exerce principalement sur une zone côtière comprise entre 0 et 3 milles nautiques, à une profondeur de 0 à 200 mètres. Cette région est considérée comme une zone où la pression de pêche est faible par rapport au reste de la Méditerranée (Relini et al. 1999). Cependant des études ont montrées que les eaux corses ont pu être exposées à des pressions de pêche beaucoup plus importantes que précédemment supposé (Le Manach et al. 2011). Un suivi halieutique des activités de pêche artisanale sur l'ensemble de la Corse est effectué par la Station de Recherche Océanographiques et sous-marines (STARESO). Depuis 2004, les données récoltées se concentraient sur la langouste puis à partir de 2009 la récolte des données s'est élargie à l'ensemble des espèces exploitées. Ainsi avec une production estimée en 2009 à 28,3 tonnes, les captures de denti par la pêche artisanale en Corse sont élevées (Francois 2011). Au carrefour des activités traditionnelles et de celles en voie de développement, la pêche récréative regroupe toutes les activités halieutiques non lucratives. Si les techniques sont connues, l'effort et les captures ont commencé à faire l'objet d'un suivi précis depuis 2005 dans la Réserve naturelle des Bouches de Bonifacio (RNBB), alors qu'un suivi de la pêche artisanale a été commencé dès 2000. Il semblerait qu'il y ait eu au cours de ces dernières années une augmentation de l'effort de pêche. Pour le denti, l'arrivée et le développement de nouvelles techniques telles que la pêche au « Jig » ou « Jigging » a semblé particulièrement affecter cette ressource en Corse. Par conséquent, il a été fait le constat qu'il existait très peu d'informations disponibles sur l'exploitation, la biologie et la structure de population du denti en Corse. C'est dans ce contexte, que ce travail de recherche, initié par l'Université de Corse, a uni en une volonté commune, scientifiques (STARESO), gestionnaires (OEC/RNBB) et pêcheurs, pour améliorer l'état des connaissances.

I.8 Objectifs de la thèse

L'objectif principal de cette thèse vise à améliorer l'état des connaissances sur l'exploitation, la biologie et la structure de population du denti en Corse, afin de contribuer à la gestion halieutique durable de cette espèce. Les sept chapitres de ce travail de recherche ont été conçus pour répondre aux objectifs spécifiques suivants :

Le **Chapitre I** est une introduction générale décrivant le contexte de l'étude, et la problématique de recherche. Le **Chapitre II** est une synthèse de la littérature sur la biologie, l'écologie, la parasitologie, la structure de population, l'exploitation, et les mesures de gestion associées pour le denti sur l'ensemble de son aire de répartition. Les principales lacunes dans les connaissances actuelles sont identifiées et de futures directions de recherches sont proposées pour résoudre ces questions fondamentales. Le **Chapitre III** étudie les facteurs (spatio-temporels) qui influencent les captures de denti de la pêche artisanale à l'échelle de la Corse. Des « hot spots » de captures sont identifiés et la structure démographique (taille et âge) de la population exploitée y est décrite. Ensuite (**Chapitre IV**), il est réalisé une analyse comparative de l'exploitation du denti par la pêche artisanale et récréative dans une aire marine protégée (RNBB). Il y est montré l'influence des mesures de gestions sur les niveaux de captures de ces deux activités. Le **Chapitre V** compare trois différentes méthodes d'estimation d'âge (écailles, otolithes entiers et sectionnés). L'objectif est de déterminer quelle structure et quelle méthode de préparation est la plus fiable et précise. Mais aussi de définir les paramètres de croissance du denti en Corse. Le **Chapitre VI** étudie la structure de population du denti autour de la Corse à l'aide d'une combinaison de marqueurs qui ont une échelle d'intégration différente au niveau spatial et temporel (Microsatellites, analyse de la forme des otolithes et les communautés de parasites). Enfin, l'ensemble de ces résultats est discuté dans le cadre d'une discussion générale et des perspectives de recherche inscrites dans la continuité de ces travaux de thèse sont proposées (**Chapitre VII**).

Chapitre II

A review of biology, fisheries and population structure of *Dentex dentex* (Sparidae)

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II.1 Introduction

The common dentex *Dentex dentex* (Linnaeus, 1758) is an iconic marine coastal bony fish in the Mediterranean Sea. It holds an important place as a fishery resource for both professional and recreational fishing, and a key position at the top of the food chain in coastal ecosystems. It belongs to the Sparidae family (Bauchot and Hureau 1986), which is represented in the Mediterranean Sea by 10 genera and 22 species that usually inhabit coastal areas (Arculeo et al. 2003). It was first described in the 18th century as *Sparus dentex* (Linnaeus, 1758), then *Sparus cetti* (Risso, 1810) or *Dentex vulgaris* (Cuvier & Valenciennes, 1839) and finally *Dentex dentex* (Linnaeus, 1758) (Tortonese 1973; Bauchot and Hureau 1986; Bauchot and Hureau 1990). This species is of great economic interest and high commercial value for artisanal fishing (Morales-Nin and Moranta 1997; Loir et al. 2001; Chemmam-Abdelkader et al. 2007). *Dentex dentex* has a high market value (Chemmam-Abdelkader et al. 2006) with prices currently ranging from a minimum of 15 €/kg for whole fish to a maximum of 38 €/kg for fillets and sliced fish. It is a highly prized catch in recreational fishing (Morales-Nin et al. 2005; Font and Lloret 2011); and is also appreciated by scuba divers (Cadiou et al. 2009). As a top predator, the common dentex is a potential indicator species for the structure and functioning of the coastal ecosystems on which it depends (Macpherson et al. 2002; Seytre and Francour 2008; Valls et al. 2012).

Dentex dentex is classified by the International Union for the Conservation of Nature (IUCN) as “vulnerable” in the Red List of Threatened Species in the Mediterranean Sea (Abdul Malak et al. 2011). There are several reasons for this ranking: the Food and Agriculture Organization (FAO) has reported that landings for this species have steadily declined over a recent 15-year period, from a peak of ~7,000 tons in 1990 to less than 1,000 tons in 2005. In addition, it is a highly sought-after food fish targeted by recreational fishing and is relatively long-lived with populations slow to recover. The common dentex is also considered as a potential candidate for aquaculture, due to its commercial success, ease of reproduction in captivity and high growth rates during the first years (Abellán 2000; Loir et al. 2001; Rueda and Martinez 2001; Giménez and Estévez 2008; Tomas et al. 2009). Accordingly, a considerable number of studies have been published concerning the biology of common dentex in captivity (Rueda and Martinez 2001; Koumoundouros et al. 2004; Suarez et al. 2009; Rigos et al. 2012).

Despite its economic and ecological importance, scientific peer-reviewed papers on the biology of this species in its natural environment are still very scant. The most important studies describe the fishing and biology of *Dentex dentex* from the Balearic Islands off Mallorca (Morales-Nin and Moranta 1997), and its age and growth on the Tunisian coast (Chemmam-Abdelkader 2004; Chemmam-Abdelkader et al. 2004). While specific studies on

this species are scarce, there is piecemeal information in scientific reports and in peer-reviewed papers regarding morphology and geographical distribution (Bauchot and Hureau 1986), the range of habitats occupied (Bayle-Sempere et al. 1991; Ramos-Esplà and Bayle-Sempere 1991), reproduction and growth (Morales-Nin and Moranta 1997; Chemmam-Abdelkader 2004), parasite communities (Radujkovic and Raibaut 1989; Euzet et al. 1993; González et al. 2004; Bartoli et al. 2005), the fishing gear used (Cetinic et al. 2002; Lelli et al. 2006; Sacchi et al. 2010; Sacchi and Dimech 2011), catches and annual production (FAO 2012), regulations (Cacaud 2003; Sahyoun et al. 2013), and on population structure and stock discrimination (Bargelloni et al. 2003; Palma and Andrade 2004). There is a lack of basic biological studies for the Mediterranean fish populations, and yet this information is most important for the conservation of biodiversity and sustainable fishery management (Tzanatos et al. 2008; Damalas et al. 2010). This review critically evaluates the current literature on *D. dentex* biology, ecology, stock structure, and fisheries, and suggests future research directions to fill important gaps in current knowledge.

II.2 General description

The common dentex has a rather short compact oval body (Bauchot 1987), with its head profile straight in juveniles and convex in adults (Bauchot 1987; Bayle-Sempere et al. 1991). The oldest specimens have a slight hump at their forehead (Bauchot and Hureau 1986). It has several rows of teeth, with 4–6 well-developed anterior teeth on each jaw (Bauchot 1987), and a succession of canine teeth that are much smaller than the frontal ones (Bayle-Sempere et al. 1991). Its gillrakers are present on the first arch, 9 or 10 lower and 8 or 9 upper (Bauchot and Hureau 1986; Bauchot 1987). Its dorsal fin has 11 spines of increasing length up to the fourth or fifth, and subequal thereafter (Bauchot and Hureau 1986). Ventral fins are characterized by one spine and five radii, the pectoral fins are composed of an average of 15 radii, and the caudal fin present 17 radii (Chemmam-Abdelkader 2004). On the anal fin, there are three spines, and between seven and nine radii (Bayle-Sempere et al. 1991). The lateral line is composed of 62–68 scales to the caudal base (Bauchot and Hureau 1986). Colour changes with age, with the young of the year displaying yellow fins (Louisy 2005) or even appearing entirely yellow (Cheminée 2012); older juveniles are greyish with vertical black bars and are blue-spotted, turning pinkish at maturity, with yellow areas on the ventral part of the head, then grey-blue in the oldest specimens. There are also dorsal spots that are variably shaded with age (Bauchot and Hureau 1986; Bauchot 1987), and green, blue, gold and purple iridescence, especially in the head region (Gonzales 2005). For Sparidae in general and in particular *Dentex dentex*, there are no characters that distinguish between sexes. The common dentex is often confused,

especially in fisheries statistical data, with other Sparidae such as the red porgy (*Pagrus pagrus*), which resembles it in shape and body colour. This precise morphological description of the species can be a reliable tool for its identification, for both biologists and Marine Protected Area (MPA) managers.

II.3 Distribution and habitat

Dentex dentex is a Mediterranean and Atlantic species (Bayle-Sempere et al. 1991). It inhabits the Mediterranean Sea most frequently south of 40°, is found occasionally in the Black Sea, and occurs in the Atlantic Ocean (occasionally around the British Isles), and also Cape Blanc, the Bay of Biscay, Madeira, the Canary Islands and southward to Senegal (Fig. 1) (Bauchot and Hureau 1986; Morales-Nin and Moranta 1997; Bat et al. 2005). In 2008, small juvenile *Dentex dentex* were observed in the Arcachon basin (Quero et al. 2009), implying that common dentex may spawn in the Bay of Biscay. Presence in this region has been reported 12 times in all: five times in the 19th century with large individuals, six times in the 20th and once in the 21st century also with the presence of juveniles (<20 cm) in the Basque country (Quero et al. 2009). *Dentex dentex* is a demersal fish found from 0 to 200 m depth, living on various substrates such as *Posidonia oceanica* meadows (L.) Delile, rocky bottom with *P. oceanica* patches, coastal detritic areas, ripples of coarse sand, sandy habitats with *Caulerpa* and *Cymodocea* and in the coralligenous community (Ramos-Esplà and Bayle-Sempere 1991; Abellán 2000; Rueda and Martinez 2001; Ballesteros 2006; Stobart et al. 2012). Juveniles of common dentex (20–50 mm TL, during June–August) inhabit shallow water (2–4 m depth), at the interface between *Posidonia oceanica* meadows and sand, or close to crevices and small caves (Dulcic et al. 2002; Valle and Bayle-Sempere 2009). The juveniles are gregarious; shoals of *Dentex dentex* have been observed with individuals of medium size (1–5 kg) especially in summer around rocky outcrops at depths between 20 and 50 m, but they are also found in shallow waters (–8 to –10 m) (Bauchot and Hureau 1986; Bayle-Sempere et al. 1991; Francour 1994; Chemmam-Abdelkader 2004; Sahyoun et al. 2013). Behaviour changes with age; the oldest adults animals are solitary (Bauchot and Hureau 1986).

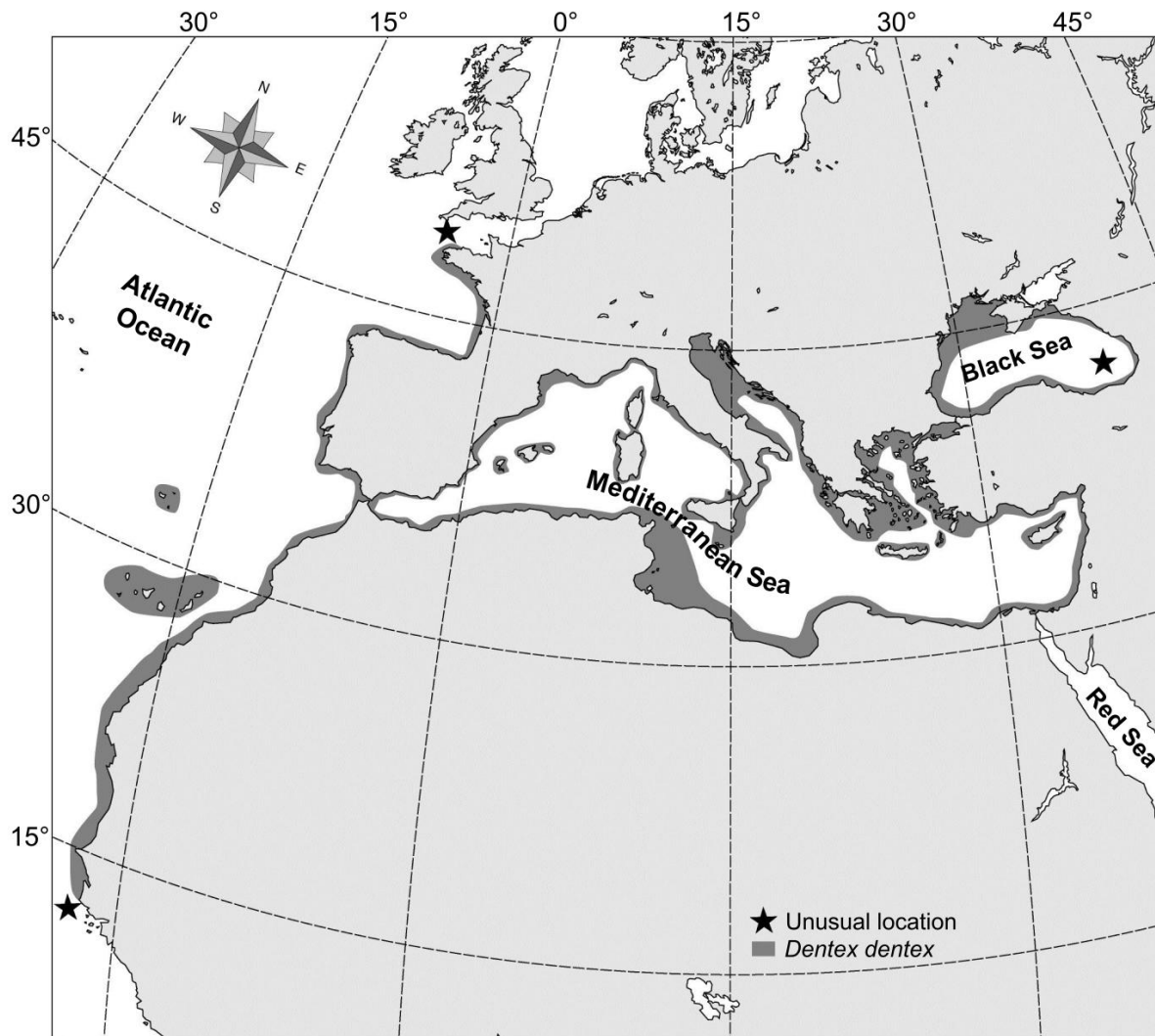


Fig. 1 Global geographical range of *Dentex dentex* (updated from Bauchot and Hureau 1986; Morales-Nin and Moranta 1997; Bat et al. 2005; FAO 2012a, b)

II.4 Feeding and behavioural ecology

Morales-Nin and Moranta (1997) reported that in the Balearic Islands, the adults feed mainly on fish from the coastal zone (74 %) and on cephalopods (26 %) as secondary prey. The smaller individuals had species from the *Posidonia* meadow in their stomachs: sparids, clupeids, gadoids, and more frequently labrids such as the peacock wrasse (*Symphodus tinca*, Linnaeus, 1758, 22.58 %). In larger specimens, fish were the predominant prey, mainly sparids, picarel and anchovy. Whole cephalopods, remains of sepia bone and unidentified beaks were also found (25.62 %). However, their prey species are diverse, and probably depend largely on availability (Morales-Nin and Moranta 1997). On the Tunisian coast the common dentex feeds preferentially on fish (84 %), crustaceans (9 %), cephalopods (5 %) and plant remains (2 %) (Chemmam-Abdelkader 2004). Pelagic fish (e.g. *Trachurus sp*, *Sardina pilchardus*, Walbaum, 1792) constitute the majority of prey (56.1 %), compared with

other fish. Crustacean preys were primarily the caramota prawn (*Penaeus kerathuru*, Forsskål, 1775), cuttlefish (*Sepia officinalis*, Linnaeus, 1758) and the European squid (*Loligo vulgaris*, Lamarck, 1798) were the main cephalopods, and *Posidonia oceanica* and species of the *Caulerpa* genus were the key plants.

The common dentex is a high level tropic predator (trophic level 4.5), and the large size of the adults probably limits the number of predators (Morales-Nin and Moranta 1997; Stergiou and Karpouzi 2001; Froese and Pauly 2011). However, a study on the food and feeding habits of the amberjack *Seriola dumerili* (Risso, 1810) indicates that the common dentex, probably at the juvenile stage, may be considered as an occasional prey for this species (Andaloro and Pipitone 1997).

II.5 Reproduction

There is almost no information on the reproductive biology of common dentex in the natural environment. Based on the macroscopic examination of gonads from 210 fish caught from the waters off Mallorca, they reported an equal sex distribution (Morales-Nin and Moranta 1997). Seasonal variations in the sex ratio of the common dentex were observed on the Tunisian coasts, with an apparent dominance of females compared with males all year round, and a dominance of males during the spawning period (April-June) (Chemmam-Abdelkader 2004). This dominance of males during the spawning period could explain the fertilization of eggs of one female by several males (Chemmam-Abdelkader 2004). In addition, macroscopic examination of *D. dentex* gonads throughout its life cycle revealed rare cases of hermaphroditism. In this study 3,727 individuals were examined, and only 14 immature individuals (with sizes between 17.5 and 24.8 cm) were observed with both male and female parts.

The species *D. dentex* can therefore be characterized by a rudimentary nonfunctional hermaphroditism, which is common throughout sparids. Reproduction (spawning period) occurs from the end of March until June (Morales-Nin and Moranta 1997). In winter most of the specimens are immature, with the development of the gonads starting in January and the first mature specimens appearing in March. The size at which 50 % of the population is mature is estimated at 34.60 cm for females and 52.02 cm for males from the Balearic Islands (Morales-Nin and Moranta 1997), and 23.32 cm for males and 22.58 cm for females from the Tunisian coast (Chemmam-Abdelkader 2004). Along the Tunisian coast, at 26 cm total length (TL), 75 % of the population is mature, and at 33 cm TL 100 % of the population is mature for both sexes (Chemmam-Abdelkader 2004). Maximum maturity occurred in the second quarter of the year, with the first post-spawn specimens appearing in the third quarter (Morales-Nin and Moranta 1997). Examination of the ovaries during the spawning period

shows that they have different amounts of oocytes corresponding to different stages of oocyte release (nearly full, half full, almost empty) (Chemmam-Abdelkader 2004). The analysis of the frequency distribution of egg size shows the existence of four modes corresponding to four categories of oocytes laid at four different periods (Chemmam-Abdelkader 2004). The common dentex is a partial spawner, it emits eggs of the same spawning over several days (Chemmam-Abdelkader 2004). Absolute fecundity of *Dentex dentex*, on average, is equal to 164,195 eggs per fish, and the average relative fecundity is estimated at 217 eggs per gram of fish (Chemmam-Abdelkader 2004).

Concerning the spawning areas, there is no information reported in the literature, however, we collected information in Corsica (France) based on the knowledge of fishers. According to their observations during the spawning period, the populations of common dentex gather periodically on spawning sites at between 40 and 100 m depth to form shoals. These sites are characterized by hard substrates such as rocky outcrops or wrecks. Observations made by seine fishers using sonar suggest that mating occurs mainly during the day, but may also occur at night during the full moon.

II.6 Age, growth and condition

Dentex dentex may reach a maximum length of 100 cm and a weight of 13 kg (Ramos-Esplà and Bayle-Sempere 1991; Morales-Nin and Moranta 1997). There are no morphological differences between the two sexes, and the size-weight relationship is similar in both (Morales-Nin and Moranta 1997). Growth is rapid in the first 2 years of life, with 31 % of the maximum length being reached in the first year (24.1 cm) (Morales-Nin and Moranta 1997) and reported estimates of von Bertalanffy growth parameters similar among studies (Table 1) (Culioli 1986; Morales-Nin and Moranta 1997; Chemmam-Abdelkader et al. 2004).

Dentex dentex has the physiological capacity to withstand long periods of fasting, which seems to form part of its life cycle (Navarro and Gutierrez 1995; Vigliano et al. 2002). Several factors, such as seasonal environmental fluctuations, reproduction, including pre-spawning and migration, or availability of prey are responsible for this natural fasting (Pérez-Jiménez et al. 2012). Results suggest that common dentex possess a high capacity to face such nutritional challenges, given that the reduction in body mass induced by prolonged starvation is far lower than that reported for other sparid fish (Pérez-Jiménez et al. 2012). *D. dentex* are a relatively long-lived species, its maximum lifespan exceeding 20 years (Morales-Nin and Moranta 1997), with up to 33 years reported (Chemmam-Abdelkader et al. 2004). It exhibits a low species-specific production rate per unit biomass (P/B value of 0.24) (Valls et al. 2012) and a low population resilience, with a minimum population doubling time of 4.5–14 years (Froese and Pauly 2011). For these reasons, its populations are considered as slow-

recovering (Abdul Malak et al. 2011). However, the calculated values of natural mortality rate (0.201 year^{-1} for both sexes combined, Morales-Nin and Moranta 1997; 0.24 year^{-1} , Valls et al. 2012) indicate a relatively low natural mortality.

Table 1 Growth parameters of Von Bertalanffy equation estimated for *Dentex dentex*. L_t^∞ = theoretical maximum size, TL = Total Length, K = growth rate, t_0 = age at which the length at age t is theoretically equal to 0, M = Male, F = Female, M/F = Male and Female.

L_t^∞ (cm)	Length type	K	t_0 (years)	Sexe	Country	Locality	Citations
110.000	TL	0.077	-2.304	M/F	France	Calvi	(Culioli 1986)
84.400	TL	0.100	-2.854	M	Spain	Mallorca	(Morales-Nin and Moranta 1997)
85.622	TL	0.102	-2.874	F	Spain	Mallorca	(Morales-Nin and Moranta 1997)
95.051	TL	0.077	-1.796	M	Tunisia	Tunisian coasts	(Chemmam-Abdelkader et al. 2004)
97.354	TL	0.072	-1.933	F	Tunisia	Tunisian coasts	(Chemmam-Abdelkader et al. 2004)
96.804	TL	0.073	-1.892	M/F	Tunisia	Tunisian coasts	(Chemmam-Abdelkader et al. 2004)

II.7 Parasitology

Parasites have been widely used as biological tags to provide information for fisheries management on the movements and population connectivity of their fish hosts (Williams et al. 1992). Just as there is a need to correctly identify a stock before it can be appropriately managed, parasites also need to be correctly identified before they can be used as biological tags (Catalano et al. 2013). The main factor limiting the use of marine parasites as biological tags is insufficient information on their complex biology and ecology (MacKenzie et al. 2008). Numerous investigations concerning the parasite fauna of several sparid fishes from the Western Mediterranean have been published (Brian 1906; Yamaguti 1963; Bartoli et al. 1989; Ternengo et al. 2009; Kaouachi et al. 2010; Marzoug et al. 2012). However, there have been no specific studies on the parasite communities present in the common dentex, but

much reported data are nevertheless available (Table 2). These results indicate that the parasite fauna is diverse, most of these species have a wide host spectrum. However some parasite as *Cainocreadium dentecis* (Jousson and Bartoli 2001) are specific to the common dentex and have it for only host-associated. There are some studies on abundance, intensity, prevalence, and their descriptions for digeneans (Bartoli and Bray 1987; Bartoli et al. 1989; Bartoli et al. 2005; Foata et al. 2012; Greani et al. 2012). For ectoparasites, there are references to the gill parasites, especially copepods (Brian 1906; Raibaut et al. 1998; Bailly 2012), but data on monogeneans are scant (Radujkovic and Raibaut 1989; Euzet et al. 1993; González et al. 2004).

Table 2 Bibliographical review of the known parasites of *Dentex dentex*; geographical location, position of the parasites and references.

Parasite species	Class	Geographical location	Position	itations
<i>Allopodocotyle jaffensis</i> (Fischthal, 1980)	Digenea	France, Scandola	Posterior-intestine	(Bartoli et al. 2005)
<i>Aphallus rubalo</i> (Bray, 1986)	Digenea	France, Scandola	Duodenum, rectum	(Bartoli et al. 2005)
<i>Aphallus tubarium</i> (Rudolphi, 1819)	Digenea	France, Scandola	Posterior-intestine, rectum	(Bartoli and Bray 1987; Bartoli et al. 2005)
<i>Cainocreadium dentecis</i> Jousson & Bartoli, 2001	Digenea	France, Scandola	Pyloric caeca, Duodenum, mid-intestine	(Jousson and Bartoli 2001; Bartoli et al. 2005)
<i>Hemiurus communis</i> Odhner, 1905	Digenea	France, Scandola	Stomach	(Bartoli et al. 2005)
<i>Metadena depressa</i> (Stossich, 1883)	Digenea	France, Scandola	Pyloric caeca, Duodenum, mid-intestine, Posterior-intestine	(Bartoli and Bray 1987; Bartoli et al. 2005)
<i>Pachycreadium carnosum</i> (Rudolphi, 1819)	Digenea	France, Scandola	Duodenum, mid-intestine, Posterior-intestine	(Bartoli et al. 2005)

<i>Stephanostomum</i> sp. (Metacercariae)	Digenea	Spain, Balearic Islands	Gills	(González et al. 2004)
<i>Lecithochirium musculus</i> (Looss, 1907)	Digenea	Adriatic Sea		(Carreras-Aubets et al. 2012)
<i>Timoniella imbutiforme</i> (Molin, 1859)	Digenea	Italy, Triest	Intestin	(Stossich 1905)
<i>Microcotyle erythrini</i> Van Beneden & Hesse, 1863	Polyopisthocotylea	Spain, Balearic Islands	Gills	(González et al. 2004)
<i>Cathucotyle acanthura</i> (Parona & Perugia, 1896)	Polyopisthocotylea	Mediterranean sea		(Euzet et al. 1993)
<i>Udonella caligorum</i> Johnston, 1835	Monopisthocotylea	Spain, Balearic Islands	Gills	(González et al. 2004)
<i>Encotyllabe vallei</i> Monticelli, 1907	Monopisthocotylea	Montenegro		(Radujkovic and Euzet 1989; Euzet et al. 1993)
<i>Dinemoura producta</i> (Mueller, 1785)	Copepoda	Spain, Balearic Islands	Gills	(González et al. 2004)
<i>Caligus dakari</i> Beneden, 1892	Copepoda	Montenegro Kotor	Gills	(Radujkovic and Raibaut 1989)
<i>Caligus diaphanus</i> Von Nordmann, 1832	Copepoda	Spain, Balearic Islands	Gills	(González et al. 2004)
<i>Clavella denticis</i> (Krøyer, 1863)	Copepoda	Montenegro		(Yamaguti 1963)
<i>Clavellotis fallax</i> (Heller, 1865)	Copepoda	Spain, Balearic Islands Montenegro, Kotor	Gills	(Radujkovic and Raibaut 1989; Raibaut et al. 1998; González et al. 2004)
<i>Colobomatus denticis</i> (Richiardi, 1877)	Copepoda	Mediterranean sea		(Raibaut et al. 1998; Bailly 2012)
<i>Caligus vexator</i> Heller, 1865	Copepoda	Italy, Genoa Montenegro, Kotor	Gills	(Brian 1906; Radujkovic and Raibaut 1989; Raibaut et al. 1998; Bailly 2012)
<i>Parabrachiella exigua</i> (Brian, 1906)	Copepoda	Mediterranean sea		(Bailly 2012)
<i>Ceratothoa parallela</i> (Otto, 1828)	Eumalacostraca Isopoda	Mediterranean sea		(Trilles 1994)

<i>Gnathia vorax</i> (Lucas, 1849, praniza larvae)	Eumalacostraca Isopoda	Spain, Balearic Islands	Gills	(González et al. 2004)
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II.8 Stock structure and assessment

An important first step toward assessing the sustainability of an exploited population is to define the geographic boundaries, or stock units, for the species (Quinn II and Deriso 1999). Unfortunately, little is known of the global stock structure and movement of *D. dentex*. There is only one study on the population genetics of *D. dentex* at the global level. This study describes the phylogeography of three sparids including *D. dentex* based on three geographic areas: the Northeast Atlantic, and the Western and Eastern Mediterranean Sea (Bargelloni et al. 2003). For *D. dentex*, mitochondrial DNA and allozymes revealed a higher degree of genetic differentiation between the Atlantic and Mediterranean individuals. A significant degree of morphological dissimilarity between the individuals in this study and a geographical gradient were found (Palma and Andrade 2004). These results are evidence for a sharp phylogeographic break between the Atlantic and the Mediterranean populations of common dentex (Bargelloni et al. 2003; Palma and Andrade 2004).

Reported differences in fish size and growth may be due to fishing pressure, changes in oceanographic conditions, food availability, and season (Shelton and Mangel 2011). There seems to be an effective boundary between the Atlantic and Mediterranean populations of dentex, both morphologically and genetically (Bargelloni et al. 2003; Palma and Andrade 2004). It can be hypothesized that the history of the Mediterranean Sea, combined with the present hydrographic patterns, may have promoted and maintained the differentiation of the Mediterranean sub-population (Bargelloni et al. 2003; Palma and Andrade 2004). However, there is a severe lack of information on population structure, requiring further studies at a higher spatial resolution and using more accurate molecular markers (e.g. microsatellites).

To date, the only studies on the stock assessment of common dentex were conducted in Tunisia; three stocks were separately addressed according to different regions: Northern, Eastern and South (Chemmam-Abdelkader 2004; FAO 2008). In the North, the yield per recruit value was below the optimal level suggesting the stock was under-exploited. The exploitation profile in the Eastern region was optimal, and by contrast, the stock of the southern region was strongly overexploited, with a current yield above the optimum performance (Chemmam-Abdelkader 2004). The results obtained in the South Tunisian sector show that fishing is carried out on small size classes composed mainly of juveniles (Chemmam-Abdelkader et al. 2007). The current average age of the stock is estimated at 1.9 years, very low given the longevity of the species, which can be more than 30 years. For losses, the fishing mortality ($F: 1.2 \text{ year}^{-1}$) of 63 % outweighed the natural mortality ($M:$

0.18 year⁻¹) of 37 %, most probably due to overfishing (Chemmam-Abdelkader et al. 2007). The Southern stock was characterized by a young average age and a critical size close to that of sexual maturity, reflecting an overfished stock. To remedy this, current fishing effort should be reduced to 44 % compared with the optimal effort (Chemmam-Abdelkader et al. 2007). As a precautionary measure it has already been recommended not to increase fishing effort in either area (FAO 2008). At a global level, efforts need to be made to improve stock assessment of the common dentex, and better understand the stock structure including its movement and how the individuals comprising the various *D. dentex* aggregations in different localities are related.

II.9 Fisheries

The main fishing gears specifically targeting the common dentex are: bottom long-lines, trammel nets and medium-large mesh gillnets (Morales-Nin and Moranta 1997; Lelli et al. 2006; Vandeperre et al. 2006; Sacchi and Dimech 2011). However, they can also be caught as bycatch, especially at the juvenile stage, by traps nets, fyke net, basket traps, bottom-trawl, purse and beach seines, as well as “Tramata” fishing used only in the eastern Adriatic, or “Ganguì” fishing used along Mediterranean north coastline (Cetinic et al. 2002; Akyol 2003; Quero et al. 2009; Vandeperre et al. 2006; Sacchi and Dimech 2011). Trammel nets are gangs of three rectangular nets made up of two outer, large-mesh panels and one inner panel (Goñi et al. 2003). For the common dentex fishery, the smaller mesh panel reaches a size of 40 mm stretched, and the large-mesh up to 150 mm stretched. It is composed of a bottom rope with sinkers, and a head rope equipped with floats (Leleu 2012) to deploy the net vertically (up to 5.8 m) with a length of 500 m (3–4 units per vessel). In addition to wedging, gilling and entangling (i.e., held by teeth, spines or other protrusions), trammel nets also catch fish in the pocket formed by the inner smaller mesh wall of netting being pushed through one of the larger mesh outer walls (Erzini et al. 2006). A trammel net is usually installed in the evening and retrieved at dawn (between 12 and 24 h). Medium mesh size gillnets are built with a single wall of monofilament net with a stretched mesh size of 48–120 mm, and target medium size fish such as sparids on shallow sandy and mixed sandy rocky bottoms (Lelli et al. 2006). The length of these nets ranges from a few hundred meters to more than 1,000 m (Sacchi and Dimech 2011). Bottom longlines consist of a monofilament mainline to monofilament snoods with hooks about 1 m long, attached at regular intervals (Lelli et al. 2006). The most common gear used is 1.2 mm diameter mainline with 0.6 mm snood and hooks of length 3 cm and width 1.5 cm (Sacchi and Dimech 2011). The bait used is mainly cephalopods and sardines (Sacchi and Dimech 2011). On the same fishing day typical artisanal Mediterranean vessels (generally less than 12 m in length) can deploy more

than one longline unit (2–3 per vessel) of 200–300 hooks each, for a length of about 1 km (Lelli et al. 2006). In sum, the common dentex is targeted by artisanal fisheries throughout the year using different gear. We note that there is an alteration and/or combined use of this gear (top three: longline, trammel and gill net), depending on the season, habitat and geographic areas (Table 3). However, for common dentex fishing, peaks of exploitation are observed, with maximum efficiency between May and September by trammel net/gill nets and between September and April by bottom long-line. The fishing depth is mostly in the range 15–80 m, with a mean value around depth 30 m. The composition by size class also shows broad variations in terms of catches (14–83 cm). Juvenile stages (mean value 30 cm) are captured especially on the *Posidonia oceanica* meadows (by trammel net and gill net) or as by-catch (e.g. *Tramata*, *gangui*), whereas adult specimens are caught mainly on the rocky bottoms (by long-line).

Table 3 Summary of the exploitation of *Dentex dentex* (abundance), according to the season, sizes class composition, fishing gears, main depth range of operations and habitat. ¹ Contribution to total biomass of the catch %, total biomass kg, tons, CPUE, ² Occurrence frequencies %, CPUE.

Geographic Area	Sampling strategy	Sampling techniques	Sampling year	Abundance Index Biomass ¹	Abundance Index Number ²	Size class composition (cm)	Stage of life and capture	Main depth range of operations (m)	Main month activity	Habitat	Citations
Croatia (Eastern Adriatic)	Landing	Tramata	1986-99	2.4%	0.22%	Length range 14.0-40.8; Mean length 28.350 ± 0.387; Modal length 29	Juveniles (By-catch)	0-50	July-September	-	(Cetinic et al. 2002)
Croatia (Vis)	Experimental fishing	Trammel net	1995-2009	-	1.7%	-	-	0-40	-	-	(Matić-Skoko et al. 2011)
France (Bonifacio, MPA)	Onboard fishing vessel/Landing	Long line	1992-93; 2000-06	6.7 kg/100 hooks	-	-	Target species	-	-	-	(Garrido 2007)
France (Bonifacio, MPA)	Onboard fishing vessel/Landing	Trammel net	1992-93; 2000-06	70 g/50 m of net/24h	-	-	Target species	-	-	-	(Garrido 2007)
France (Bonifacio, MPA)	Onboard fishing vessel	Trammel net	2004-2006	4.8%	-	-	Target species	-	-	-	(Rocklin 2010)
France (Bonifacio, MPA)	Onboard fishing vessel	Trammel net	2001; 2007	4.04 % (2001); 4.03% (2007)	-	-	Target species	-	-	-	(Rocklin 2010)
France (Calvi-Galeria)	Landing	Trammel net, long line	1986	-	-	Length range 14-74; Median 30	Juveniles (By-catch)	-	-	-	(Culioli 1986)
France (Corsica outside Scandola MPA)	Underwater visual census	SCUBA diver	1988	4.9 g/10 m ²	0.08 ind/100 m ²	-	-	10-30	July	Rocky areas	(Francour 1991)
France (Corsica Scandola MPA)	Underwater visual census	SCUBA diver	1990-2000	-	0.14 ind/100 m ²	-	-	10-30	June-August	Rocky areas	(Francour 2004)
France (Corsica Scandola MPA)	Underwater visual census	SCUBA diver	1988	19.1 g/10 m ²	0.2 ind/10 m ²	-	-	10-30	July	Rocky areas	(Francour 1991)
France (Corsica)	Onboard sampling	Trammel net, gill net	2009-10	0-150 g/50 m of net; 2009 (28.3 tons) ; 2010 (26.5 tons)	-	-	Target species	-	-	-	(Francois 2011)

France (Côte Bleue, MPA)	Landing	Trammel net	2009-10	-	-	-	Target species	37.6 (mean value)	-	-	(Leleu 2012)
France (Cros de Cagnes)	Landing	Trammel net, long line	2002-2005	0.19%	-	-	-	-	-	-	(Leroy 2009)
France (Lavezzi Islands)	Onboard fishing vessel	Trammel net, long line	1992-93	1316 kg (5.64 %)	0.74 % (n=445)	Length range 0-40 (41%); 40-60 (37%); 60-80 (22%)	Target species	-	-	-	(Culioli 1995)
France (National Park of Port-Cros)	Underwater visual census	SCUBA diver	1989-1990	92.4 g/10 m ²	0.47 ind/100 m ²	-	-	10-30	June-September	Rocky areas	(Francour 1992)
France (National Park of Port-Cros)	Underwater visual census	SCUBA diver	2005-2006	-	0.1 ind/250 m ²	-	-	20-40	April-July	Rocky areas	(Francour 2007)
France (National Park of Port-Cros)	Landing	Small-scale fisheries (all gears combined)	2005	1.30 %	-	-	-	-	-	-	(Cadiou and Bonhomme 2006)
France (Var)	Experimental fishing	Gangui	2010	-	-	-	Juveniles (By-catch)	15-35	January-December	<i>Posidonia oceanica</i> meadow	(Sacchi et al. 2010)
France (Var)	Onboard fishing vessel	Angling	2010-2012	14%	-	-	-	-	-	-	(Bodilis et al. 2012)
France (Var, Cap Roux Fisheries Reserve)	Experimental fishing	Trammel net	2011-2012	-	0.3 ind/100 m of net (0.77%)	-	-	0-40	-	Rocky areas and Posidonia	(Arceo 2012)
France, Corsica (NW coast)	Landing	Trammel net, long line	1988-1989	3.6%	-	-	-	-	-	-	(Riutort 1989)
Greece	Declarative survey	Small-scale fisheries (all gears combined)	1993-99	Winter (1.63%) ; Spring (2.64%) ; Summer (2.13) % ; Autumn (2.37 %) ; (mean value all the year 2.27%)	-	-	-	-	January-December	-	(Tzanatos et al. 2005)
Greece (Korinthiakos)	Onboard fishing vessel/ Experimental fishing	Trammel net, gill net	2008-09	-	-	Length range 17.1-48.0; Median 28.1	-	-	June-September	-	(Moutopoulos et al. 2013)
Greece (Patraikos)	Onboard fishing vessel	Trammel net	2004-05	-	-	-	Target species	0-25	September-July	-	(Tzanatos et al. 2008)

Greece (Patraikos)	Onboard fishing vessel	Long line	2004-05	-	-	-	Target species	20-36	March-November	-	(Tzanatos et al. 2008)
Italy (North-Western Ionian Sea)	Experimental fishing	Experimental bottom trawl	1985-2008	-	0.3%	-	-	15-258	-	-	(Maiorano et al. 2010)
Italy (Otranto)	Underwater visual census	SCUBA diver	1997	-	0.1 ±0.1 ind/40 m ²	-	-	6.5–8.0	-	Seagrass and Rocky-algal	(Guidetti 2000)
Lebanon (Tyre)	Landing	Mono/Multifilament gill nets (with large mesh size)	2005-06	-	-	-	By-catch	-	October-July	-	(Lelli et al. 2006)
Lebanon (Tyre)	Landing	Bottom longline	2005-06	-	-	-	Target species	-	January-December	-	(Lelli et al. 2006)
Portugal (Setúbal and Sesimbra)	Onboard fishing vessel	Trammel net	2004-05	20.2 g/10.000 m of net	-	-	By-catch	-	-	-	(Batista et al. 2009)
Spain (Cabo de Gata, A guilas, Cabo de Palos, Isla Grosa, Cabrera, Mallorca and Columbretes, MPA)	Underwater visual census	SCUBA diver	1996	6.9 ±3.8 g/250 m ²	3.6 ±1.2 ind/250 m ² (18%)	-	-	10	-	Rocky bottom	(García-Charton et al. 2004)
Spain (Cabo de Palos, MPA)	Onboard fishing vessel /Declarative survey	Trammel net	2005-08	6.6%	-	-	Target species	30 (mean value)	April-October	-	(Esparza Alaminos 2010)
Spain (Cabo de Palos, MPA)	Onboard fishing vessel /Declarative survey	Long line	2005-08	8.7%	-	-	Target species	-	February-April; October-November	-	(Esparza Alaminos 2010)
Spain (Cabo de Palos, MPA)	Onboard fishing vessel /Declarative survey	Gill net	2005-08	13.3%	-	-	Target species	-	February-June	-	(Esparza Alaminos 2010)
Spain (Cala Ratjada, MPA)	Experimental fishing	Bottom long line	2008-09	460.5 kg (40.3%)	(n=150)	Length range 30-75; Mean length 54	-	31 (median)	-	<i>Posidonia oceanica</i> meadows, Rocky bottom with <i>P. oceanica</i> patches, Coastal detritic, Detrit Ripples of coarse sand and sediments	(Stobart et al. 2012)
Spain (Cap Creus, MPA)	Onboard fishing vessel	Trammel net, gill net, long line, basket traps	2008-10	-	-	Mean length 37.5 cm	-	-	-	-	(Lloret et al. 2012)

Spain (Cap Creus, MPA)	Landing	Long line, gill net	1991-2003	1 % (1991-98); 1.6% (1999-2003)	-	-	Target species	-	April-November	-	(Gomez et al. 2006)
Spain (Columbretes Islands, MPA)	Experimental fishing	Trammel net	1998-2006	-	0.461 ind/600 m of net	-	-	20-80	-	-	(Stobart et al. 2009)
Spain (Columbretes Islands,	Onboard fishing vessel	Trammel net	1998-2006	-	0.103 ind/600 m of net	-	-	50-100	-	-	(Stobart et al. 2009)
Spain (Denia)	Declarative survey	Small-scale fisheries (all gears combined)	1995-2009	2760 kg (2003); 5000 kg (2009)	-	-	-	-	March-May; October-December	-	(Orozco et al. 2011)
Spain (L'Estartit)	Underwater visual census	SCUBA diver	1997-99	696.0 g/1000 m ² (SD=1391,9)	-	-	-	0-30	-	Gently sloping rock	(Macpherson et al. 2002)
Spain (Mallorca)	Landing	Trammel net	1993-95	-	-	Length range 17.5-30	Juveniles	-	September-March	<i>Posidonia oceanica</i> meadow	(Morales-Nin and Moranta 1997)
Spain (Mallorca)	Landing	Long line	1993-95	-	-	Length range 17-83	Adult	-	April-June	-	(Morales-Nin and Moranta 1997)
Spain (Santa Pola)	Declarative survey	Trawl	1995-2009	2500 kg (2003); 5500 kg in (2009)	-	-	-	-	March-May; October-December	-	(Orozco et al. 2011)
Spain (Santa Pola)	Declarative survey	Small-scale fisheries (all gears combined)	1995-2009	7000 kg (2003); 19800 kg (2009)	-	-	-	-	March-May; October-December	-	(Orozco et al. 2011)
Spain (Tabarca, MPA)	Underwater visual census	SCUBA diver	2005-06	110.84 ±44.67 (g/125 m ²); (5.95 %)	-	-	-	-	-	<i>Posidonia oceanica</i> meadow	(Forcada et al. 2008)
Spain (Tabarca, MPA)	Underwater visual census	SCUBA diver	2005-06	486.25 ± 2002.24 (g/125 m ²); (11.90 %)	-	-	-	-	-	Rocky bottom	(Forcada et al. 2008)
Spain (Tabarca, MPA)	Landing	Small trap net (Morunas)	1988-1989	less than 1%	-	-	-	-	-	-	(Ramos-Esplà & Bayle-Sempere 1990)
Spain (The Medes Islands, MPA)	Underwater visual census	SCUBA diver	1997-99	622 g/1000 m ² (SD=28.7)	-	-	-	0-30	-	Gently sloping rock	(Macpherson et al. 2002)

Spain (The Medes Islands, MPA)	Underwater visual census	SCUBA diver	1997-99	38456.7 g/1000 m ² (SD=3847.6)	-	-	-	0-30	-	Large broken rocks	(Macpherson et al. 2002)
Spain (The Medes Islands, MPA)	Underwater visual census	SCUBA diver	1997-99	3191.3 g/1000 m ² (SD=24.6)	-	-	-	0-30	-	<i>Posidonia oceanica</i> meadow	(Macpherson et al. 2002)
Spain (Tossa)	Underwater visual census	SCUBA diver	1997-99	2186.5 g/1000 m ² (SD=372.9)	-	-	-	0-30	-	Gently sloping rock	(Macpherson et al. 2002)
Spain (Vilanova i la Geltrú, MPA)	Cabled video observatory	Digital image acquisitions	2009-10	-	1.6% (individuals detected in digital images taken at hourly intervals during daytime over the course of 12 months; n = 366)	-	-	20	May-November	Close to an artificial reef	(Condal et al. 2012)
Tunisia	Landing/ Declarative survey	Trammel net, gill net, long line	1995-2002	301.484 tons	-	Mean length 31.32 (1997-98)	Trammel net and gillnets (Juveniles); Long line (Adult)	-	May-July; November-January	-	(Chemmam 2004)
Tunisia	Landing/ Declarative survey	Trawl	1995-2002	27.643 tons	-	Mean length 31.32 (1997-98)	-	-	May-July; November-January	-	(Chemmam 2004)
Tunisia	Landing/ Declarative survey	Basket traps, traps net, fyke net	1995-2002	3.259 tons	-	Mean length 31.32 (1997-98)	Juveniles (By-catch)	-	May-July; November-January	-	(Chemmam 2004)
Tunisia (Southern region)	Landing	Trammel net, long line, trawl	2004	-	-	Length range 13-73 (18-25 represents 69%)	Juveniles	-	-	-	(Chemmam-Abdelkader et al. 2007)
Turkey (Antalya)	Landing	Bottom trawl net	2009	16.5 kg/nm ² (SE=5.92)	248.8 ind/nm ²	-	-	25-200	August	-	(Kebapçıoğlu et al. 2010)
Turkey (South of Izmir)	Landing	Beach seine	1996	1.75%	0.49%	-	-	4-30	May-September	-	(Akyol 2003)

Fish from the *Sparidae* family are widely distributed along the coastal waters of the Mediterranean Sea, being considered traditionally as an important resource for small-scale fishing (Coppola 2001) and are of considerable economic importance (Chemmam-Abdelkader et al. 2006). FAO data on global capture production for the last 60 years for *D. dentex* (Fig. 2) show interannual fluctuations. Time-series analyses show four peaks of production, the first between the years 1950 and 1953 with a maximum production of 5,400 tonnes (T)/year, the second during the years 1962–1964 with a production that reached 8,700 T/year, the third between 1976 and 1980 with a production of 4,143 T/year and finally between 1990 and 1994 with a production of 10,329 T/year.

At the national level only two countries contribute significantly to catches of common dentex. The main one is Spain, which alone accounted for almost all the overall common dentex production until 1980, when its production declined until 2010. Considering in detail the catch data for Spain during the years 1950 to 1980, it appears that most fish were caught in Eastern, Central and Northeast Atlantic regions. However, these areas are not usually the main areas for common dentex; hence caution is needed in data interpretation. From the years 1965–1970 Italian production increased, with peaks and troughs, reaching its highest level in 1992. Production then declined abruptly until 2000, stabilizing at lower levels until 2010. It is possible that the rapid increase in the exploitation rate observed during the years 1956–1963 in Spain, and 1981–1992 in Italy may have led to sudden depletion, a scenario already reported for other demersal species (Hidalgo et al. 2009; Quetglas et al. 2012). These two countries have successively dominated production from 1950 to 2000, although at the national level there is broad heterogeneity of the catches over time. It seems that researchers and artisanal fishers share the same opinion on the existence of cyclic fluctuations of *D. dentex* populations (Bayle-Sempere et al. 1991), although without estimates of fishing effort such suggestions need to be treated with caution. Indeed, one of the key reasons for cyclic changes in production may be the fact that fishing effort fluctuates over a range of time scales (technological changes or advances, management zonation, changes in markets etc.). Secondly, three main ecological hypotheses can be proposed to explain possible fish population fluctuations: (1) changes in species interactions, such as predator–prey interactions (2) strongly nonlinear single-species dynamics and/or (3) environmental variations (Shelton and Mangel 2011).

The marked cyclical fluctuations in the abundance of some species seem to be linked not only to exploitation, but also to the influence of climate on these populations (Walther et al. 2002). In the common dentex, interannual changes in production, indicating possible changes in abundance, seem to be more pronounced in the northern Mediterranean sector (Catalonia, France, Ligurian Sea, Northern Adriatic) and may be the result of longer-term environmental changes in the coastal waters (Ramos-Esplà and Bayle-Sempere 1991;

Francour et al. 1994). Environmental influences are suggested to be the basis of the inter-annual fluctuations observed in landings of the region's most important demersal resources (Massuti et al. 2008). Climate may affect marine fish populations through many different pathways, operating at a variety of temporal and spatial scales (Ottersen et al. 2010). If there is a strong message from ecology for the 21st century, it is that we should not expect a single mechanism to be solely responsible for generating fluctuating populations but recognize the potential contribution of each and work toward understanding how these factors interact to affect the variability of natural populations (see references in Shelton and Mangel 2011). Consequently, the interaction between fishing exploitation and environmental variables can have a synchronic effect on the population dynamics of exploited populations (Quetglas et al. 2012). However many other factors, such as biological interactions, variations in recruitment, habitat degradation and nonclimatic environmental factors can also have impacts on fish stocks (Bayle-Sempere et al. 1991; Brander 2010).

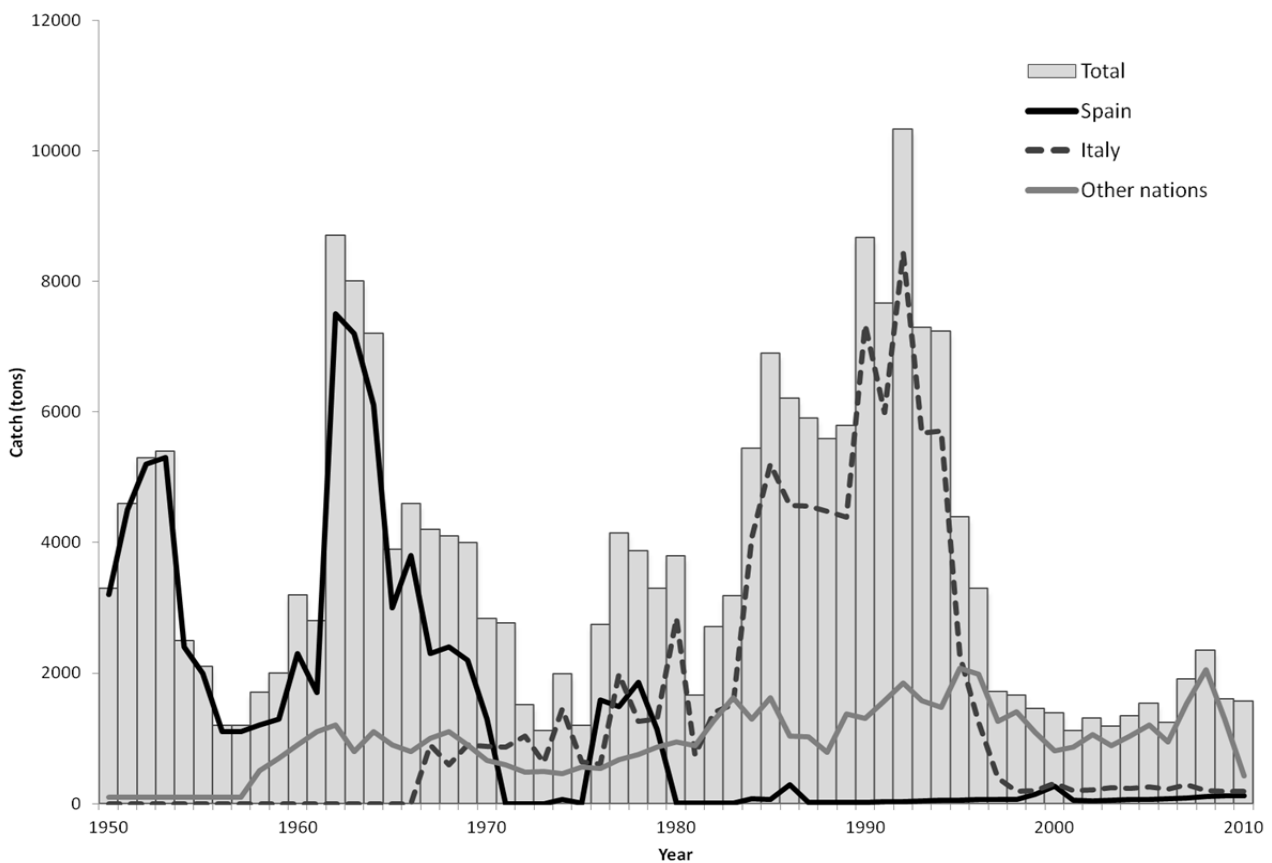


Fig. 2 Annual catch of common dentex for all nations combined (grey bars), for Spain and Italy, the two highest contributor nations (lines) and the remaining nations (lines; Albania, Bosnia-Herzegovina, Croatia, Cyprus, Egypt, France, Greece, Latvia, Libya, Malta, Montenegro, Portugal, Romania, Serbia, Tunisia, Turkey) for the years 1950–2010 (based on FAO 2012)

II.10 Recreational fishing

Recreational fishing has economic, social, and cultural roles in the Mediterranean (Morales-Nin et al. 2005), being recognized as one of the most common leisure activities in coastal zones (Albouy et al. 2010). The common dentex, due to its large size, flesh quality, and high commercial value, is considered an iconic species, and is therefore also targeted by recreational fishing. There are few data regarding fishing effort or total catch from most recreational fisheries of any species (Lloret and Font 2013), and recreational fishing for common dentex suffers from similar deficiencies. The most common methods used in recreational fishing for *D. dentex* are boat fishing, spear fishing, line and shore fishing (Morales-Nin et al. 2005; Lloret et al. 2008a; Gordo 2009; Abdul Malak et al. 2011; Font and Lloret 2011). The angling techniques generally used to catch *D. dentex* are varied; bait can be alive or dead, or artificial lures can be used. Along the coast of the marine reserve of Cap de Creus, live fish such as *Serranus cabrilla* (Linnaeus, 1758) or *Coris julis* (Linnaeus, 1758) are used to catch valuable fish such as *D. dentex*, and represent 9.9 % of the total bait used by shore anglers in 2007 and 2009. For the common dentex, cephalopods (body portions or whole dead animals) such as squid, cuttlefish, octopus and bobtail squid, constitute 15.5 % of the total baits used, and sardines (*Sardina pilchardus*) 13.7 % (Font and Lloret 2011). There is a relatively high mean vulnerability and trophic level of rocky benthic fish species caught by shore fishing and spear fishing; this is mainly due to relatively large catches in terms of weight of top predators such as *D. dentex* (Lloret et al. 2008b; Font and Lloret 2011). Commercial and recreational fishing have similar demographic and ecological effects on fished populations, and they can have equally serious ecological and economic consequences (Cooke and Cowx 2004; Font and Lloret 2011). In some geographic areas spear fishers are perceived as the main competitors for artisanal fishers, who become strong market competitors by selling their catches (illegally) to local restaurants at a high price without a commercialization license, therefore affecting demand (Maynou et al. 2013). There is clear evidence that recreational activities not only impact marine resources quantitatively, but in addition modify their population structure (Rocklin et al. 2011). In particular, the removal of large individuals can adversely affect the reproductive potential of these vulnerable fish populations (Lloret et al. 2012; Prato et al. 2013).

II.11 Regulations and minimum fish sizes

The common dentex seems to be a heavily exploited species, and it is considered as “vulnerable” in the Mediterranean Sea (Abdul Malak et al. 2011). Considering the potential effects of commercial fishing and recreational fishing on coastal ecosystems, it seems important to create new regulation policies (Albouy et al. 2010; Lloret and Font 2013) for both these activities. Measures could consider limiting catches through permanent or seasonal closures during the spawning season, the establishment of a minimum legal length (based on the species size at maturity) and/or the enlargement of existing no-take locations in critical areas (Lloret et al. 2008b; Abdul Malak et al. 2011). For recreational fishing (including spear fishing), as stated previously, there is a general lack of knowledge on this activity, and it seems urgent, in the light of its potential impact, to implement effective measures for regulation and control. For commercial fishing, in some Mediterranean countries, there is a regulation imposing a minimum landing size of common dentex (Table 4). Unfortunately, depending on the country, even when there is a minimum landing size, this remains well below the size at which 50 % of the population is mature, namely 34.60 cm for females and 52.02 cm for males (Morales-Nin and Moranta 1997).

Table 4 Minimum landing sizes of *Dentex dentex* for commercial fishing in some Mediterranean countries

Country	Minimum fish sizes (cm)	References	Citations
Morocco	12	Decree No. 1154-1188 of 3 October 1988 (as amended and supplemented by decree No. 352-89 dated 2 February 1989, by decree No. 652-92 of 1 October 1993 and decree No. 373-01 dated 21 February 2001),	(Cacaud 2002)
Algeria	15	Decree No. 04-86 of 26 Moharram 1425 corresponding to 18 March 2004 fixing the minimum market sizes of biological resources.	Official Journal of the Republic of Algeria (24/03/2004)
Mauritania	15	Decree No. 2002-073 of 1 October 2002 laying down general rules for the application of Law No. 2002-025 of 24 January 2000	Official Journal of the Islamic Republic of Mauritania (30/10/2002)
Turkey	20	Act fisheries No. 1380 of March 22, 1971 as amended, supplemented with fisheries regulations No. 22223 of March 10, 1995 and section 15 of circular No. 33/1	(Cacaud 2003)
Tunisia	22	Decree of 28 September 1995 regulating the practice of fishing is the main text of application of Law No. 94-13 of January 31, 1994	(Cacaud 2002)
Albania	25	Law No. 7908 of 5 April 1995 on fisheries and aquaculture Regulations No. 1 of March 26, 1997	(Cacaud 2003)
Croatia	30	Based on the Article 48 paragraph 3 bullets 1, 2 and 3 of the Marine Fisheries Act (Official Gazette No. 46/97).	(Martín and Kekez 2009)

II.12 Conclusion and directions for future research

Here we have shown that although the common dentex species is of great interest, both economically and ecologically, some very important questions still remain unanswered about the life and populations of this iconic fish. As a top predator, it is a key species in the functioning of coastal food webs, and for this reason there is a need to improve the state of knowledge on the biology and ecology. In order to implement proper fishery management strategies aimed at avoiding stock decline, information about connectivity among stocks and populations is critical. There is still great progress to be made in understanding the larval and juvenile stages and the reproductive behavior of the common dentex. There should also be a clear vision of the population state (demographic parameters) and the spatial and temporal structure of the stocks, to implement sustainable management of fisheries in the Mediterranean Sea. Genetic techniques using specific microsatellite loci may provide a more comprehensive analysis of the genetic population structure of the common dentex (Bargelloni et al. 2003). Other approaches that could be relevant in determining the stock structure include parasite taxonomy and abundance (e.g Williams et al. 1992; MacKenzie and Abaunza 1998; Williams and Lester 2006), stable isotope analysis (e.g Rooker et al. 2007) and otolith shape and/or microchemistry (e.g Turan 2006; Hamer et al. 2012). Examination of the movement of individuals, for example using electronic tagging, would also be important especially for examining aggregations at the time of reproduction (e.g Pastor et al. 2009). Ideally, simultaneous multiple approaches such as analysis of fisheries data, population genetics, and otolith chemistry would be used (see Papetti et al. 2013).

In terms of exploitation via recreational fishing, it is necessary to have near-term accurate biological, social and economic data to evaluate this activity (Pitcher et al. 2002; Arlinghaus et al. 2010). Recreational catches are often poorly quantified, but such catch data are essential for estimating total mortality in stock assessments, especially where the recreational catch is high compared with the commercial catch (Lloret and Font 2013), as is suspected in this case. Despite its importance, knowledge about fleets and their characteristics, fishing gear, seasonality, catches, and the yields of the professional artisanal sector is still limited (Battaglia et al. 2010). It is necessary to develop standardized data collection routines and indicators of fishing effort for the Mediterranean artisanal fishery that make data comparable on a spatial and temporal basis (Colloca et al. 2004). Data on the global catch of common dentex suggests a possible cyclic fluctuation of the populations, with the appearance of multiannual peaks of activity. Notwithstanding that suitable effort data is unavailable, there are indications that the abundance of the common dentex has fluctuated over the last 60 years on a multidecadal time scale, possibly declining significantly since the 1990s. Such declines may be linked to levels of artisanal and recreational fishing but more

information is urgently needed in this regard. Fishing gear such as trawl or seine may make a particular impact on vulnerable populations, especially in spawning areas (mature adults) or nursery areas such as in the *Posidonia oceanica* meadows (juveniles and young of the year). Additionally, the interaction between fishing exploitation and environmental variables can have synchronous effects on the population dynamics of exploited marine fishes (Quetglas et al. 2012). The improved management of human interactions with marine ecosystems can undoubtedly play an important role in adapting to the impacts of climate change (Brander 2010). Natural resource managers should consider the implementation of specific measures to safeguard the reproductive potential of coastal top predator species, such as *D. dentex* (Lloret et al. 2012). There is an urgent need to implement effective protection measures for this species, whether based on a maximum daily catch, minimum catch size, protection through marine protected areas, or other measures to allow a period of biological recovery. It would be also desirable to engage artisanal fishers in a partnership with scientists and fishery and MPA managers, since this could help foster their participation in the management of the fish populations they exploit. *D. dentex* has recently been classified as “vulnerable” in the Red List of Threatened Species in the Mediterranean Sea (Abdul Malak et al. 2011) and so effective management is now required.

Acknowledgments

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Chapitre III

Spatio-temporal catch variation and demographic structure of common dentex (*Dentex dentex*) exploited by Mediterranean artisanal fisheries

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III.1 Introduction

For centuries, artisanal fishing has been an essential economic activity and one of the pillars of Mediterranean culture and related cultural diversity (Guidetti 2012). Artisanal fishing is an activity performed along the entire Mediterranean coast, with a considerable number of vessels (42,000 vessels) and fishermen (about 280,000) (Griffiths et al. 2007; Morales-Nin et al. 2010). Artisanal and small-scale fisheries are characterized as commercial fishers operating in small boats (less than 12 m in length), exploiting areas near the coast (0–200 m deep), using a large number of gears and techniques, typically manned by a single fisherman or a pair of fishermen and targeting a high diversity of species (Colloca et al. 2004; Forcada et al. 2010; Lloret and Font 2013). One relevant feature of artisanal fishing is the great diversity of gears and fishing techniques adopted all over the Mediterranean, with a vast range of variations and/or distinctive features (Di Franco et al. 2014b).

Due to the complexity of this activity, very few studies have quantified effort and catch (Maynou et al. 2011b). The lack of quantitative data on the spatial and temporal scales strongly reduces the opportunity of developing the management measures required to make fishing methods sustainable in the long term (Colloca et al. 2004). Therefore understanding the spatiotemporal patterns of artisanal fishing and identifying the allocation of exploitation is essential. These data are critical to the effective planning and management of threatened marine species (Pressey et al. 2007; Cleguer et al. 2015). There is an urgent need to evaluate the potential impact that the different types of fishing activities, alone and in combination, can have on the sustainability of coastal resources (Albouy et al. 2010). The fishing gears used can have an effect on the biodiversity and abundance of marine resources and on ecosystem structure and functioning (Coll et al. 2014). Over the last 20 years, catches of several commercial stocks have declined in the western Mediterranean Sea (Morales-Nin et al. 2005). Among species, the global commercial catch of common dentex (*Dentex dentex*, Linnaeus, 1758) has fluctuated over the last 60 years and declined significantly since the 1990s (Marengo et al. 2014b). The landings for this species have declined steadily from a peak of 10,000 tons in 1992 to 1,300 tons in 2012 (FAO-FISHSTAT 2015).

Dentex dentex is a Mediterranean and Atlantic species. It inhabits the Mediterranean Sea most frequently south of 40°, is found occasionally in the Black Sea, and occurs in the Atlantic Ocean, British Isles, Cape Blanc, the Bay of Biscay, Madeira, the Canary Islands and Senegal (Morales-Nin and Moranta 1997; Marengo et al. 2014b). It is a demersal sparid fish (0–200 m) that grows to a maximum length of 100 cm and a weight of 13 kg, with a relatively long life span (more than 20 years) (Ramos-Esplà and Bayle-Sempere 1991; Morales-Nin and Moranta 1997). As a high trophic level predator, it holds a key position in coastal marine

food webs. Due to its large size, flesh quality, and high commercial value, the common dentex is considered as a trophy fish and is targeted by both artisanal and recreational fishing (Marengo et al. 2015). The main artisanal fishing gears used to catch the common dentex are: trammel nets, gillnets and bottom long-lines (Vandeperre et al. 2006). It is targeted throughout the year by modifying and/or combining these gears, depending on the season, habitat and geographic area (see Marengo et al 2014). The common dentex appears to be a heavily exploited species and is classified by the International Union for the Conservation of Nature (IUCN) as “vulnerable” on the Red List of Threatened Species (Abdul Malak et al. 2011). Despite its ecological and economic importance, fisheries data on this species are still very scarce and little is known of the space-time dynamics of common dentex at regional scales.

The aim of this study is to provide new information on the artisanal fishery of common dentex around the island of Corsica (NW Mediterranean) over a 5-year period. In detail, we (i) analyze the relationship between the catch per unit effort (CPUE, by weight and number) and possible factors that might have caused the trends observed, (ii) study the temporal and spatial trends in CPUE, (iii) identify the spatial distribution of fishing effort, and (iv) compare the size distribution and age structure of catches.

III.2 Materials and methods

III.2.1 Study area

This study was performed around the island of Corsica (France; NW Mediterranean). It is located southeast of the French mainland and north of Sardinia (Italy) (42° N and 9° E). Corsica is the fourth largest island of the Mediterranean Sea and is characterized by a mountainous landscape and a highly disparate underwater morphology, featuring a steep descent to low depths along the western part of the island (down to 3,000 m, 10 km offshore) (Pluquet 2006). In contrast, wide expanses of shallow waters are present along the east coast. It has a surface area of 8722 km² and a total coastline of 1047 km, representing more than half of the French Mediterranean coast. In 2015, 91% of the 195 active boats of the Corsican fleet were included in the artisanal fisheries group. This region is among the least intensively fished areas in the whole of the northern Mediterranean Sea and, to date, it has been studied very little by fish biologists (Relini et al. 1999).

III.2.2 Data collection

Sampling was carried out in fishing vessels covering the main fishing harbors and sectors of Corsica between 2009 and 2013 (April to September). The fishing catches were collected by scientific observers onboard fishing vessels, in collaboration with professional fishermen. The observers were on board and inspected catches as they were pulled on to the boat. 1425 km of nets were sampled over the five-year period, corresponding to 531 observation days (= fishing parties). Days and fishing gears were chosen at random. The survey provided information on fishing operations (fishing gear, length of nets, duration, depths, locations, total catch, and weight). All the common dentex caught were measured and their total weight was estimated.

Total length (TL) was measured and size class correspondences were used for weight estimates: Small: 0-40 cm = 0.3828 kg; Medium: 40-60 cm = 2.1053 kg; Large: 60-80 cm = 5.4653 kg; (Marengo et al. 2013), for 2009-10. Total length (TL) was measured to the five nearest centimeters for 2011 and to the nearest centimeters for 2012-13. For these years, weight estimates were derived using length-weight relationships published in FISHBASE [<http://www.fishbase.org/>], based on Morales-Nin and Moranta 1997. To standardize the data collected, total Catch Per Unit of Effort (CPUE) was expressed for nets (including retained fish and discards), in grams by piece of net (50 m) (CPUE of biomass: $\text{g}\cdot 50\text{m}^{-1}$), and per number of individuals caught by piece of net (50 m) (CPUE of individuals: $\text{ind}\cdot 50\text{m}^{-1}$). In this study, the "Spiny Lobster net" is defined by duration of fishing operation of at least two days at a depth exceeding or equal to 50 m. The "Fish net" covers any type of net that does not correspond to the first definition (Pere 2012). For spatial analysis, six strata (Ajaccio, Calvi, Cap Corse, Plaine, Porto, Bonifacio) were defined, divided into fishing grounds (Pere 2012)(Fig. 1).

III.2.3 Age determination

Scales were collected from 90 individuals during the survey for the years 2012-13. For each individual, four scales were selected from among the non-regenerated ones and cleaned with sodium peroxide to remove any remaining traces of organic matter (Panfili et al. 2003). They were placed between two glass slides for observation using a stereomicroscope (Zeiss Discovery.V20) connected to a camera (Sony XCD-U100CR) and a computer equipped with TNPC 7.0 software, an image analysis application dedicated to sclerochronology. The readings were carried out twice by the main reader and independently by a second reader on a sub-sample of 50%, with no reference to the previous readings and without any knowledge of the fish specifications. The second readings of the main reader

were kept after comparison with the second reader on the estimated subsample. These estimations agreed with those of the second reader and were therefore considered the most accurate.

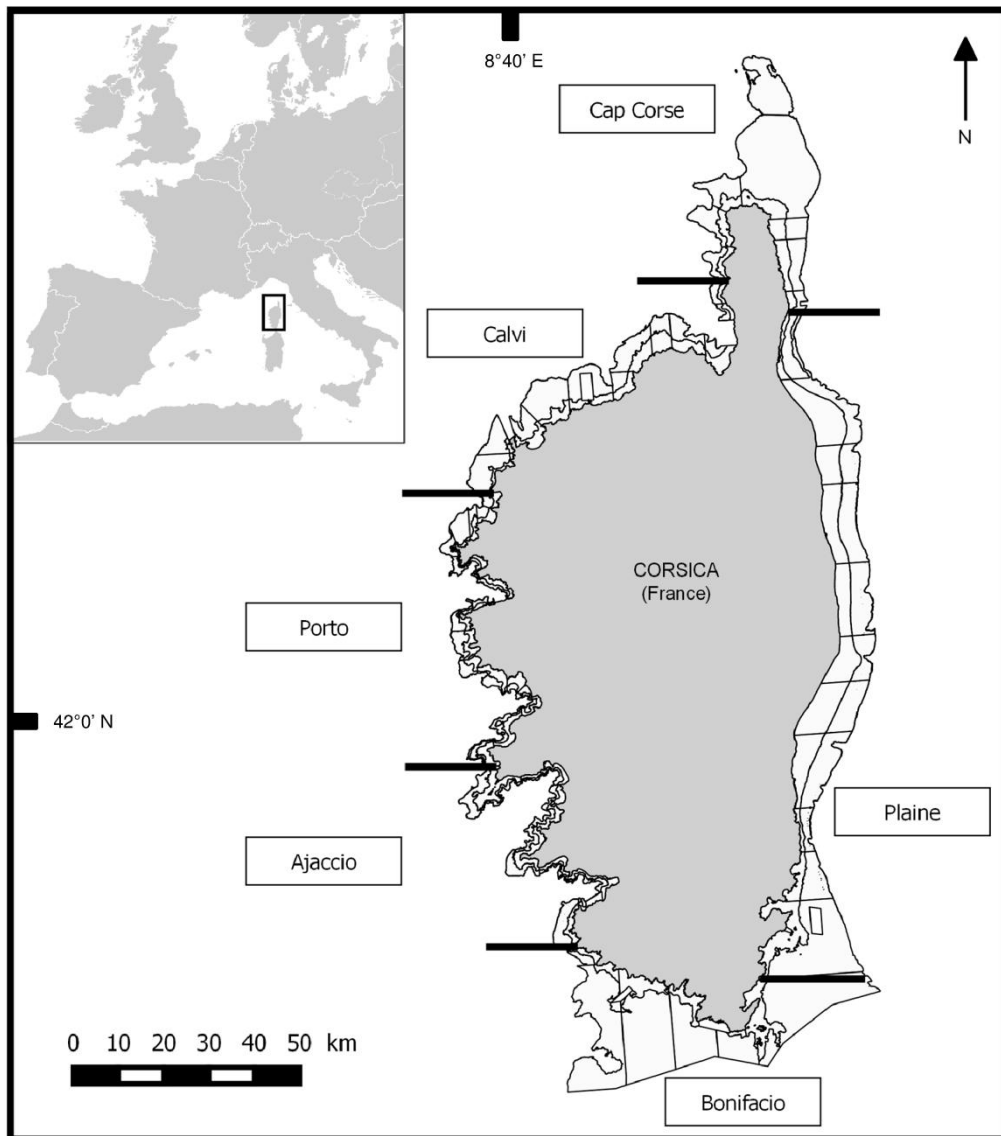


Fig.1 A map of Corsica (NW Mediterranean, France), showing the six strata (Ajaccio; Calvi; Cap Corse, Porto, Plaine; Bonifacio) and fishing grounds.

III.2.4 Data analysis

The CPUE values were log transformed using $\text{Log}(\text{CPUE} + 1)$, to better meet assumptions of normality for multivariate tests. A Student's t-test was conducted to determine any differences in catch rates (weight and number) between the two fishing gears identified (Fish net and Spiny Lobster net). Multivariate analysis of variances (MANOVAs) were used to test the effect of year (2009-13), month (April to September), depth (0 to more than 100 m

deep), and strata (Ajaccio, Calvi, Cap Corse, Plaine, Porto, Bonifacio) on mean CPUE values (weight and number) for the Fish net and Spiny Lobster net. The variables were not normally distributed ($P < 0.05$, Kolmogorov–Smirnov test); however, MANOVA is robust to skewed distributions and performs reasonably well with non-normal data (Paukert and Wittig 2002; Ridenour et al. 2009). Whenever the MANOVA tests indicated a significant effect, a *posteriori* univariate ANOVA and a *post hoc* Tukey’s honestly significant difference test (HSD) were used to identify the modalities of the factor associated with the variation in the response variable. Catch and effort spatial distribution were plotted using a Geographical Information System (GIS, QGIS 2.6.1).

III.3 Results

III.3.1 Catch variation

The bathymetric distribution of the species in this study was between 10 m (minimum) and 142 m depth (maximum). There were significant differences between the Fish net and Spiny Lobster net for the CPUE of biomass ($P < 0.0001$, t-test) and the CPUE of individuals ($P < 0.0001$, t-test).

- For Fish net, MANOVA results indicated that there were significant differences in the CPUE of biomass between months ($P < 0.001$), depths ($P < 0.05$) and strata ($P < 0.001$) (Table 1).

Table 1 MANOVA results for testing the effects of year, month, number of piece of net (50m) and strata on artisanal fisheries CPUE (weight and number) of *Dentex dentex* around Corsica and *F*-values of the tests used (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Fishing gear\Factor	Year		Month		Depth		Strata	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Fish net								
CPUE of biomass	1.60	0.172	5.81	<0.001***	2.24	0.014*	6.56	<0.001***
CPUE of individuals	1.17	0.321	3.95	0.001**	3.82	<0.001***	6.77	<0.001***
Spiny Lobster net								
CPUE of biomass	2.26	0.061	2.07	0.67	3.58	0.003**	2.71	0.019*
CPUE of individuals	4.11	0.003**	3.47	0.004**	3.62	0.005**	2.28	0.05

Using one-way ANOVAs with *post hoc* HSD, CPUE differed significantly by strata ($P < 0.001$), with Cap Corse being higher than Calvi, Bonifacio and Ajaccio (Fig. 2A). This species showed seasonal variability in captures, with a clear maximum during May followed by a decrease during the summer. The highest monthly value was May, which was significantly different ($P < 0.001$), then June, July, August and September (Fig. 2B). CPUE differed significantly by depth ($P < 0.05$), with 10-20 m being higher than 30-40 m (Fig. 2C).

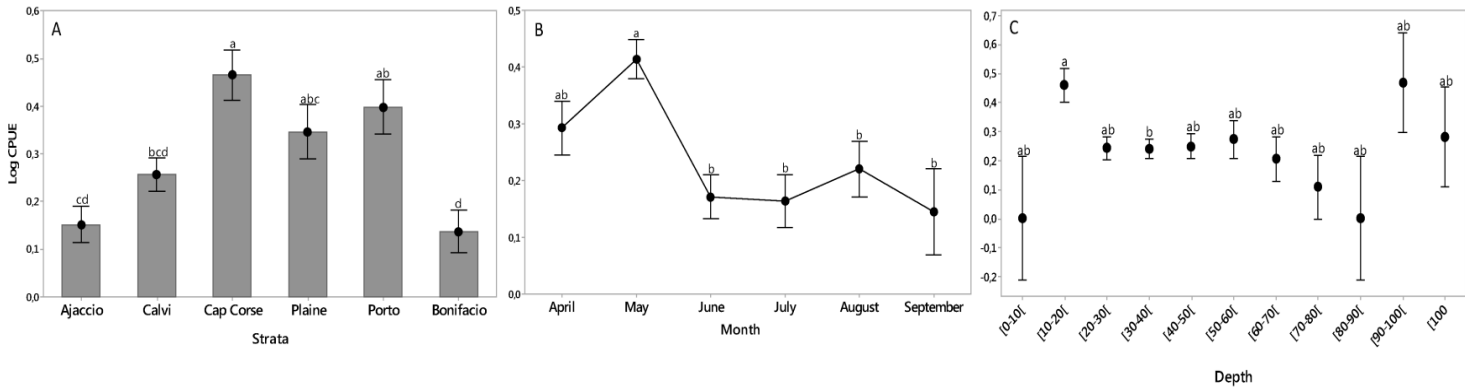


Fig.2 Variations of mean Log CPUE of biomass (g.50m^{-1} of net; $\pm\text{SE}$) between strata (A), month (B), depth (C), caught by Fish net (2009-13) in Corsica for *Dentex dentex*. The values sharing no letter are significantly different (ANOVA+ *post hoc* Tukey's; * $p < 0.05$).

MANOVA results indicated significant differences in the CPUE of individuals between months ($P < 0.01$), depths ($P < 0.001$) and strata ($P < 0.001$) (Table 1; see Fig.3 for more details).

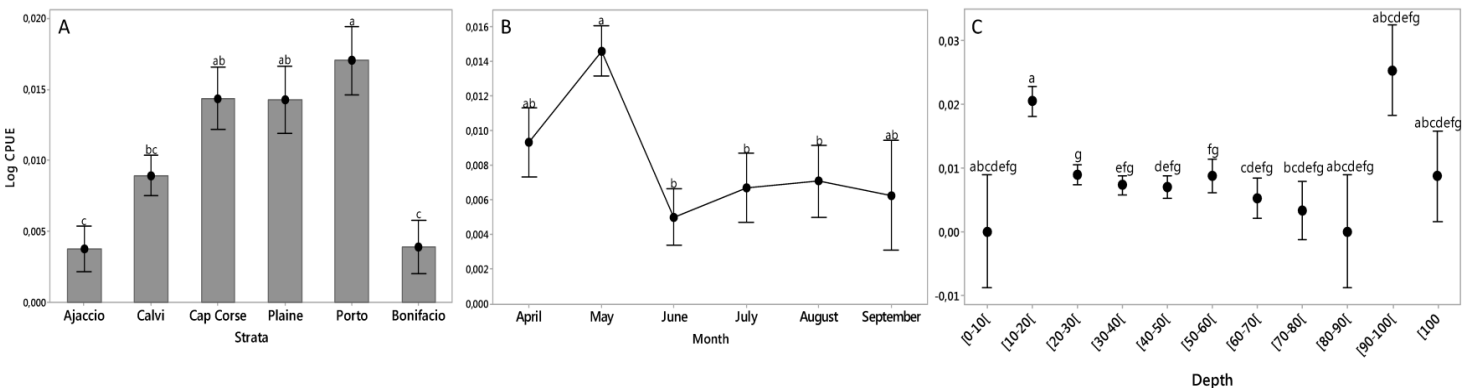


Fig.3 Variations of mean Log CPUE of individual (ind.50m^{-1} of net; $\pm\text{SE}$) between strata (A), month (B), depth (C), caught by Fish net (2009-13) in Corsica for *Dentex dentex*. The values sharing no letter are significantly different (ANOVA+ *post hoc* Tukey's; * $p < 0.05$).

- For the Spiny Lobster net, strata ($P < 0.05$) and depth ($P < 0.01$) significantly affected the CPUE of biomass (Table 1). The strata with the highest values were Plaine and Calvi. Two peaks of exploitation were observed for depth, with maximum efficiency between 50-60 m and 90-100 m (Fig. 4).

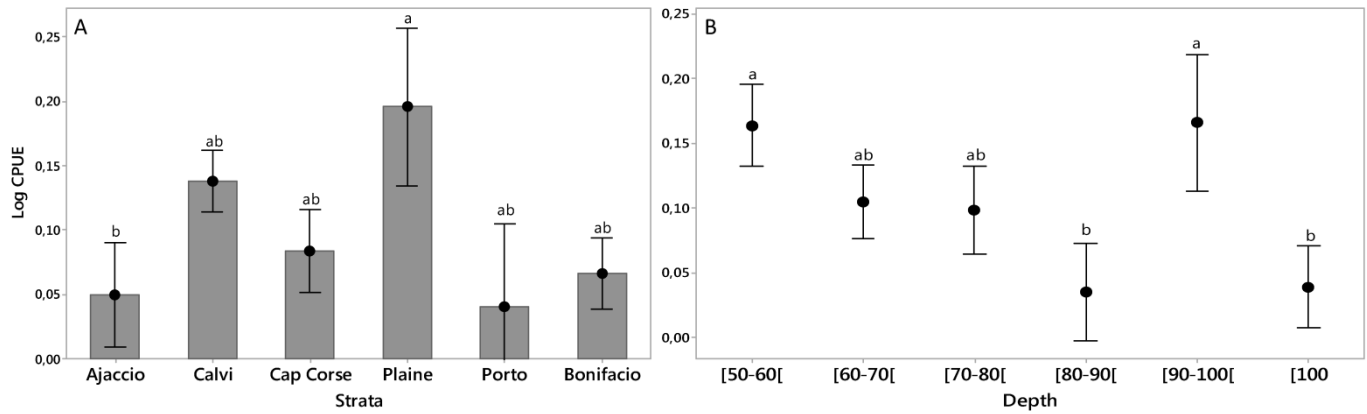


Fig.4 Variations of mean Log CPUE of biomass (g.50m^{-1} of net; \pm SE) among strata (A), depth (B), caught by Spiny lobster net (2009-13) in Corsica for *Dentex dentex*. The values sharing no letter are significantly different (ANOVA+ *post hoc* Tukey's; * $p < 0.05$).

The CPUE of individuals varied by year, month and depth (MANOVA, $P < 0.01$), whereas it did not seem to be affected by strata. Catches (individual) were maximal in May, at a depth of 50-60 m, and significantly higher ($P < 0.001$) in 2013 than in the other years (see Fig. 5 for more details).

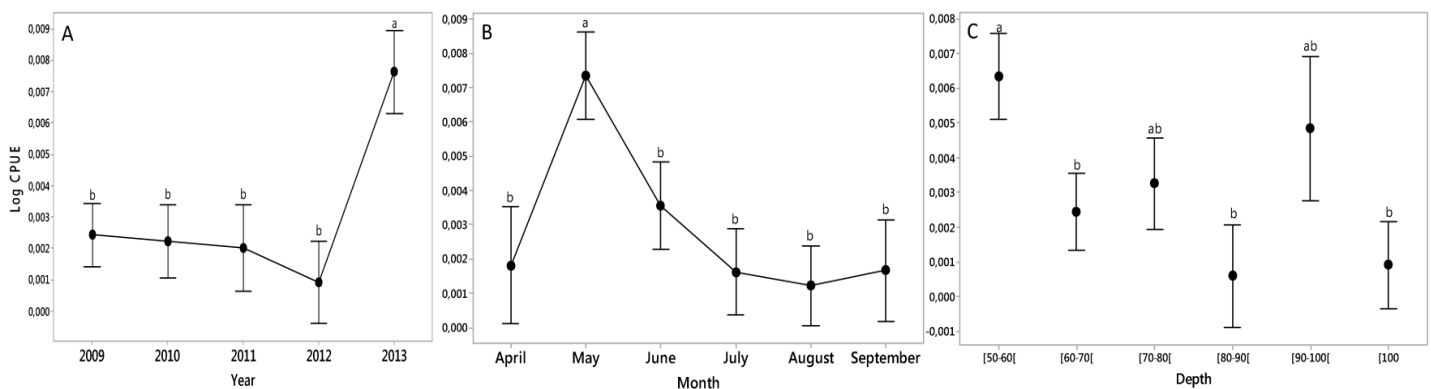


Fig.5 Variations of mean Log CPUE of individual (ind.50m^{-1} of net; \pm SE) between year (A), month (B), depth (C), caught by Spiny lobster net (2009-13) in Corsica for *Dentex dentex*. The values sharing no letter are significantly different (ANOVA+ *post hoc* Tukey's; * $p < 0.05$).

III.3.2 Age structure

A total of 90 common dentex were sampled between 2012 and 2013. Using scales, six age classes were identified, ranging from 0 to five years old and older (Fig. 6). The scales over 5 years old were illegible on account of the poor definition of the annual rings and the abundance of false rings, therefore they were classified in the aged five years and over category. Analysis of age structure showed that the sample was dominated by three age classes (2, 3, 5 and over). 38% of the specimens caught (age classes, 0, 1, 2) had not reached the age of sexual maturity (2 years old, the size at which 50% of the population was mature, Morales-Nin 1997). The Fish net had a broad spectrum of capture (six age classes), while the Spiny lobster net tended to target older specimens (two years old and over).

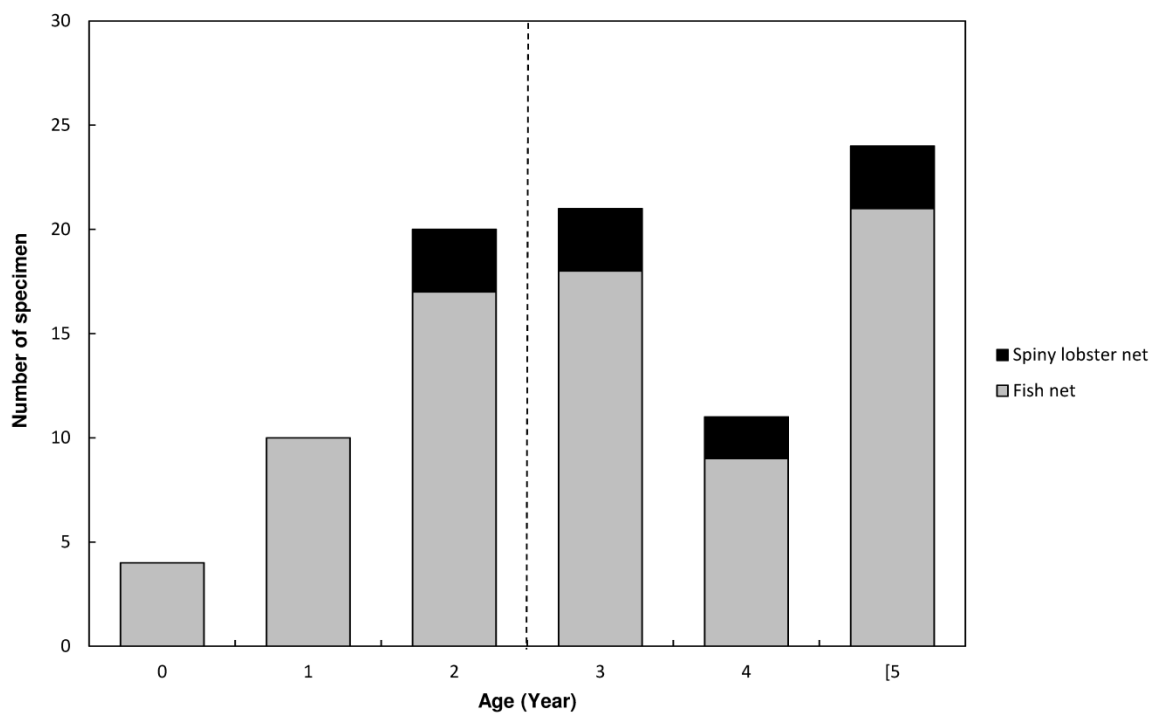


Fig.6 Frequency histogram of ages of *Dentex dentex* exploited by artisanal fisheries (Fish net and Spiny lobster net) in Corsica (2012-2013; n= 90). Vertical dotted lines show approximate age at maturity (from Morales-Nin and Moranta, 1997).

III.3.3 Size distribution

A total of 140 common dentex were sampled between 2011 and 2013. Length-frequency histograms for *D. dentex* (Fig.7) showed that a wide range of life-stages of this species, from juveniles to adults, were caught by artisanal fisheries around Corsica

Island (Fig. 7). Fish size ranged from 15 cm to 90 cm (Total length, TL). The analysis of size distribution showed that there was a predominance of four distinct modes (25-30, 30-35, 35-40 and 40-45 cm) (Figure 4). The vast majority of fish sampled were caught by Fish net (n=124, 89%). 43% of the specimens (modes, 15 to 35 cm) had not reached the length of sexual maturity (35 cm, size at which 50% of the population was mature, Morales-Nin 1997), mainly caught by Fish net.

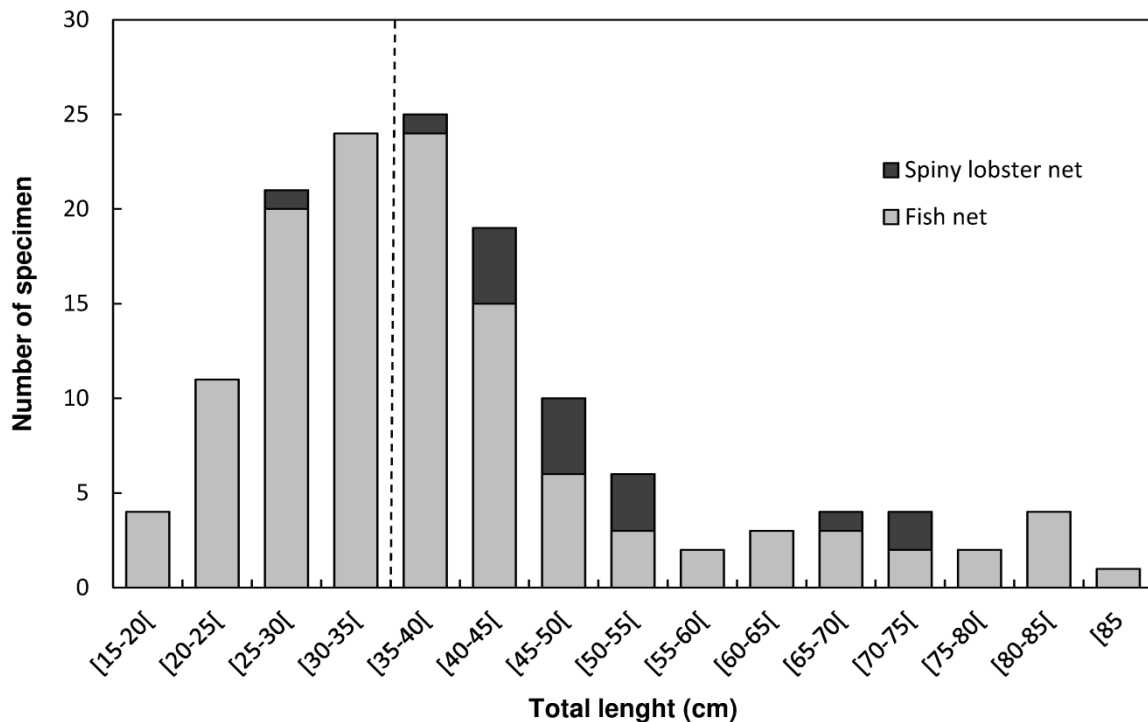


Fig.7 Length-frequency histogram for *Dentex dentex* captured in Corsica (2011-2013; n=140) by artisanal fisheries (Fish net and Spiny lobster net). Vertical dotted lines show approximate total lengths at maturity (from Morales-Nin and Moranta, 1997).

III.3.4 Spatial distribution of catches

The spatial distribution of fishing grounds showed a heterogeneous distribution of common dentex around Corsica. The highest CPUEs (biomass and individual) were mainly located in the north west of Corsica (Porto, Calvi, Cap Corse) (Fig. 8). These fishing grounds were mainly at depths between 10 m and 50 m. While lower CPUEs were found in the east of Corsica (e.g., Plaine). The highest CPUEs (biomass) were identified during the spawning period, in ten fishing grounds within four stada (Porto, Calvi, Cap Corse and Bonifacio) (Fig. 9A). Several units supporting very high common dentex abundance (weight) were located near/inside two Marine Protected Areas: “*La Réserve Naturelle des Bouches de Bonifacio*”

and “*La Réserve Naturelle de Scandola*”. Analysis of size distribution within these “hot spots” areas showed that the specimens caught were mainly medium to large individuals (between 40 and 100 cm) (Fig. 9A). In general, these grounds were the most significant areas sampled in terms of fishing effort (Fig. 9B). Fishermen concentrated their effort mainly around their home harbors.

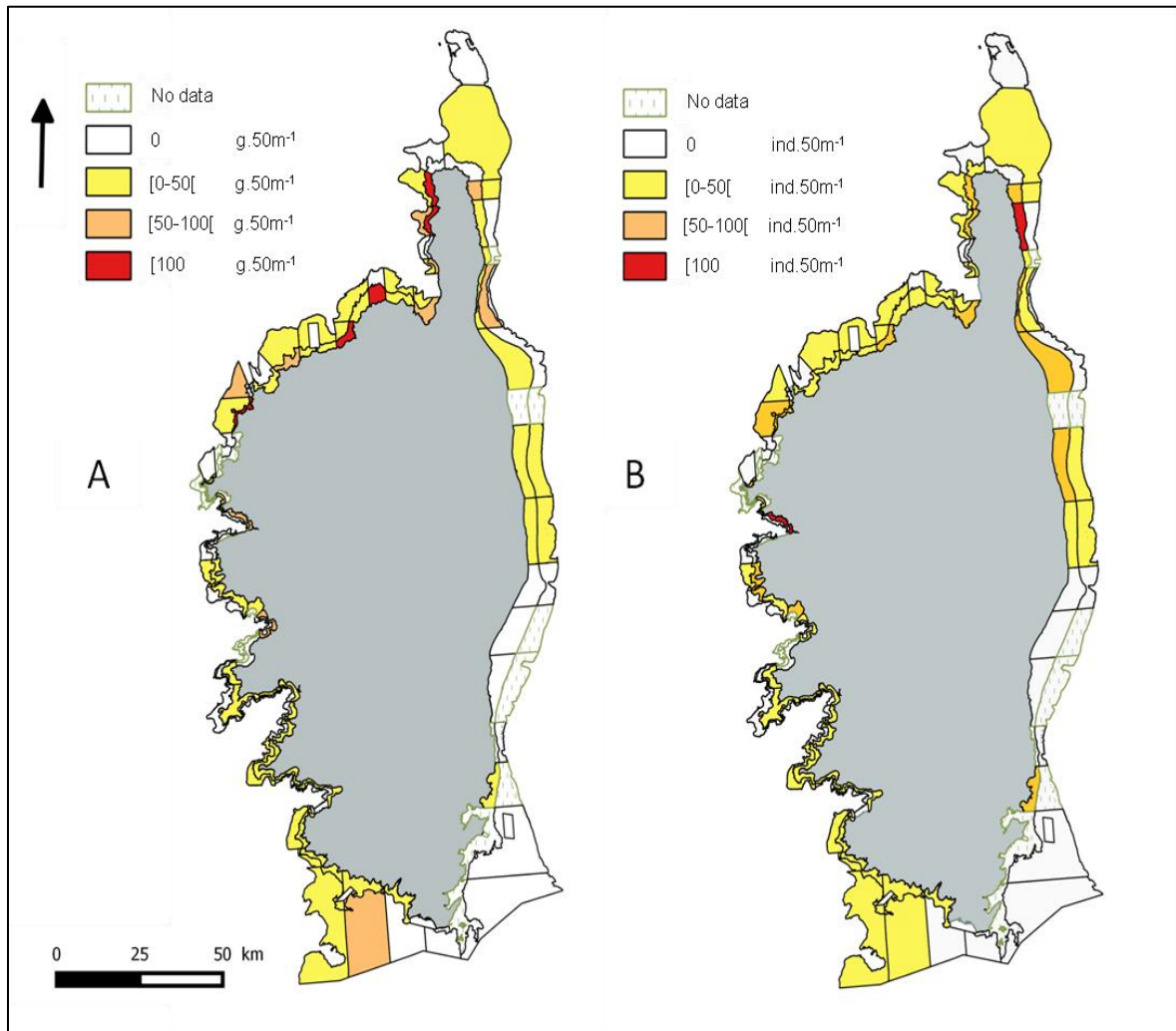


Fig.8 Map of fishing grounds around Corsica showing CPUE of biomass (g.50m⁻¹ of net; A) and CPUE of individual (ind.50m⁻¹ of net; B) (2009-13) for *Dentex dentex* caught by artisanal fisheries.

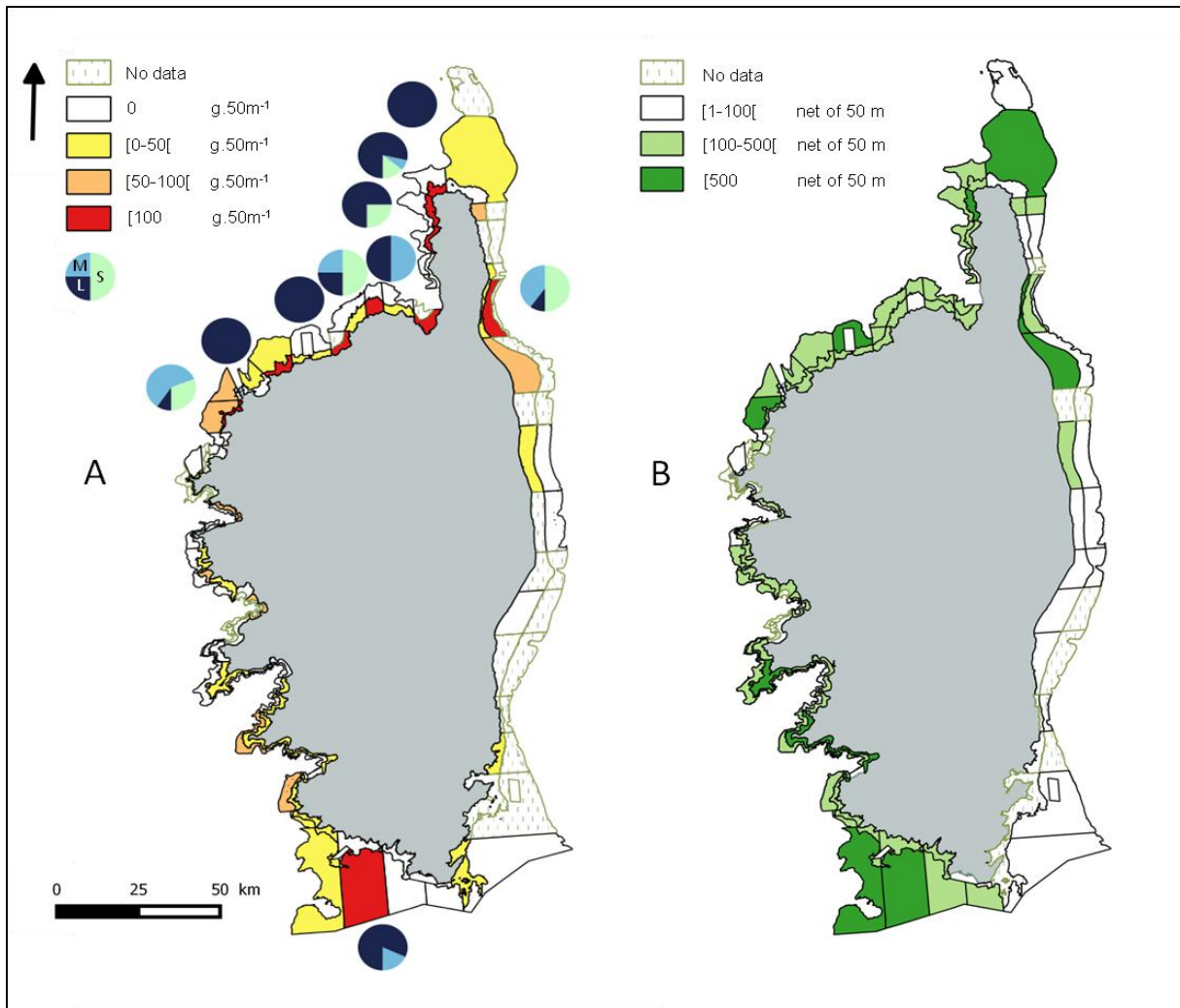


Fig.9 Map of fishing grounds around Corsica Island showing CPUE of biomass ($\text{g}\cdot 50\text{m}^{-1}$ of net; A) during the spawning period (April-May) for the years 2009-13 for *Dentex dentex* caught by artisanal fisheries. Diagrams represent size class composition (Total length in cm: Small: [0-40[; Medium: [40-60[; Large: [80) within “hot spots” areas. Spatial distribution of fishing effort during the sampling period (2009-2013; B).

III.4 Discussion

In light of the state of the majority of living resources, understanding the impact of different gears that compete for the same resources is vital for improved management and conservation (Erzini et al. 2006). First, it should be noted that the bottom long-line is used in Corsica for the exploitation *D. dentex*. However, since this activity is mostly practiced between September and April (period of low activity), data were not available and therefore not considered in this study. We found significant differences in the catch rates of *Dentex dentex* between the Fish net and Spiny Lobster net. The Fish net is the most profitable gear for the common dentex fishing considered in this study. Preference for the use of Fish nets

was apparent in areas where *D. dentex* is concentrated, such as the rocky bottoms close to the coast, and generally at depths of less than 50m or at the limit of *Posidonia oceanica* meadows (L. Delile). These results were consistent with previous studies in the Mediterranean Sea (Morales-Nin and Moranta 1997; Stobart et al. 2012).

The artisanal CPUE of *Dentex dentex* varied over spatial and temporal scales. The catch rates by gear show annual stability throughout the time period considered: however, there was a noticeable increase in the number of individuals caught by the Spiny lobster net during 2013. Fluctuations in fish abundance depended not only on the effects of fishing or other anthropogenic impacts, but also on key processes such as recruitment, predation and migration, which may also be linked to environmental fluctuations and climate change (Rijnsdorp et al. 2009). Seasonal variations in catch rates for the Fish net and the Spiny Lobster net (both biomass and individual) were found. The study revealed a seasonal pattern in CPUE for common dentex exploited by artisanal fishing around Corsica. Monthly variability showed that exploitation reached a peak during May, with lower rates during the rest of the year. Seasonal variations obtained in this study were similar to those reported from other Mediterranean locations (Morales-Nin and Moranta 1997; Chemmam-Abdelkader et al. 2004). This seasonal increase of captures in spring was probably related to the reproductive strategies of this species mainly during this period, *i.e.* from March till June (Morales-Nin and Moranta 1997). This could be due to mating behavior prior to fertilization when individuals aggregate for reproduction, or/and seasonal migrations towards spawning grounds (Tzanatos et al. 2006; Henriques et al. 2013). Several species concentrate during spawning which can promote high CPUE values, since fishermen use their knowledge to exploit this phenomenon (Petitgas et al. 2003). During this season (April-May) common dentex probably become more active or expand their area of activity to find partners, therefore becoming more accessible to fisheries (*i.e.*, catchability increases) (Muñoz et al. 2013). It is possible that increased fishing pressure on these species during this period might have a negative impact on stocks (Tzanatos et al. 2008). Depletion induced by exploitation can indeed contribute to the loss of spatial structure, and can potentially eliminate a single stock or a deme within a sympatric population system or a metapopulation complex (Ciannelli et al. 2013). It is primarily the overharvesting of local populations/aggregations (*i.e.* sub-units; often those closest to ports suffer first) that erodes population structure (Ciannelli et al. 2013). Many aggregations have declined or collapsed due to overfishing, and several aggregating species are at risk of extinction (De Mitcheson et al. 2008). When fishing pressure is low, and a relatively small proportion of spawners is removed, aggregations persist (Sadovy et al. 1994). However, when fishing pressure removes a high proportion of aggregating fish each year, aggregations may quickly decline and totally cease to form within a few years (Sadovy et al. 1994). Recent evidence has shown that spawning aggregations may exhibit

hyperstability, a situation where catch per unit effort of aggregation is relatively stable over many years while the abundance of fish within the aggregation declines to critical levels and possible collapse (Sadovy and Domeier 2005). Fishing of spawning aggregations can have a wide range of effects on target species and local fishery productiveness (Nemeth et al. 2007).

Ours results showed that the size class composition of the captures during the spawning period was mainly composed by mature individuals (Medium and Large). Fishing mortality tends to remove larger and older individuals from the population, especially the Big Old Fat Fecund Female Fish (the BOFFFF concept) (Field et al. 2008; Hixon et al. 2014). This often leads to strong truncation of age and size distributions within fished populations, known as Age Truncation Effects (ATE) (Berkeley et al. 2004). The removal of these individuals can include negative effects: (i) a shortening and change in timing of the spawning season, (ii) behavioral change in migratory pathways; (iii) a decrease in the production of eggs and larvae, (iv) a decrease in the average survival potential of larvae, and (v) a reduction in genetic heterogeneity (Berkeley et al. 2004; Field et al. 2008; Ciannelli et al. 2013). Such effects may seriously damage the resilience of the populations and increase population variability and extinction risk, without giving a clear signal of decline in total population biomass in fisheries data (Hsieh et al. 2010). Effective management of fish spawning aggregations requires detailed understanding of the dynamics of spawning behavior and associated fishing activities in both time and space (Sadovy and Domeier 2005; Erisman et al. 2012).

The lower captures observed after this spawning period (June-September) may be partially due to the fishing-induced mortality of the preceding months, a change in social behavior after reproduction, or to a return to normal non-reproductive behavior (Goñi et al. 2003). However, seasonal variations in catch rates are influenced not only by the natural behavior of the species, but also by a multitude of factors like recent catch and income, market demand, fishers' experience, weather conditions, distance to fishing grounds, cultural/traditional aspects and fishery management measures (Tzanatos et al. 2006; Battaglia et al. 2010).

The length and age frequency histograms of the common dentex showed that exploitation (essentially during June-September) was mostly composed of small/young and immature individuals that had not yet reached first sexual maturity (Morales-Nin & Moranta 1997). Not allowing these smaller individuals to reach maturity can lead to population declines because they are removed from the population before having the opportunity to reproduce and contribute to its growth (Hupfeld and Phelps 2014). The exploitation of juveniles threatens the reproductive potential of the species (Lloret et al. 2012) and the removal of immature fishes contributes to the decline of stocks, bringing about the type of overfishing known as growth overfishing (Jennings et al. 1999). Growth overfishing also has important economic

repercussions, inasmuch as the immature, small-sized individuals could be caught later at a much larger size and thus attain higher prices (Jennings et al. 1999).

Our spatial approach revealed a heterogeneous catch distribution of common dentex at the scale of Corsica and identified major exploitation areas. It should be noted that the sampling effort was not the same throughout the study area and for certain strata (Bonifacio/Plaine) the number of nets sampled was less consistent. However, the identification of the fishing grounds exploited clearly indicated the existence of 'hot spots', which probably represent essential habitats, such as spawning or nursery grounds in the life history of the common dentex and associated species. It is worth stressing that more than one habitat can be favorable, but often at particular phases of life history, such as the seasonal spawning or settlement period, often involving ontogenic shifts in habitat use (Macpherson et al. 1997). The "hot spots" identified for common dentex were mainly located near or inside a Marine Protected Area (MPA). Catches of common dentex obtained by artisanal fishers inside the MPAs show higher rates in biomass and density than outside them. This effect was described previously and was consistent with the results of previous studies, which showed that common dentex tends to respond positively to protection from fishing (Forcada et al. 2010; Guidetti et al. 2010; Marengo et al. 2015).

Variability in the recruitment of sparids is also very high at small spatial scales (Vigliola et al. 1998). Geographical differences could also be partially explained by larval dynamics, which in turn depend on reproductive success at regional scale, larval mortality, occurrence of settlement episodes and/or post-settlement survival, and the general hydrodynamic regime (García-Charton et al. 2004). A fishery's impact on its own resources is determined in large part by the distribution of fishing effort (Diogo et al. 2015). The use of GIS applications to allocate fishing effort constitutes a powerful tool that helps decision makers to evaluate the decisions taken and to assess the effectiveness of policy changes (Caddy and Carocci 1999). This study generated the first fine scale maps showing the spatial exploitation of common dentex and the distribution and intensity of fishing activities during the fishing season.

The significant differences in catch rates between depths are another implication of the complex association of organisms with the spatial component. Depth and substrate preferences of different fish sizes/ages can be linked to prey preferences and availability such as different prey compositions between depth zones and sizes (Tzanatos et al. 2008). Numerous authors have demonstrated that several environmental variables linked to the bathymetric gradient, such as water temperature, salinity, or other habitat features, could also strongly influence the organization patterns of fish assemblages (Demestre et al. 2000; Gaertner et al. 2005).

III.5 Conclusion

The present study makes a significant contribution to the knowledge of several aspects of the exploitation of common dentex by a typical Mediterranean artisanal fishery. A wide range of life-stages of this species, from juveniles to adults, were caught by artisanal fisheries around Corsica. However, we showed that *D. dentex* were mainly caught during the reproduction season, when individuals concentrate in certain “hot spot” areas.

A combination of management tools and specific measures to safeguard the reproductive potential of this species should be promoted: (i) such as limiting or banning their capture through seasonal closures during the spawning season, (ii) a national minimum landing size exceeding the age at first maturity, (iii) reducing bycatch mortality wherever possible, and (iv) the establishment of permanently closed marine reserves in key areas, such as spawning grounds and diversity hot spots (Nemeth et al. 2007; Matić-Skoko et al. 2015).

Management will also need to keep in mind that potentially multiple populations could be present within a single management area and that there is a risk of localized depletion if management measures are inappropriate for all the populations within a managed area (Ballagh et al. 2012). One alternative for professional fishers may be to change their fishing activity to another related activity, such as fishing tourism, which in other Mediterranean areas is already a well-established alternative source of income (Maynou et al. 2013). Sustainable use of fishery resources can involve a balance between protecting fish when they are most vulnerable to exploitation, while not stifling the need for fisheries to operate economically and efficiently (Hilborn 2011).

The preferences of artisanal fisheries for these areas (hot spots) identify them as important socio-economic fishing locations whose sensitivity should be borne in mind in fishery management decisions (Pascual et al. 2013). It would be desirable to engage artisanal fishers in a partnership with scientists and fishery and MPA managers. The more the fishermen are engaged in management processes, the more successful the management will be (Di Franco et al. 2014b). Our study also shows the importance of continuous monitoring of the artisanal fisheries around Corsica. Little is known of the reproductive movements of the common dentex. Further studies using fishery-independent research (e.g., passive and active acoustic telemetry, external tags, direct observations) are needed to better understand the reproductive behavior over time and space of this species.

Understanding the factors influencing behavior during spawning may provide predictable patterns that can be used in management. There is a pressing need to incorporate knowledge of mating systems in stock assessments (Lloret et al. 2012). Finally, this information will be useful in designing sustainability scenarios, in terms of maximum sustainable yield for artisanal fisheries (Pascual et al. 2013).

Chapitre IV

Comparative analysis of artisanal and recreational fisheries for *Dentex dentex* in a Marine Protected Area

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IV.1 Introduction

The Mediterranean Sea is a marine biodiversity hot spot under intense pressure, where ecological and human influences meet and strongly interact (Coll et al. 2010; Lejeusne et al. 2010). Among ecological factors, such as direct habitat modification, species tropicalization, and seawater acidification, fishing represents the activity having the greatest impact because it has driven most stocks to overexploitation (Quetglas et al. 2013).

To reduce such negative impacts, marine protected areas (MPAs) have been implemented as part of an ecosystem-based approach to coastal management (Albouy et al. 2010). Multiple-use MPAs have been widely implemented due to their potential to achieve conservation objectives while allowing human uses and minimizing conflicts, by including some degree of protection for commercial species and important habitats as well as promoting the use of local fisheries and a range of recreational activities (Lester et al. 2009; Rocklin et al. 2011; Horta e Costa et al. 2013). More generally, MPAs are increasingly used as a tool for fishery management (Rocklin et al. 2011). They have the potential to sustain the fisheries adjacent to protected areas while safeguarding species and habitats within them (Francour et al. 2001). The expected benefits of MPAs for fishes include an increase in abundance (net emigration of adults and juveniles across borders, termed “spillover”), biomass and fecundity (the increased production and exportation of pelagic eggs and larvae), as well as a potential benefit for biodiversity (Francour et al. 2001; Gell and Roberts 2003).

Artisanal fisheries or small-scale coastal fisheries are particularly important in the Mediterranean, where they constitute about 80% of the fishing fleet (European Commission 2004). Artisanal fishing is a complex system characterized by commercial fishers operating in small boats, exploiting areas near the coast, using a large number of gears and techniques, typically manned by a single fisherman or a pair of fishermen and targeting a high diversity of species (Colloca et al. 2004; Gomez et al. 2006; Lloret and Font 2013). In the Mediterranean, fish are heavily exploited by commercial fishing but recreational fishing is also intensive along the Mediterranean coast (Seytre et al. 2013). Recreational fishing in the Mediterranean can be defined as follows: all non-commercial fishing carried out mainly for pleasure or sport, where the catch - the sale of which is illegal - is used for private consumption (Font et al. 2012). Recreational fishing has economic, social, and cultural roles; it has been recognized as one of the most common leisure activities and is now a thriving activity in Mediterranean coastal areas (Morales-Nin et al. 2005; Albouy et al. 2010; Font and Lloret 2011). In the Mediterranean, recreational fishing is particularly important because it represents more than 10% of the total production of all fishing (European Commission 2004).

Recreational and artisanal sectors often compete for limited coastal resources and the intensification of recreational fishing magnifies pressure on species already in an advanced state of exploitation (Diogo and Pereira 2013; Lloret and Font 2013). Commercial and recreational fishing can have similar demographic and ecological consequences on fished populations and may provoke serious ecological and economic damage (Coleman et al. 2004). Despite this similarity, generating a variety of impacts on marine ecosystems, much less research is performed on recreational fishing compared to commercial fishing, due in part to the difficulties involved in collecting data on recreational fishing (Font et al. 2012). There is an urgent need to evaluate the potential impact that the different types of fishing activities, alone and in combination, can have on the sustainability of coastal resources and on the general functioning of coastal ecosystems (Albouy et al. 2010).

The common dentex *Dentex dentex* (Linnaeus, 1758) is an iconic marine coastal fish in the Mediterranean Sea. It is a demersal sparid fish (0-200 m) that grows to a maximum length of 100 cm and weight of 13 kg, with a relatively long life span (more than 20 years) (Morales-Nin and Moranta 1997). As a high trophic level predator, it holds a key position in coastal marine food webs. The global commercial catch of common dentex has fluctuated over the last sixty years on a multidecadal time scale and declined significantly from a peak of ~7,000 tons in 1990 to less than 1,000 tons in 2005 (Abdul Malak et al. 2011; Marengo et al. 2014b). *D. dentex* is now classified by the International Union for the Conservation of Nature (IUCN) as “vulnerable” on the Red List of Threatened Species in the Mediterranean Sea (Abdul Malak et al. 2011). Despite this status, there is no Minimum Landing Size (MLS) to safeguard the reproductive potential for this species. *D. dentex*, due to its large size, flesh quality, and high commercial value is of great economic interest for both artisanal and recreational fisheries (Morales-Nin and Moranta 1997; Loir et al. 2001). The main fishing gears used by artisanal fishing, specifically targeting the common dentex are: bottom long-lines, trammel nets and medium-large mesh gillnets (Morales-Nin and Moranta 1997; Sacchi and Dimech 2011). The most common methods used in recreational fishing for *D. dentex* are boat fishing, spearfishing, line and shore fishing (Morales-Nin et al. 2005; Font and Lloret 2011). There is an alteration and/or combined use of this gear, depending on the season, habitat and geographic area (Marengo et al. 2014b). Despite its economic and ecological importance, data on this species regarding fishing gear, seasonality, fishing effort, catches and the yields of the artisanal and recreational sector are still limited.

The aims of this study were to: (i) characterize the artisanal fishing of common dentex in the Bonifacio Strait Natural Reserve (BSNR, Corsica, NW Mediterranean Sea) in terms of temporal variability; (ii) compare and quantify, over a four year period, the catch rates, fishing techniques, catch composition of the artisanal and recreational common dentex fisheries and determine the influence of management measures (protected areas) on the captures by both

activities; (iii) and estimate the production of the common dentex for both artisanal and recreational fishing.

IV.2 Materials and methods

This study was performed in the Bonifacio Strait Natural Reserve (BSNR), located in southern Corsica (France; Mediterranean Sea, Fig. 1). Several activities take place in this MPA such as artisanal fishing (mainly trammel nets and longlines), recreational fishing (mainly longlines, hook fishing and spear fishing), diving and sailing.

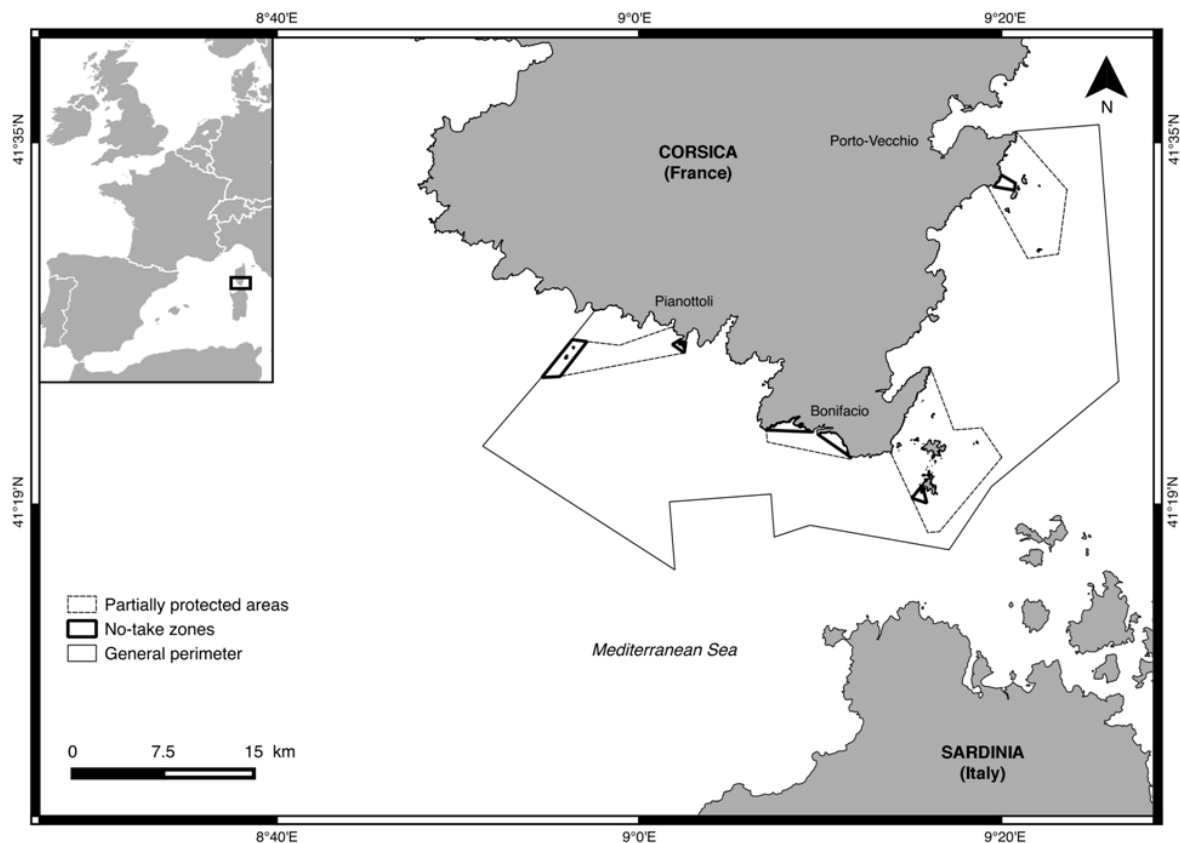


Fig. 1 Map of the study area showing the boundaries of the Bonifacio Strait Natural Reserve with zoning implemented by the management plan.

It was created in September 1999 and encompasses the Lavezzi Islands Reserve created in 1982 (Mouillot et al. 2002). Its bottom substrate is predominantly covered by a mosaic habitat of rocks, sand and seagrass beds of *Posidonia oceanica* (L. Delile), and the maximum depth is 158 m. Its marine surface area of 79 640 ha includes four zones of Partially Protected Areas (PPA; 12 300 ha), where spearfishing is forbidden (artisanal fishing authorized), and six No-Take Zones (NTZ; 1130 ha) closed to all types of fishing activities (both artisanal and recreational) as well as diving (Mouillot et al. 2002). See <http://www.rnbb.fr/> for more details about legislation.

IV.2.1 Data collection

Fishery data were collected from different artisanal fishing surveys (from 2000 to 2012; except 2009) and recreational fishing surveys (2006, 2008, 2011, 2012) carried out in BSNR (see Table 1 for a summary of the survey details). Over the study period, 962 commercial boats (=fishing parties) and 459 recreational boats (=fishing parties) were sampled.

Table 1 Information on the different recreational and artisanal fishing surveys in which data were collected. The years and months when surveys were conducted, the survey type, and the number of boats sampled are shown.

Survey	Years	Months	Survey type	Number of boats sampled
Artisanal fishing	2000	May-July	Landing	154
	2001	May-July	Landing	152
	2002	May-July	Landing	76
	2003	May-July	Landing	110
	2004	May-July	Onboard fishing vessel	59
	2005	May-July	Onboard fishing vessel	29
	2006	May-July	Onboard fishing vessel	57
	2007	May-July	Landing	125
	2008	May-July	Onboard fishing vessel	56
	2010	May-July	Landing	92
	2011	May-July	Onboard fishing vessel	16
	2012	May-July	Onboard fishing vessel	36
Total				962
Recreational fishing	2006	July-September	Roving-roving	32
	2008	June-October	Roving-roving	82
	2011	May-August	Roving-roving	264
	2012	March-May	Roving-roving	81
Total				459

IV.2.2 Artisanal fishing surveys

Catches were collected by BSNR scientists onboard fishing vessels or on landing, only on retained fish (see Table 1), in collaboration with fishers of the prud'homie of Bonifacio from four main ports (Pianottoli, Bonifacio, Sant'Amanza, Porto-Vecchio) and three shelter ports (Piantarella, Santa Giulia, La Chiappa). All the common dentex caught were measured (mm), and their total weight was estimated using size class correspondences: small: 0–40 cm = 0.3828 kg; medium: 40–60 cm = 2.1053 kg; large: 60–80 cm = 5.4653 kg (Marengo et al. 2013). The fishing area, duration, type, characteristics of the gear deployed and fishing effort were recorded. To standardise the data collected, catch-per-unit-effort (CPUE) was expressed for nets, in grams by piece of net (50 m) (CPUE mass: $\text{g}\cdot 50\text{m}^{-1}$), and per number of individual caught by piece of net (50 m) (CPUE num: $\text{ind}\cdot 50\text{m}^{-1}$). In this study, the spiny lobster net is defined by duration of fishing operation of at least 2 days at a depth exceeding or equal to 50 m. The fish net covers any type of net that does not correspond to the first definition. For longlines, CPUE was expressed g per 100 hooks and ind per 100 hooks. Fishing yield data are expressed in $\text{g}\cdot \text{day}^{-1}$ per boat.

IV.2.3 Recreational fishing surveys

Surveys covered the summer (tourist) season. During fishing activity, a study on boat fishing was conducted at sea using a boat and several interviewers in the BSNR (roving). For each fishing set, the data collected included type of fishing gear, date, duration of each fishing operation and catch (only retained fish). Weight estimates for common dentex were obtained with a spring balance (accuracy ± 20 g) or were derived using length–weight relationships published in FISHBASE (<http://www.fishbase.org/>; based on Morales-Nin & Moranta 1997). CPUE mass was recorded as $\text{g}\cdot \text{boat}^{-1} \text{h}^{-1}$ and CPUE num as $\text{ind}\cdot \text{boat}^{-1} \text{h}^{-1}$.

IV.2.4 Estimation of fishing effort and production: Artisanal fishing

Fishing effort was expressed as the mean number of active fishing boats per day and the mean number of trips performed during the whole fishing season (Farrugio and Le Corre 1993). BSNR annual production was estimated using this previous information combined with the mean daily biomass caught per boat (yields data) for the years 2006, 2008, 2011 and 2012.

IV.2.5 Estimation of fishing effort and production: Recreational fishing

BSNR annual production was estimated using several key assumptions; a heuristic approach was developed to estimate the fishing effort. Information for the study was gleaned from a multiple approach based on fishing authorisations and roving data, for more reliable assessments of the actual numbers of recreational anglers and their fishing effort and yields. The number of fishers practicing in the RNBB was obtained from the number of declaration of intent of fishing made in 2013 within the BSNR. A new regulation (Arrêté préfectoral no 2013165-0001) requires all recreational fishers to declare themselves to the managers. From this survey, fishing effort was calculated based on: number of fishers, their profiles, type of activity, mean duration of fishing and number of trips per year. Annual production was estimated from the average yield for trolling (based on the study period 2006–2008–2011–2012) and the annual effort values, expressed as total catch per fisher and hour of fishing, and total number of fishing trips per fisher and year (2013), respectively.

IV.2.6 Data analysis

Data sets were not normally distributed; therefore, assessments were tested for significance using nonparametric tests. Annual trends (2000–2012) in the fishing yields were assessed using the Mann–Kendall test to test whether there was a trend in the time series and the Pettitt's test assessed whether a shift occurred. A smoothing method was also used (moving average) on these data sets. For artisanal fishing, differences in the CPUE between the sectors (PPA, GP, Out) were analysed using the Kruskal–Wallis analysis of variance, with the Dunn post hoc test and the Bonferroni correction. For recreational fishing, differences in the CPUE between sectors (PPA, GP) were analysed using the Mann–Whitney U-test. Analyses were performed using XLSTAT software, Addinsoft, Paris, France (with the Time package).

IV.3 Results

IV.3.1 Time series analyses

No significant temporal trend in fishing yield for artisanal fishery (2000–2012) was found (Mann-Kendall: $P = 0.86$), and no shift was detected (Pettitt's test: $P = 0.212$). However, by segmenting the time series, a significant increasing trend was detected between 2000 and 2006 (Mann–Kendal: $P < 0.05$), while no significant temporal trend was detected between 2007 and 2012 (Mann–Kendal $P > 0.05$). Furthermore, graphically, the

moving average showed two main trends during these years: (1) increase between 2000 and 2006, with a yield in 2000 of 654 g.day⁻¹ per boat, reaching peak exploitation in 2006 of 3750 g.day⁻¹ per boat and (2) a relatively stable yield (moving average), but highly variable with strong interannual fluctuations between 2007 and 2012. The yield varied from a minimum of 566 g. day⁻¹ boat⁻¹ in 2007 to a maximum of 4721 g.day⁻¹ boat⁻¹ in 2011 (Fig. 2). The number of fishing vessels exploiting the MPA (average of 13 boats per day) did not change between 2000 and 2012.

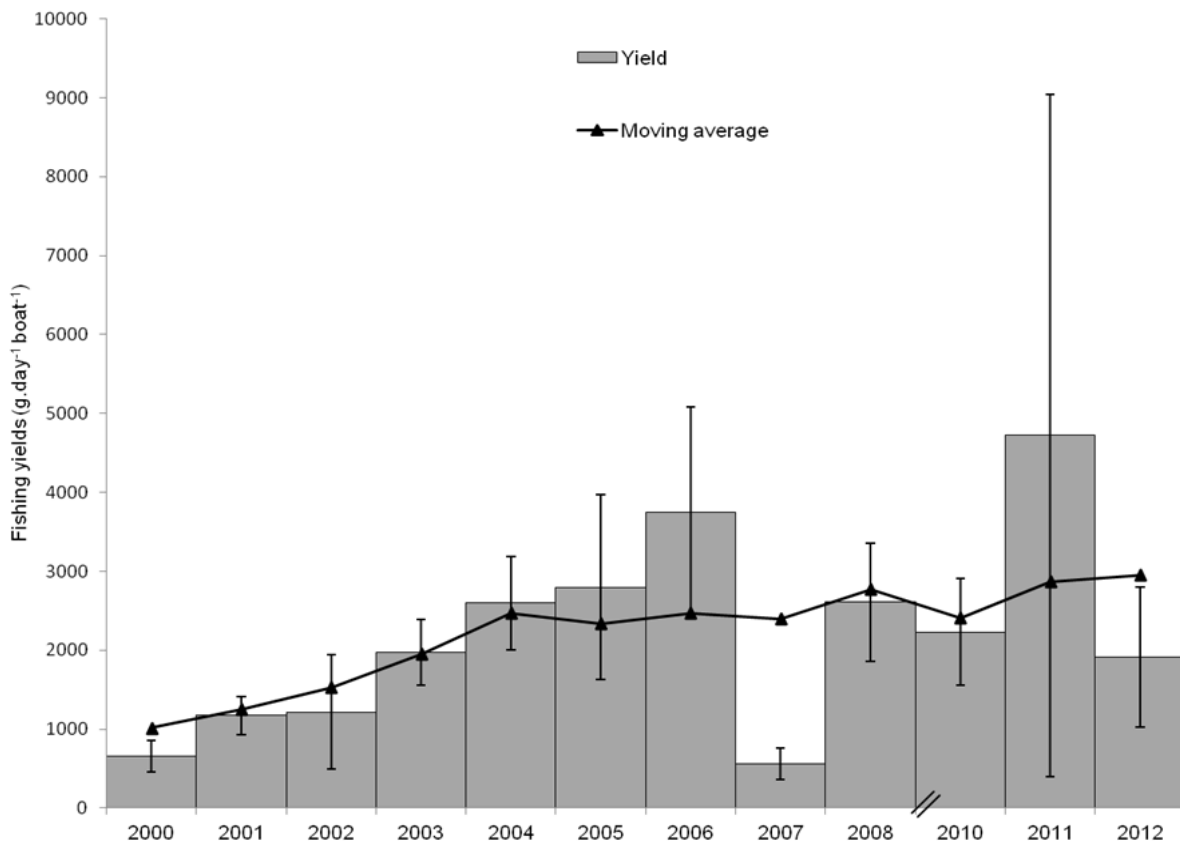


Fig. 2 The mean fishing yield (g.day⁻¹ boat⁻¹) (\pm SE) and moving average for artisanal fishing in the BSNR during the period 2000-08; 2010-12.

IV.3.2 Catch composition

For artisanal fishing, the fishing method with the largest number of specimens caught was the fish net (65% of catches) followed by longline (25% of catches) and spiny lobster net (10% of catches) (Fig. 3a). For recreational fishing, the fishing method with the largest number of specimens caught was (bottom) trolling (90% of catches), followed by spear fishing (6% of catches) and boat angling (4% of catches) (Fig. 3a). As regards to size representativeness in the catch for artisanal fishing (Fig. 3b), spiny lobster nets (*SL*) and fish nets (*FI*) have a broad spectrum of capture: the three size classes were well represented

(SL, S: 24%, M: 48%, L: 28%; FI, S: 32% M: 46% L: 22%), with a predominance of the medium size class. Individuals caught using longlines (LL) were essentially large specimens (LL, M: 22%, L: 78%). For recreational fishing, trolling (TF = T in Fig. 3b) captured the most large individuals (TF, S: 11%, M: 17%, L: 72%); for spear fishing (SF = S Fig. 3b) and boat angling (or handlining) BA = A Fig. 3b), the only size class found in the sample was the category medium (SF and BA; M: 100%).

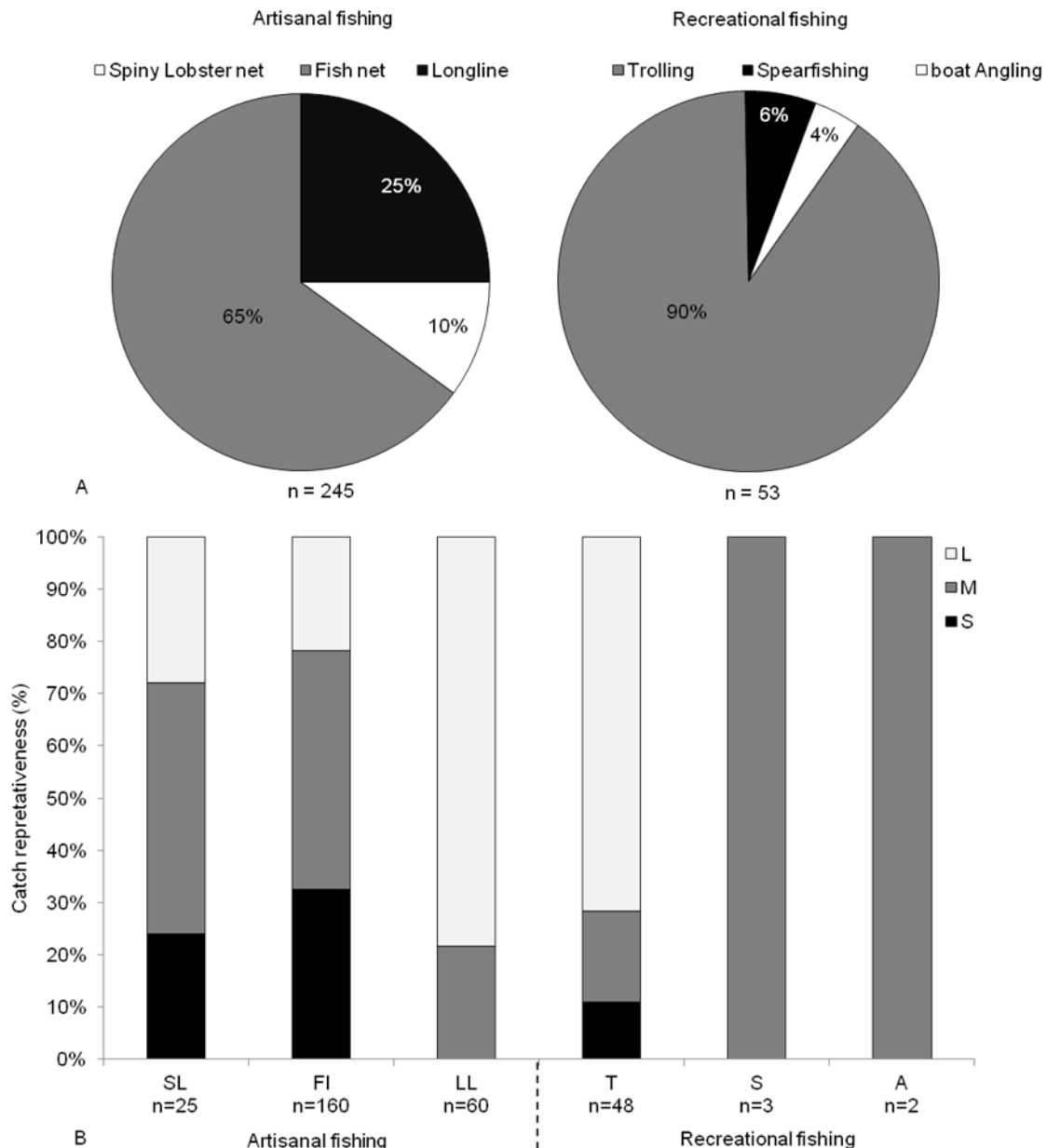


Fig. 3 Catch representativeness in % according to the total number (A) of individuals (n) caught for each fishing type by artisanal fishing and recreational fishing. Catch representativeness in % according to their size class (B) (L: large, M: medium, S: small), for each fishing type caught by artisanal fishing (SL: Spiny Lobster net; FI: Fish net, LL: Longline) and recreational fishing, n= number of *D.dentex* recorded during the surveys (2006-08-11-12).

IV.3.3 Fishing gears

Six types of fishing gear targeting the common dentex were identified in the study area for both artisanal and recreational fishing (Table 2). For artisanal fishing, longlining had the highest rates of exploitation (3554 g.100⁻¹ hooks) followed by the fish net (70 g.50 m net⁻¹) and spiny lobster net (31 g.50 m net⁻¹). Although these fishing gears were used in a wide range of depths, most of the effort was deployed between 48 and 68 m depth. For recreational fishing, trolling reached the highest levels of exploitation (359 g.boat⁻¹ h⁻¹). By comparison, spear fishing and boat angling had much lower levels of exploitation (68 and 13 g.boat⁻¹ h⁻¹, respectively).

Table 2 Characterization of fishing gear used by artisanal and recreational fishing (2006-08-11-12) with their catch per unit effort (CPUE).

Type of fishing	Fishing gear	Sampling years	Mean CPUE Mass (\pm SE)	Unit	Depth of operations (Mean)	Mean CPUE Num (\pm SE)	Unit
Artisanal	Spiny Lobster net	2006; 2008; 2011-12	31.49 (\pm 9.75)	g.50m of net ⁻¹	64 m	0.011 (\pm 0.003)	Ind.50m of net
Artisanal	Fish net	2006; 2008; 2011-12	69.53 (\pm 11.12)	g.50m of net ⁻¹	34 m	0.032 (\pm 0.005)	Ind.50m of net
Artisanal	Longline	2004-06; 11-12	3554.28 (\pm 770.52)	g.100 hooks ⁻¹	48 m	0.779 (\pm 0.175)	Ind. 100 hooks ⁻¹
Recreational	Trolling fishing	2006; 2008; 2011-12	358.50 (\pm 72.61)	g.boat ⁻¹ h ⁻¹	-	0.077 (\pm 0.015)	Ind.boat ⁻¹ h ⁻¹
Recreational	Spearfishing	2006; 2008; 2011-12	68.02 (\pm 44.74)	g.boat ⁻¹ h ⁻¹	-	0.028 (\pm 0.017)	Ind.boat ⁻¹ h ⁻¹
Recreational	boat Angling	2006; 2008; 2011-12	12.73 (\pm 9.29)	g.boat ⁻¹ h ⁻¹	-	0.007 (\pm 0.005)	Ind.boat ⁻¹ h ⁻¹

IV.3.4 Differences between protection levels

For artisanal fishing, there were significant differences between the CPUE values according to zone [out of reserve (OUT), general perimeter (GP), partial protected area (PPA)] (Kruskal–Wallis $P < 0.0001$). Multiple pairwise comparisons using Dunn's procedure found CPUE values within the OUT were significantly higher than within the GP; CPUE values within the PPA were significantly higher than within the GP. The mean CPUE was 26 g.50m net⁻¹ (\pm SE 6.6) in the OUT zone, 17 g.50m net⁻¹ (\pm SE 4.9) for GP and 99 g.50m net⁻¹ (\pm SE 17.4) for the PPA zone (Table 3).

For recreational fishing, CPUE values within the PPA were significantly higher than within the GP. The mean CPUE was 56 g.boat⁻¹ h⁻¹ (\pm SE 26.4) in the GP, and 355 g.boat⁻¹ h⁻¹ (\pm SE 87.1) in the PPA (Mann–Whitney $P = 0.014$) (Table 3).

Table 3 Mean values (\pm SE) of CPUE by artisanal fishery (g.50m⁻¹ of net) and recreational fishery (g.boat⁻¹h⁻¹) in the BSNR (2011-12), according to zone (PPA: Partial Protected Area, GP: General Perimeter, OUT: Out of reserve).

Zone	CPUE Artisanal Fishery	CPUE Recreational Fishery
OUT	26,2 (\pm 6,6) g.50m of net ⁻¹	-
GP	17,4 (\pm 4,9) g.50m of net ⁻¹	55,5 (\pm 26,3) g.boat ⁻¹ h ⁻¹
PPA	98,6 (\pm 17,4) g.50m of net ⁻¹	355,1 (\pm 87,1) g.boat ⁻¹ h ⁻¹

IV.3.5 Fishing production

Estimated mean annual production (based on the study period) in BSNR was 5.8 and 3.4 t for artisanal and recreational fishing modalities considered in this study, respectively. Proportionally, recreational fishing represented 58% of the total captures of artisanal fisheries for this species. Recreational fishing amounted to 37% of the total catch (artisanal and recreational production combined) of the species in this MPA. Total annual fishing production estimated in the BSNR area for common dentex is 9.2 t.

IV.4 Discussion

The common dentex is considered as a trophy fish, and it is therefore targeted by both artisanal and recreational fishing. Time series results for artisanal fishing in the Bonifacio Strait Natural Reserve (BSNR) despite strong intra- and interannual variability showed two prominent periods (an increase from 2000 to 2006 and relatively stable yield from 2007 to 2012). Even if time series data of the present study started just after the creation of the

BSNR, one possible explanation for the increased yield from 2000 to 2006 might be the direct effect of protection measures that first contributed to the increase of the common dentex and, second, to maintaining its exploitation. In the BSNR, a restrictive policy has been enforced on fishing activities since the creation of the marine protected area (MPA) in 1999: number of professional licenses and minimum mesh size were controlled and various protected perimeters were delimited (Albouy et al. 2010). These restrictions tend to decrease fishing pressure on the protected parts and increase catches in terms of CPUE in these areas (Mouillot et al. 2008). The increase in the abundance of exploited species can be rapid, but the recovery of age- and size-structures might only occur after a longer period of protection (Seytre et al. 2013). A likely hypothesis is that a long term period (several decades) of fishing prohibition is necessary to reach a complete reserve effect that could lead to an increase in catches for fishermen outside the protected zone, as part of a density-dependent process (Seytre and Francour 2008).

Stabilisation of the yield for artisanal fishing (2007–2012) could be explained by the combined impact of recreational fishing and marine tourism. Technological advances for the recreational fishery has led to major advances in the ability to capture fish: (i) with equipment for traveling longer distances, e.g., more powerful motors; (ii) several gear modifications, e.g., using light, prey mimics, additional chemicals, motion and sound to increase bait attractiveness; (iii) the affordability of sophisticated fishing technologies, e.g. electric fishing reels (Cooke and Cowx 2006). Progress has also been made in locating fish more rapidly and effectively: (i) e.g., global positioning systems and sonar and (ii) the improved transfer of knowledge, e.g. internet forums (Cooke and Cowx 2006). Such investments generally result in increased capacity or efficiency (e.g., better access to current fishing grounds) and an extension to existing fishing strategies (e.g., access to new fishing grounds) (Torres-Irineo et al. 2014).

In addition, the large numbers of recreational boats that can be found in the MPA of BSNR during summer can have a number of effects on its coastal marine environment. In 2006, 14 003 boats visited the two main tourist ports of the BSNR (Bonifacio, Porto-Vecchio). The rapid growth in the numbers of recreational boats is causing stresses to the marine environment and to many aspects of the biology and ecology of fishes. These stresses include pollution (e.g. heavy metal deposits), habitat alteration (e.g. increased turbidity, physical damage to bottoms by anchoring); behavioral alteration due to pressure wave disturbance and sound disturbance (e.g., avoidance of boating traffic by fish) and invasive species propagation (e.g., direct and indirect introduction of invasive aquatic biota) (Whitfield and Becker 2014). The difficulty in controlling such an influx of tourists is a problem well recognized by the managers of all of those MPAs where marine tourism is practiced (e.g., Port-Cros, Bonifacio, Medes), and does not yet seem to have been resolved (Francour et al.

2001). However many other factors, such as biological interactions, variations in recruitment, and environmental variations can also influence ecosystem functioning and have impacts on fish stocks (Pinnegar et al. 2000; Brander 2010).

For the first time, our results characterize all fishing boat activities targeting the common dentex within an MPA, with an inventory of the fishing gear used, their selectivity and their rates of exploitation. Our study showed that in the BSNR, common dentex were targeted by both artisanal and recreational fishing using a wide variety of gears. In the BSNR, for common dentex fishing, Longline fishing essentially targets large specimens, whereas the composition by size class for Fish net and Spiny lobster net fishing shows broad variations in terms of catches. The catch by Fish net mainly corresponds to a peak of exploitation, with maximum efficiency in May during the spawning period when individuals aggregate or during seasonal migration. The catch by “Spiny lobster net” is low and mainly corresponds to a bycatch. These results are in agreement with previous studies conducted in the Mediterranean Sea for common dentex (reviewed by Marengo *et al.* 2014).

The gears used most frequently for recreational fisheries in this area are Trolling, followed by Spearfishing and boat Angling. Trolling clearly has the greatest impact in terms of biomass removed, targeting essentially large specimens. Spear fishing might have a relatively minor impact compared to trolling. These results do not agree with the conclusions of Abdul Malak *et al.* (2011), who identified spearfishing as the main threat to the exploitation of the common dentex in the Mediterranean.

The combined impact of artisanal and recreational fishing (e.g Longline, Trolling), targeting large specimens can have serious consequences on the state of stocks of *D. dentex*.

The removal of large individuals can adversely affect the reproductive potential of vulnerable fish populations because larger females are proportionally more fecund, reproduce over an extended period, and spawn better quality eggs and larvae with better survival rates (Birkeland and Dayton 2005). Size selective fishing may not only reduce the biomass but may induce: compensatory mechanisms, truncation of age and size structure, loss of genetic variability, and evolutionary changes (Lewin et al. 2006).

CPUE data have been evaluated inside and outside the MPA using the same gear. This allows the use of CPUE as an indicator of population abundance of fish communities according to protection levels (Guidetti et al. 2010). This study showed that catches obtained by artisanal and recreational fishermen inside the PPA and outside these areas were consistently different. On average, catches were quantitatively higher in PPA relative to GP and OUT. This effect has been described previously and was consistent with the results of previous studies, which show a higher increase in the biomass and density of common dentex inside the MPAs than outside them (Guidetti et al. 2010; Forcada et al. 2010). There is a body of evidence suggesting that the differences observed between average CPUEs

inside and outside the MPA are likely due to different fishery managements (Guidetti et al. 2010). The higher trophic levels tend to show greater responses to protection, likely because higher predators tend to be targeted by fisheries (Lester et al. 2009). Other factors can explain a substantial proportion of the variation observed in the abundance of fish species such as habitat structure (Lizaso et al. 2000; Miller and Russ 2014; Harasti et al. 2014). In this case, two main hypotheses could explain the high catch rates of common dentex in the PPA: (i) the banning of spearfishing in the PPA and (ii) the “refuge effect”.

Firstly, Rocklin *et al.* (2011) demonstrated in the BSNR that spearfishing can modify species assemblage structure. The dramatic effects of spearfishing on some of these species have been well established (Coll et al. 2004). Secondly, one of the most important benefits to marine coastal species is that MPAs can act as refuges into which fish move to escape fishing (Lester et al. 2009). The common dentex is one of those species that benefit from this protection measure, as it is especially targeted by both recreational and artisanal fishing. The trophic balance of an aquatic ecosystem can be disrupted by the direct and indirect effects of commercial and recreational fishing (Cooke and Cowx 2006). Depending on role and dominance within the ecosystem, the removal of a substantial part of a population can significantly affect the trophic process and the community structure (Lewin et al. 2006). Cascade processes concern interconnected changes in predation interactions involving keystone species at different trophic levels, which are induced by modifications affecting the identity or the activity rate of top-predators (Francour et al. 2001). The abatement of their stocks in overfished areas and, conversely, their replenishment in protected areas may thus trigger cascade processes (Steneck 1998). In Port de la Selva (Spain), the proportion of a top predator such as *Dentex dentex* in total landings increased after the establishment of the MPA to the detriment of *Octopus vulgaris* (Cuvier, 1797), *Diplodus sargus* (Linnaeus, 1758), *Scorpaena sp* (Linnaeus, 1758), and *Palinurus elephas* (Fabricius, 1787) (Gomez et al. 2006). For example, in the Bonifacio straits (France) the significant decrease of *Serranus cabrilla* (Linnaeus, 1758) could be explained by the significant increase of *D. dentex* (Rocklin *et al.* 2011). The explanation for this difference was based on increased predation within the reserve due to a number of larger predators such as *Dentex dentex* (Francour et al. 2010). Such a trend is generally not expected after the implementation of an MPA, but can be explained by trophic interactions between species through the top-down effect, by which an increase of predators would lead to a decrease of its preys (Pinnegar et al. 2000; Seytre and Francour 2008). However, the role of these keystone species is fundamental to ecosystem functioning and their protection is an insurance against the erosion of functional diversity (Sergio et al. 2008).

The recreational fishing modalities considered in this study catch around 3.4 tons of common dentex per year, which is equivalent to 58% of the artisanal fishery production in the MPA

(artisanal fisheries catch 5.8 tons.year⁻¹ of common dentex). The comparison of recreational catch estimates from this study with artisanal catch estimates of common dentex in the MPA suggests that recreational fishing (i) contributes significantly to fishing mortality, (ii) and it can exacerbate the magnitude of the negative effects of artisanal fisheries on the common dentex. However, it is noteworthy that the recreational and artisanal fishing catches reported in this study were probably underestimates. Recreational catches have a degree of imprecision due to the constraints associated with onsite survey methods (Lockwood 2000), and discards and illegal catches were not estimated in this study.

It is becoming increasingly apparent that recreational fishing is contributing significantly to the total fishing mortality of some species in certain regions (Coleman et al. 2004).

Other studies have also shown that recreational fishing can represent a significant part of total landings (Cooke and Cowx 2004). Overall, recreational fishing's share of total catches ranges by as much as 10% to 50% of the total commercial fishing catch (European Commission 2004; Morales-Nin et al. 2005; Lloret and Font 2013). However, for specific species recreational catches may often be equal to, or exceed, commercial catches (Zischke et al. 2012).

This activity may challenge the sustainability of artisanal fisheries sharing the same areas and the same resources (Rocklin et al. 2011). Within the BSNR, artisanal and recreational fishing activities generate combined pressure on the ecosystem (Albouy et al. 2010). Although rarely considered to be an important factor, the result of recreational fishing has the potential to produce effects that parallel those of commercial fisheries (e.g., reduced stock size, decreasing mean size, genetic changes, ecosystem level changes and habitat degradation) (Cooke and Cowx 2006).

D. dentex is a vulnerable species included on the red list of the IUCN and also a highly important target of artisanal fishing and recreational boat fishing in the BSNR. The data collected and the results presented in this study make a significant contribution to knowledge on several aspects of the artisanal and recreational fishing of common dentex in the Mediterranean, providing an overview of the pressure levels and catches arising from these practices. In this work, we showed that the common dentex was favored by protection measures in Western Mediterranean MPAs. In brief, MPAs are an essential tool for protecting overexploited populations and threatened species (Hackradt et al. 2014). Managers of the BNSR predict an increase in recreational fishing activities while the fishing effort from artisanal fisheries may stabilize (Albouy et al. 2010). Considering the effect of recreational fishing, it seems important to formulate new regulation policies for recreational activities (Albouy et al. 2010). It should be noted that since June 2012, new management tools have been tested by managers within the BSNR to limit the impact of recreational fishing (e.g. daily bag limitations, the restriction of recreational fishing in the PPA).

For the common dentex in the BSNR, managers should consider the implementation of specific measures to safeguard its reproductive potential, such as the establishment of Minimum landing sizes (MLS). It is essential to adjust MLS values so that they are larger than size at maturity, especially for the most vulnerable species (Font and Lloret 2014). Based on the size at first maturity and life history traits of the common dentex (Morales-Nin and Moranta 1997), it would be necessary to establish an MLS of 40 cm.

Common efforts devoted to educating fishers would be also necessary, especially to develop the practice of “catch-and-release”. Unlike in other parts of the world where catch and release is common practice (Cooke and Cowx 2004, 2006), it is not widespread in the Mediterranean. Fish mortality after catch-and-release is an essential element to evaluate in order to adapt fishing regulations; however, it is highly dependent on variables such as the species considered, the gear used (Bartholomew and Bohnsack 2005) and seawater temperature (Gale et al. 2013). Thus, it is recommended that the factors influencing the post-release mortality of released fish be studied to allow accounting for post-release mortalities when estimating fishing mortalities and to assist in the development of best-practice guidelines (Ferber et al. 2013).

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Chapitre V

Comparison of otolith and scale readings for age and growth estimation of *Dentex dentex*

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The common dentex, *Dentex dentex* L. 1758, is a Mediterranean and Atlantic species (Marengo et al., 2014). This demersal sparid fish (0-200m) may reach a maximum total length (TL) of 100 cm and a weight of 13 kg (Ramos Esplà and Bayle-Sempere, 1991; Morales-Nin and Moranta, 1997), with a relatively long lifespan over 20 years (Marengo et al. 2014). It is classified by the International Union for the Conservation of Nature (IUCN) as “Vulnerable” (Carpenter and Russell, 2014). Despite its conservation status, economic value and ecological importance, there is currently poor information about its demography. Machias et al. (2002) performed age validation on scales and whole otoliths of common dentex of known age up to four years old from aquaculture. Morales-Nin and Moranta (1997) and Chemmam-Abdelkader et al. (2004) studied age and growth of *Dentex dentex*, however using the two different structures, *i.e.* whole otoliths and scales respectively. Unfortunately, no study really assessed the precision of the age estimation between structures and preparation. In this study, three methods of age estimation were compared for *D. dentex*: scales, whole otoliths and sectioned otoliths.

A total of 224 common dentex ranging from 15 to 91 cm TL were obtained from commercial, recreational fishing activity and scientific monitoring in 2012 and 2013 from several sampling areas around Corsica (France). Both scales and otoliths were collected from 104 individuals, and scales only were collected from 120 other individuals. At least four scales were removed from the area under the pectoral fin on each side, where regeneration is less frequent and leaves few visible traces for fish marketing. They were cleaned with sodium peroxide to remove any remaining traces of organic matter (Panfili et al., 2002) then placed between two glass slides for observation using a stereomicroscope (Zeiss Discovery.V20) connected to a camera (Sony XCD-U100CR) and to a computer equipped with TNPC 7.0 software. The readings were carried out twice by the main reader and independently by a second reader on a sub-sample of 50%. The second readings of the main reader were kept after comparison with the second reader on the subsample estimated. These estimations were consistent with those of the second reader and were therefore considered the most accurate.

Regarding otoliths, age estimation was first performed on the whole otolith. The left sagitta was immersed in glycerol to highlight the growth increments on the distal face (Abecasis et al., 2008 ; Cengiz et al., 2013) and observed under reflected white light against a dark background with a compound stereoscope. Otolith growth increments were counted from the nucleus towards the pararostrum end, twice by the main reader and once by a second reader, independently. As estimations were different for 18% of the samples, the two readers made a fourth common reading. Afterwards, the otoliths were embedded in clear epoxy resin (Araldite 2020) and cross-sectioned. The sections were stained with toluidine blue 5% to improve the visibility of annual rings. The sectioned otoliths were read under a microscope (Olympus BX53) connected to a camera (Olympus PEN Lite E-PL3). Readings were

performed in the same way as for whole otoliths by the same persons, and a fourth common reading was carried out and used for subsequent analysis. Finally, after discarding illegible structures, ages of sliced otoliths and scales were compared for 90 specimens and ages of sliced and whole otoliths were compared for 93 specimens.

Specimens' length distribution ranged in size from 15 to 91 cm for scales sampling, and from 18 to 91 cm for otoliths sampling. With scales, the age of the common dentex studied ranged from 0 to 16 years old. The range was larger with whole otoliths, from 0 to 28 years old. Finally, the sectioned otoliths presented a wide age range: age class 0 to 36 years old.

Otolith age determination is thought to be more accurate because, unlike scales, otoliths have a higher priority in the utilization of calcium (Carlander, 1987) and continue to grow as the fish ages (Beamish and McFarlane, 1983). They are almost never resorbed, except under conditions of extreme stress, so all the growth marks recorded are preserved (Panfili et al., 2002). As the fish gets older, otoliths thicken and become more opaque, thus sectioned otoliths often ensure better age estimation for old specimens (Dwyer, 2003; Brouwer and Griffiths, 2004; Stransky et al., 2005; Paul and Horn, 2009; Matić-Skoko et al., 2011). Assuming that age determination on sliced otoliths was the most reliable method, these age estimations were compared to scales and whole otoliths respectively with a Student's t-test for paired samples followed by the McNemar test of symmetry (Hoenig et al., 1995; Evans and Hoenig, 1998). Significant differences were detected between age estimations from scales and sectioned otoliths (Student's t-test, $t_{89} = 4.950$, $p < 0.001$) with significant asymmetry (McNemar test, $Kh^2_1 = 32.36$, $p < 0.001$), starting from 6 years (Fig. 1).

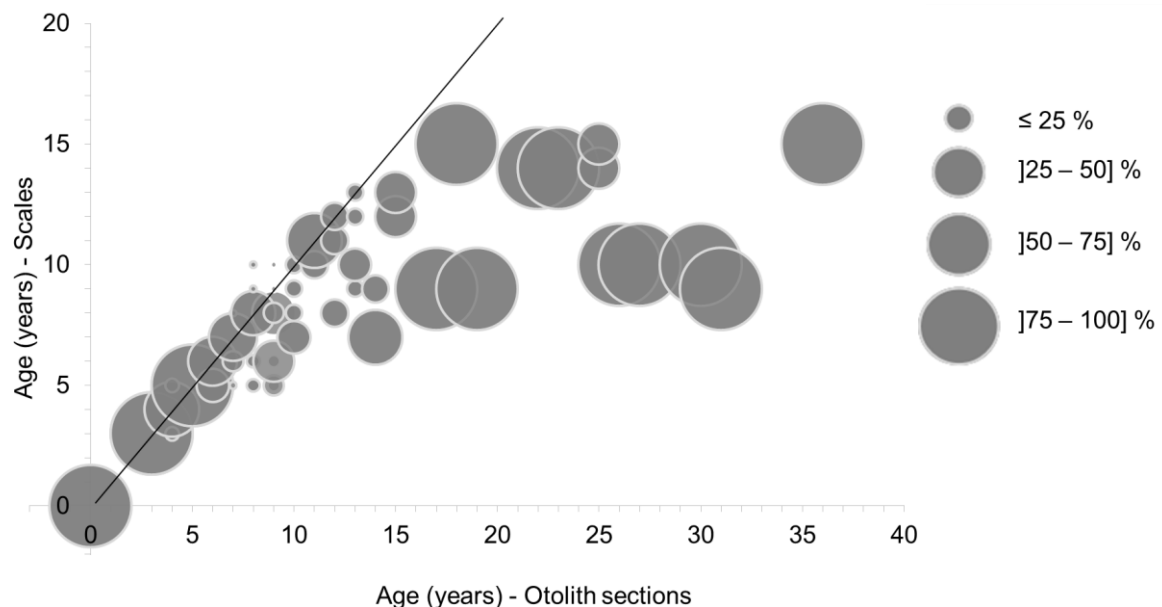


Fig. 1 Symmetry of ages determined from sectioned otoliths and scales of *D. dentex* collected around Corsica in 2012 and 2013 ($n = 90$). Circles are proportional to the percentages of the specimens classified for the estimated age considered.

There was an underestimation of ages determined from scales. There was also a significant difference between age estimations from whole and sectioned otoliths (Student's t-test, $t_{92} = -3.250$, $p < 0.01$) with significant asymmetry (McNemar test, $Khp_1 = 15.125$, $p < 0.001$) starting from 13 years (Fig. 2), showing an underestimation of ages determined from whole otoliths.

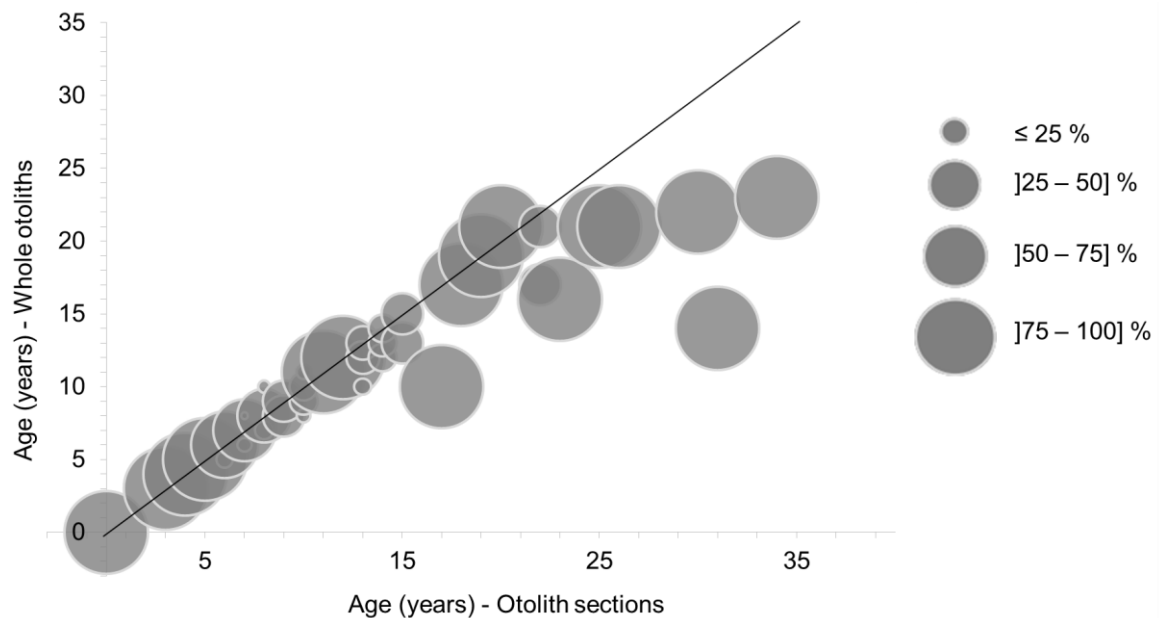


Fig. 2 Symmetry of ages determined from sectioned otoliths and whole otoliths of *D. dentex* collected around Corsica in 2012 and 2013 ($n = 93$). Circles are proportional to the percentages of the specimens classified for the estimated age considered.

The Von Bertalanffy growth equation $TL_t = TL_{\infty} (1 - \exp(-k(t-t_0)))$ was fitted using the estimated ages in relation to the total length (where t is time, TL_t is total length, k is the growth rate and TL_{∞} is the asymptotic length at which growth is zero and t_0 age at which the organisms would have had zero size). The growth equation was obtained from the total sample with a limitation for ages determined from scales to five years (according to previous findings; $n = 194$). The growth parameters estimated for all common dentex around Corsica were $TL_{\infty} = 81.203$, $k = 0.147$ and $t_0 = -2.369$ (Fig. 3).

The present study is the first to use different methods to assess the quality of ageing information according to the calcified structure chosen for common dentex (see Fig. 4. for illustration). The analyses demonstrated that scale reading is reliable up to five years only. Morales-Nin and Moranta (1997) mentioned previously that the scales of specimens older than five years were illegible for age reading on account of the poor definition of the annual rings and the abundance of false rings. Thus it strongly calls into question the previous findings based on scales by Culioli (1986) and Chemmam-Abdelkader (2004) in terms of age

estimation. Estimating ages using otoliths is generally much more accurate (Stransky et al., 2005; Abecasis et al., 2008; Matić-Skoko et al., 2011). Moreover, the use of sectioned otoliths substantially improves the readability of *annuli* since a specimen of 36 years old was identified, making it the oldest known common dentex. According to structural comparisons, it appears that whole otoliths allow good age estimation up to 12 years old (for a size of about 71 cm). Age estimation with whole otoliths for *D. dentex* was used by Morales-Nin and Moranta (1997) with a maximum age assessed at 28 years for the Balearic Islands. In the present study, otolith sections revealed many older individuals than had appeared with previous whole otolith readings. The main difficulty for this structure resides in the opacity of older otoliths and their crystallization, which substantially limits reading of the otolith. Therefore, sectioned otoliths appear to be the most accurate approach for fish age estimation throughout the lifespan of the species.

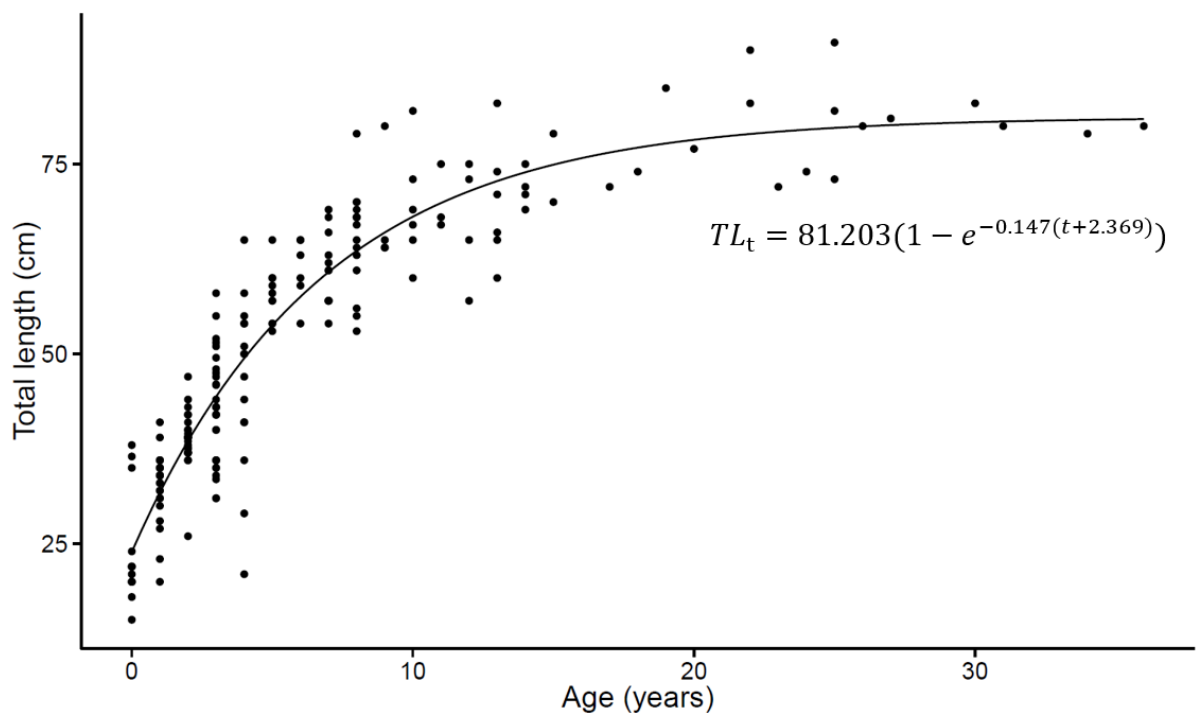


Fig. 3 Illustration of the three reading methods and age estimations for the same specimen of *D. dentex* ($TL = 72$ cm). The white points represent the *annuli*. (a) Scale, 13 years old, magnification 6.5x; (b) Whole otolith, 16 years old, magnification 6.5x and (c) Stained sliced otolith, 23 years old, magnification 40x.

The growth curve of common dentex from Corsica helped to define its growth parameters, which could be compared to those already published for this species in other areas of the Mediterranean Sea. Asymptotic length was similar to that found in the Balearic Islands by Morales-Nin and Moranta (1997) ($L_t^\infty = 84.4$ cm for males and 85.6 cm for females) computed from whole otoliths, but lower than that computed by Chemmam-Abdelkader et al.

(2004) in Tunisia ($L_t^\infty = 96.8$ cm) and even much lower than that calculated by Culioli (1986), near Calvi (Corsica, France – $L_t^\infty = 110$ cm). The growth rate was very high compared to that calculated for Calvi ($k = 0.077$), the Tunisian coast ($k = 0.073$) and for the Balearic Islands ($k = 0.100$ for males and $k = 0.102$ for females). The comparison must be considered with caution because age estimation in previous studies were based either on scales (Culioli 1986; Chemmam-Abdelkader et al., 2004) or on whole otoliths (Morales-Nin and Moranta 1997), which provided inconsistent estimation throughout the lifespan of this species. However, these studies would have had the tendency to under-estimate age and therefore over-estimate growth. Differences between all the estimated parameters could be attributed to several factors such as: (i) sampling locations, (ii) types of sampling gear, (iii) difference in age groups applied to fit the growth function, (iv) difference in genetic structure or/and (v) in temperature, density of food and diseases (Duan et al., 2014). The growth of the Corsican common dentex seems quite fast but it is still slow compared to the maximum potential reached by the species in aquaculture ($k = 0.507$, Machias et al., 2002). Overall, growth estimation for common dentex around Corsica could serve as a reference for future work on population dynamics for this species.



Fig. 4 Illustration of the three reading methods and age estimations for the same specimen of *D. dentex* ($TL = 72$ cm). The white points represent the *annuli*. (a) Scale, 13 years old, magnification 6.5x; (b) Whole otolith, 16 years old, magnification 6.5x and (c) Stained sliced otolith, 23 years old, magnification 40x.

The maximum estimated age of 36 years found for *D. dentex* in this study using state of the art technique based on sectioned otoliths extends the estimated life span of the species beyond the maximum of 33 years mentioned in previous reports using scales (Chemmam-Abdelkader et al., 2004), and confirms that it can be considered as a relatively long-lived species. To conclude, scales appear suitable for estimating age between 0 and 5 years old. Beyond this age, whole otoliths can be used up to 12 years. Finally, sectioned otoliths are the most accurate and reliable structure for all age ranges.

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Chapitre VI

Combining microsatellite, otolith shape and parasites community data as a holistic approach to assess population structure of *Dentex dentex* around Corsica Island

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VI.1 Introduction

The stock structure identification of exploited fish species is fundamental to fisheries management and provides the basis for the determination of appropriate spatial management units (Begg and Waldman 1999). The term 'stock' referring as a population unit of a single species has several meanings. Some authors consider a stock to be an ecological unit (Marques et al. 2006), and some an evolutionarily significant unit (Waples 1991). A stock can be defined as a spatially distinct group of marine organisms exhibiting no significant mixing with neighbouring individuals, being essentially self-reproducing and having similar life-history characteristics (Lester and MacKenzie 2009; Charters et al. 2010). Fish stocks can, however, show varying degrees of mixing with other stocks, which can complicate the identification of discrete sub-units of the population or metapopulation (Stephenson 1999). In a marine context, a metapopulation is in fact a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals (Kritzer and Sale 2004).

Many methods have been used to identify and discriminate stocks: life history (e.g. growth, reproduction), natural markers (body and otolith morphometrics, meristics, genetics, parasites, otolith elemental composition, and fatty acid profiles), and applied marks (internal and external tags, electronic tags, and otolith thermal marking) (Cadrin et al. 2013). There has been a recent shift in fisheries research towards using combinations of these complementary stock identification techniques, known as "a holistic approach". From an operational perspective a holistic approach can be defined as one that utilizes multiple techniques for fish stock identification, in a single study on the same samples (Begg and Waldman 1999). Using more than one technique, however, greatly increases the likelihood of detecting different stocks where they exist (Abaunza et al. 2008). It also gives greater certainty where the evidence supporting the hypothesis of more than one stock is insufficient (i.e. there is a spatially homogeneous or single stock present). Analysis of stock structure is also more effective when several techniques are used because of the different temporal, spatial and evolutionary scales addressed by each method (Welch et al. 2015). In these cases, it is possible to expect that applying all the techniques on the same specimen would facilitate the interpretation of the results and comparison of the performance of the different techniques (Waldman et al. 1997). Adopting a multidisciplinary approach combining genetic markers with biological characteristics is therefore recommended in the context of fishery stock management (Cadrin et al. 2013).

Among all available techniques, genetic methods have been long recognized for their usefulness in defining stock structure of fish (Ward 2000a). In genetic approaches to stock

delineation, microsatellite DNA markers, due to their high levels of variation and large numbers of alleles, provide great resolution for identifying population structure (O'reilly and Wright 1995). Genetic variation between stocks can provide a direct basis for stock structure but can prove inadequate where low and inconsistent levels of differentiation may still mask a high degree of demographic separation between stocks (Ward 2000a; Mariani et al. 2005). This situation often translates into populations presenting low genetic differences at neutral loci, but significant differences for other biological characteristics that are labile on a shorter timescale (e.g. morphology, parasite load, otolith elemental composition) and have yielded better small-scale resolution (Ihssen et al. 1981; Valentin et al. 2014). These biological characteristics might reflect adaptive differentiation and biocomplexity, thus revealing population structure (Cadrin 2000; Conover et al. 2006; Hauser and Carvalho 2008).

Otolith morphology has been proven to be relevant feature for stock identification issues (Campana and Casselman 1993; Stransky 2005; Cañás et al. 2012; Sadighzadeh et al. 2014). Otolith shape is species-specific, and the gross morphology can often vary geographically within a species (intra-specific variation) (Campana and Casselman 1993; Lombarte and Leonart 1993). In particular, variability in the sagitta otolith shape has been shown to be attributable to ontogenetic, genetic and environmental influences (e.g. depth, water temperature, salinity, diet regime, substrate type) (L'Abée-Lund 1988; Lombarte and Leonart 1993; Cardinale et al. 2004; Vignon and Morat 2010). Thus, otolith morphometry can be considered as a natural mark and can be used as an indirect way to infer connectivity among fish stocks that occupy distinct geographical regions (Calò et al. 2013).

Among natural tags, parasites have an extensive history of use in fish population studies (Boje et al. 1997; Moore et al. 2003; Timi et al. 2008; Durieux et al. 2010; Hermida et al. 2013). The use of parasites as biological tags presents a promising alternative approach that has been used in the identification of discrete fish stocks (MacKenzie 2002). The basic principle underlying the use of parasites as tags is that fish can become infected with a parasite only when they come within the area suitable for the transmission of that specific parasite (MacKenzie and Abaunza 2005). The ability to differentiate stocks on the basis of their parasites reflects the variations in ecological and environmental conditions in the regions that the hosts inhabit, resulting in non-uniform distributions and abundances of the parasites final and intermediate hosts (MacKenzie et al. 2013). The common dentex *Dentex dentex* (Linnaeus, 1758) is an iconic marine coastal fish of the Mediterranean Sea. The species is a demersal sparid fish (0–200 m), that grows to a maximum length of 100 cm and a weight of 13 kg, with a relatively long life span (more than 20 years) (Morales-Nin and Moranta 1997). It inhabits the Mediterranean Sea most frequently south of 40°, is found occasionally in the Black Sea, and occurs in the Atlantic Ocean (occasionally around the British Isles), and also Cape Blanc, the Bay of Biscay, Madeira, the Canary Islands and

southward to Senegal (Morales-Nin and Moranta 1997; Bat et al. 2005). Due to its large size, flesh quality, and high commercial value, the species is of great economic interest for both artisanal and recreational fisheries (Marengo et al. 2014b). *D.dentex* is classified by the International Union for the Conservation of Nature (IUCN) as “vulnerable” in the Red List of Threatened Species (Carpenter and Russell, 2014). Overexploitation and eutrophication are considered among the major threats identified by IUCN in parts of its range. Despite its economic and ecological importance, data on the population structure of this species are still very limited. For *D. dentex*, mitochondrial DNA and allozymes revealed a higher degree of genetic differentiation between the Atlantic and Mediterranean individuals (Bargelloni et al. 2003). Evidencing for a sharp phylogeographic break between the Atlantic and the Mediterranean populations (Bargelloni et al. 2003). However, there is a severe lack of information on population structure, requiring further studies at a smaller spatial resolution and using more accurate molecular markers (e.g. microsatellites).

The aim of this study was to identify the stock structure of the common dentex around Corsica Island, using a combination of markers that have different spatial and temporal scales of integration: microsatellite DNA markers, otolith shape analysis and parasites communities.

VI.2 Materials and methods

VI.2.1 Sample collection

The common dentex were collected from the local artisanal and recreational fisheries, mostly captured by gill net, long line and trolling between October 2012 and May 2013. Total length (TL, cm) and total weight (W, g) were measured for all fish sampled. A total of 77 specimens of *D.dentex* were sampled in coastal waters of the Corsica Island (NW Mediterranean Sea) in four localities: Ajaccio (n=6), Bonifacio (n=27) Cap Corse (n=18), Galeria (n=26), (Fig. 1). In this study, the analyses were carried out on the same individuals of *D.dentex* for microsatellites, otoliths shape and parasites communities analyses.

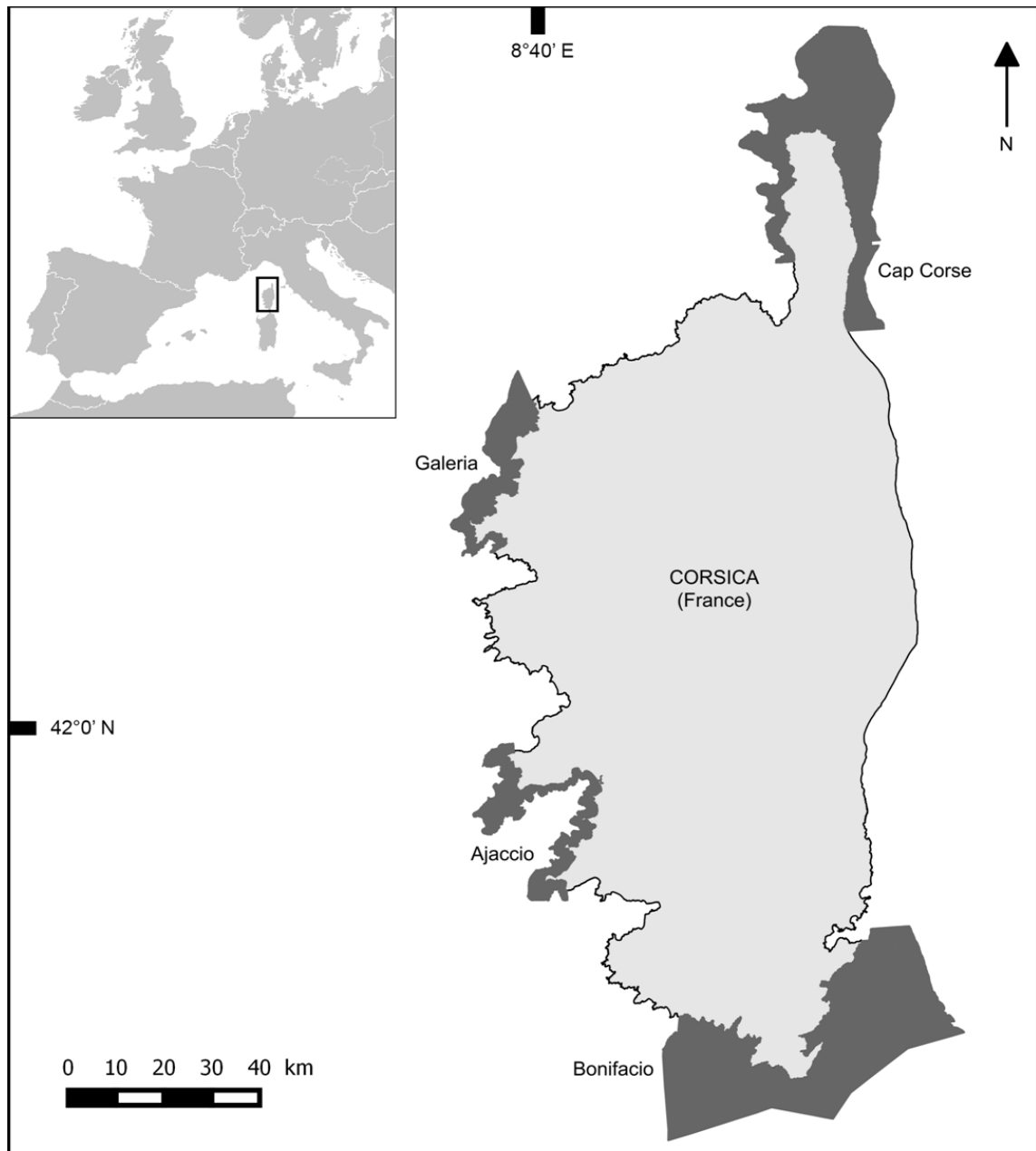


Fig.1 A map of Corsica Island, North Western Mediterranean, France, showing the four sample areas for *Dentex dentex*: Ajaccio; Bonifacio; Cap Corse and Galeria.

VI.2.2 DNA extraction and amplification

DNA was extracted from fins in ethanol following the Chelex protocol (Walsh et al. 1991). Six microsatellite loci were selected for the study, previously isolated from different Sparidae species (Table 1) (Batargias et al. 1999; De la Herrán et al. 2005). Polymerase chain reaction (PCR) was performed under the following conditions: preheating at 95° C for 5 min, followed by 35 cycles of denaturing (95 °C, 45 s), hybridization (primer melting temperature or T_m, 45 s indicated in Table 1) and elongation at 72° C for 30 s. The PCR

ended with a final polymerization for 5 min at 72° C. Amplifications were carried out in a total reaction volume of 10 µl containing 1× buffer, MgCl₂ 1,5-2 mM, DNA polymerase buffer 0,2 mM dNTP, 0,5 µM of each primer, 0,03 U Taq DNA polymerase and DNA extract (Table 1). The samples plates were preserved in a refrigerator (+4°C) until their introduction in the acrylamide gel.

Table 1 Microsatellite loci for *Dentex dentex*, including size range of alleles (base pairs), cloned sequence repeat motif, primer sequence (Forward primer listed above Reverse), MgCl₂, Tm primer melting temperature.

Locus	Size (bp)	Sequence	Amorce Forward (5'-3')	MgCl ₂ (mM)	Tm (°C)	Reference
Ds24	239-243	(GT) ₁₇	GGAGCCGGTGGGAAGAGTTAC GACGTGAAGGGTGAACACG	1.5	61	De la Herrán et al., 2005
Ds33	204-216	(GT) ₁₇ C(GT) ₂	AGAGTTCTCCAACCCAGAGC GGAGTAATGTGCGGGTAGATG	1.5	61	De la Herrán et al., 2005
Dxd11	235-295	(CA) ₆ GC(CA) ₁₂	CCAGAAAGGAGTGTGTAGAA TGAGAGAAAGAGCAGGAAT	2.0	60	De la Herrán et al., 2005
Dxd16	111-129	(GT) ₁₅ (GA) ₁₈	TGCTCTGTACTTTTCCCCTTG ACCGTACACCCATTACTGGAC	2.0	56	De la Herrán et al., 2005
Dxd21	267-281	(AC) ₁₄	CTCCCAGGATTGACAGACAG ACCAAGACCCACACAGGAC	2.0	58	De la Herrán et al., 2005
SaGT41b	148-192	(GT) ₆ AT ₃ (GT) ₂	GGAGGCACTTGCAAGTGCAG AGATGGCAGAGGTCTGGTAG	1.5	61	Batargias et al., 1991

VI.2.3 Genotyping

The PCR products were electrophoresed in 6% denaturing polyacrylamide gels (Bio-Rad, Marnes-le-Coquette, France) and visualized with a FMBIO-II fluorescent imaging system (Hitachi, Yokohama, Japan). Allele sizes were based on a fluorescently labeled ladder 100–600 bp (Promega, Madison, WI, USA) and the fluorescence of the fluorochrome carried by the F primer. The software FMBIO® Image Analysis 8.0 analyzer was used to measure the size of the different alleles and thus define the genotypes of each individual.

VI.2.4 Microsatellites statistical analysis

Polymorphism within the samples was evaluated from the unbiased expected heterozygosity (Nei 1978). Deviations from the Hardy–Weinberg equilibrium were examined for each population at each locus by calculating the fixation index F_{is} tested by 1000 permutations with the software GENETIX. The null hypothesis of independence between loci (no linkage disequilibrium) was tested using the same software. Levels of genetic differentiation between all sampling sites were analysed by calculating Wright's pairwise F_{st} statistics with software GENETIX tested by 5000 permutations of genotypes among samples (Weir and Cockerham 1984). The Bayesian clustering analysis implemented in the program STRUCTURE was used to identify the number of clusters, K (from a range of 1–4), with the highest posterior probability. Ten replicates were performed (STRUCTURE parameters: 100,000 burn-in) for $K = 1$ to $K = 4$ genetic clusters. The software tests the clusters and calculates the percentage of each individual belonging to different clusters. The optimal model (i.e. number of genetic clusters) was identified by the lowest associated Bayesian information criterion (BIC) for models of $K = 1$ –4. The most likely number of genetic groups was estimated using the Evanno et al. (2005) method through STRUCTURE HARVESTER (Earl and von Holdt 2012). The Discriminant Analysis of Principal Components (DAPC) is designed to investigate the genetic structure of biological populations optimizing the separation of individuals into predefined groups. This multivariate method consists in a two-steps procedure. First, genetic data are transformed (centred, possibly scaled) and submitted to a Principal Component Analysis (PCA). Second, principal components of PCA are submitted to a Linear Discriminant Analysis (LDA). Based on the retained discriminant functions, it is possible to derive group membership probabilities, which can be interpreted in order to assess how clear-cut or admixed the clusters are (Jombart et al. 2010). The datasets were analysed by DAPC using the *adegenet* package for the R software. The Mantel test was used to test correlation between genetic distances, expressed as Cavalli-Sforza chord distances as metrics, and geographic distance, expressed as km using 10 000 randomizations, using XLSTAT software (Addinsoft, TM). The shortest distance between sites was estimated using Google Earth 7.1.

VI.2.5 Image acquisition and otoliths shape analysis

Sagittal otoliths were removed, cleaned of membranes and tissues and stored dry. When possible, right otoliths were used for shape analysis, otherwise left one were used instead. A total of 72 right otoliths and 5 left otoliths were used in this study. A digitization of the otoliths was performed to obtain the morphological data, using a Canon® (EOS 7D)

attached to a Zeiss® (KL 200 LED) Stereomicroscope. Right otoliths were placed convex side up, positioned *sulcus* facing downwards with the rostrum pointing to the right (upwards) in a horizontal line under reflected light. Left otoliths were transposed accordingly for analysis.

Geometric morphometric was used to a direct comparison of shape differences. It focuses on the coordinates of biologically definable landmarks and the geometric information about their relative positions (Nasreddine et al. 2009). Geometric outline methods quantify boundary shapes so that patterns of shape variation within and among groups can be evaluated (Cadrin et al. 2013). Images were binarized (TNPC) and contour extraction was carried out using the image-analysis system TPS software.

The outline of each otolith was stored as pixel coordinates (X–Y coordinates) which were reduced to 50 points equally spaced (using contour length as a parameter) along the contour, the tip of the rostrum being taken as the origin (Monteiro et al. 2005; Ponton 2006; Vignon and Morat 2010). This reference point (biologically corresponding among individuals) is referred to as a landmark and the remaining 49 points as semi-landmarks (see Vignon and Morat 2010). Generalized orthogonal least square procrustes superimpositions of landmark and semi-landmark coordinates were then computed using Morpho-J, version 1.02d software (Klingenberg 2011). TpsRelw version 1.45, minimizing bending energy with respect to a mean reference form (Green 1996, Bookstein 1997) to determine the criteria for sliding semi-landmarks along outlines (Rohlf and Slice 1990). The shape differences between otoliths were estimated using the procrustes distances. Subsequent analyses were all performed on aligned (semi-)landmarks.

VI.2.6 Otolith statistical analysis

Multiple regressions were applied to test the influence of endogenic variables (TL and weight). It appeared that these two variables contribute significantly to otoliths shape variations (Goodall's F tests, $P < 0.05$). After weight-size adjustment analyses were carried out on the standard residuals. Otoliths were then geographically discriminated using a Quadratic Discriminant Function Analyses (QDFA) that, contrary to linear DFA, does not require homogeneity of within-group covariance matrices (Quinn and Keough 2002). The percentage of correctly classified individuals gives a measure of the morphological distinctness of the samples. This classification success into groups was tested by jack-knife cross-validation (the method of leaving-out-one case at time), and Wilks λ was used to evaluate the discrimination power.

An additional canonical variate analysis (CVA) was computed using MorphoJ. to maximally discriminate among groups (Weinberg et al. 2009). In the space defined by canonical variates, populations are arranged according to their morphological similarity; the more alike

two populations are, the shorter is the spatial distance between them (Linde et al. 2004). The statistical significance of pairwise differences in mean shapes was assessed with permutation tests using Procrustes distances as the test statistic (10 000 permutations per test). A Mantel test was used to test correlation between otoliths shape differences (using the Procrustes distances in tangent space as metrics), and geographic distance (expressed as km) using 10 000 randomizations.

VI.2.7 Parasite extraction and analysis

The viscera of the specimens were removed and stored frozen at -20°C until examination. After thawing, the viscera are best divided into key organs (pyloric caeca, middle intestine, posterior intestine and rectum) for examination. The dissections were carried out using standard parasitological techniques, the “Gut Wash” method (Cribb and Bray 2010). All organs were examined individually, washed with saline water and sieved through a 200 µm filter. All the material retained was inspected stereomicroscopically at x16 and x40. The parasites collected from each fish were sorted, counted, placed in Bouin's fluid and preserved in 70% ethanol and subsequently identified to the lowest taxonomic level possible, following taxonomic guides and original descriptions in the literature. When needed, parasites were colored using Carmin 40 and observed under light microscope for identification.

VI.2.8 Parasite statistical analysis

The parasitological indices of prevalence (the percentage of infected fish), mean abundance (the mean number of parasites per fish) and mean intensity (mean number of parasites per infected fish) were calculated in each sample (Bush et al. 1997). Because fish size can influence the abundance and composition of parasites, the TL was compared between locations by means of a Mann-Whitney U test.

Chi-square analysis (χ^2 test) was performed to test for the significance values of the differences in prevalence between zones. Kruskal-Wallis ANOVA (H) and a posteriori Dunn's test were used to analyze the effects of locality on abundance of each parasite species. Values of $P < 0.05$ were considered statistically significant. The natural logarithm of the parasite (x) plus one $\log(n + 1)$ was used to minimize the variance of the abundance data. These transformed data were used throughout the analyses. A Linear Discriminant Function Analysis (LDFA) based on Mahalanobis distances, was used to assess whether the site of capture of each *D.dentex* could be reliably determined from parasite assemblage abundance. The nematoda group has not been included for the discriminant analysis since

none was corresponding to several major criteria in choosing a parasite species as a biological tag. In order to qualify as an appropriate biological tag, parasite communities must be present with contrasted infection levels in the fish host within the study area, must remain in the host for long periods of time, and should not cause serious pathology or alter its host's behaviour (MacKenzie and Abaunza 1998). The classification success of the discriminant analysis was tested by jack-knifed cross-validation (the method of leaving-out-one case at time) and Wilks λ was used to evaluate the discrimination power. A Mantel test was used to test correlation between parasites abundance, expressed as Bray-Curtis distance as metrics (Poulin et al. 2011), and geographic distance, expressed as Km using 10 000 randomizations.

VI.2.9 Combination of microsatellite, otoliths shape and parasites communities markers

The Mantel test was used to test pairwise correlation between the matrices of: 1) genetic distances (Cavalli-Sforza chord distances) and otolith shapes (Procruste distances), 2) genetic distances and parasites abundance (Bray-Curtis distances), 3) otolith shapes and parasites abundance and 4) the three combined, genetic, otoliths and parasites. This test was done to assess the overall concordance between the markers datasets, in describing population structure. A non-metric Multidimensional Scaling (nMDS) (Kruskal 1964) was used to conduct multivariate analyses on genetic, morphometric and parasite. The analysis was performed with the SMACOF (Scaling by MAjorizing a COnvex Function) included in XLSTAT 2014 that minimizes the "Normalized Stress" (De Leeuw and Heiser 1980).

VI.3 Results

VI.3.1 Microsatellites

Tests for conformity to Hardy-Weinberg Equilibrium (HWE) was applied for multilocus and locus by locus by localities. It revealed a number of deviations, mainly due to deficits of heterozygotes and few excesses. It appears that the sites of Bonifacio and Galeria showed significant but moderate deviations relative to the HWE ($P < 0.05$), the multilocus heterozygote deficits were $F_{is} = 0.0717$ and 0.0691 , respectively (Table 2). The locus-by-locus analysis within Galeria sample indicated two significant deviations from HWE for loci Ds24 and Dxd16. These loci show a significant excess of homozygotes with $F_{is} = 0.3704$ for Ds24 ($P < 0.01$) and $F_{is} = 0.1935$ for Dxd16 ($P < 0.05$). The other two localities, Ajaccio and Cap Corse were in Hardy-Weinberg equilibrium with F_{is} values of 0.0186 and 0.0713 , respectively.

Table 2 Estimates of F_{is} for each sampled zones of *Dentex dentex* (Ajaccio, Bonifacio, Cap Corse, Galeria) by multi-locus and locus by locus; asterisks refer to values that were significant (* $p < 0.05$; ** $p < 0.01$).

F_{is}	Multi-locus	Ds24	Ds33	Dxd11	Dxd16	Dxd21	SaGT41b
Ajaccio	0,01861	-0,15385	0,48718	-0,14286	0,25926	-0,05263	-0,21951
Bonifacio	0,07178 *	0,13971	0,05282	0,05272	-0,04000	0,07787	0,18202
Cap Corse	0,07138	0,10660	0,17982	0,05882	0,11194	0,08197	-0,15104
Galeria	0,06915 *	0,37041**	-0,08324	0,01877	0,19355 *	-0,00654	-0,12202

Pairwise multilocus F_{st} revealed no significant genetic differentiation ($P > 0.001$). Pairwise F_{st} between samples were low and non significant, ranged from negative values (considered as null) to 0.0081 (Table 3). Genetic homogeneity was observed among the four localities. Pairwise F_{st} comparisons at individual loci suggested that there were significant differences ($P < 0.05$) between samples of Bonifacio and Galeria ($F_{st} = 0.0472$) at the Ds33 locus and between Cap Corse and Galeria at the SaGT41b locus ($F_{st} = 0.0007$). All pairwise F_{st} values were no significant ($P > 0.001$) in the others localities (Ajaccio, Bonifacio, Cap Corse) (data not shown).

Table 3 Estimates of pairwise comparisons of F_{st} by multi-locus for each *Dentex dentex* sampled zones (Ajaccio, Bonifacio, Cap Corse, Galeria).

F_{st}	Ajaccio	Bonifacio	Cap Corse	Galeria
Ajaccio	0	-0,01148	-0,01086	-0,00488
Bonifacio	-	0	-0,00502	0,00817
Cap Corse	-	-	0	0,00687
Galeria	-	-	-	0

The test of Evanno et al. (2005) was used to estimate the plateaus of log likelihood, detecting the best K (number of partitions/groups to consider in the analysis) in STRUCTURE assignment analysis. Assignment test performed using STRUCTURE software produced non-significant results since the partition was done inside each individual and not among them (Fig. 2). This is the definitive demonstration of the incapacity of STRUCTURE to find any cluster all around the island.

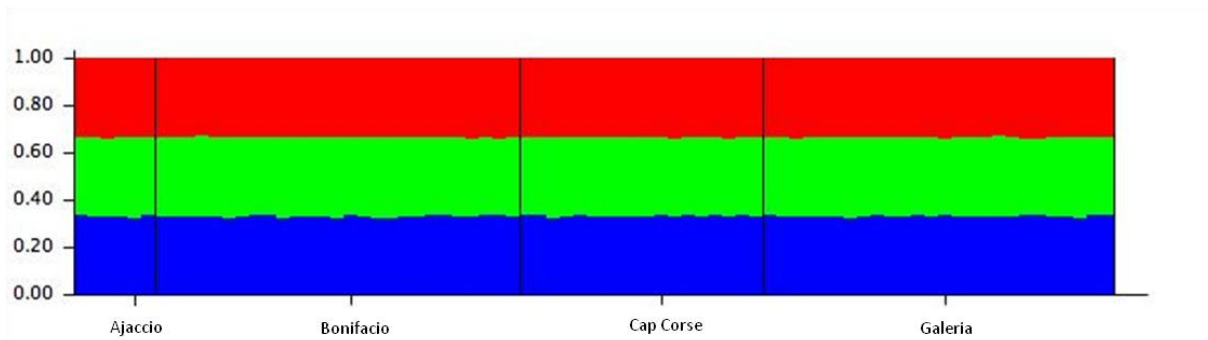


Fig.2 Bayesian cluster analysis using STRUCTURE with a K=3, estimated from the analysis of six microsatellite loci representing four *Dentex dentex* Corsican localities.

60 Principal Components were selected for the discriminant analysis. The curve of Bayesian Information Criterion (BIC) indicates a number of clusters of K=3. The principal components retained of the multivariate DAPC, explained 99.76% of the total variance. The three clusters comprised a mix of individuals belonging to the four localities (Fig. 3).

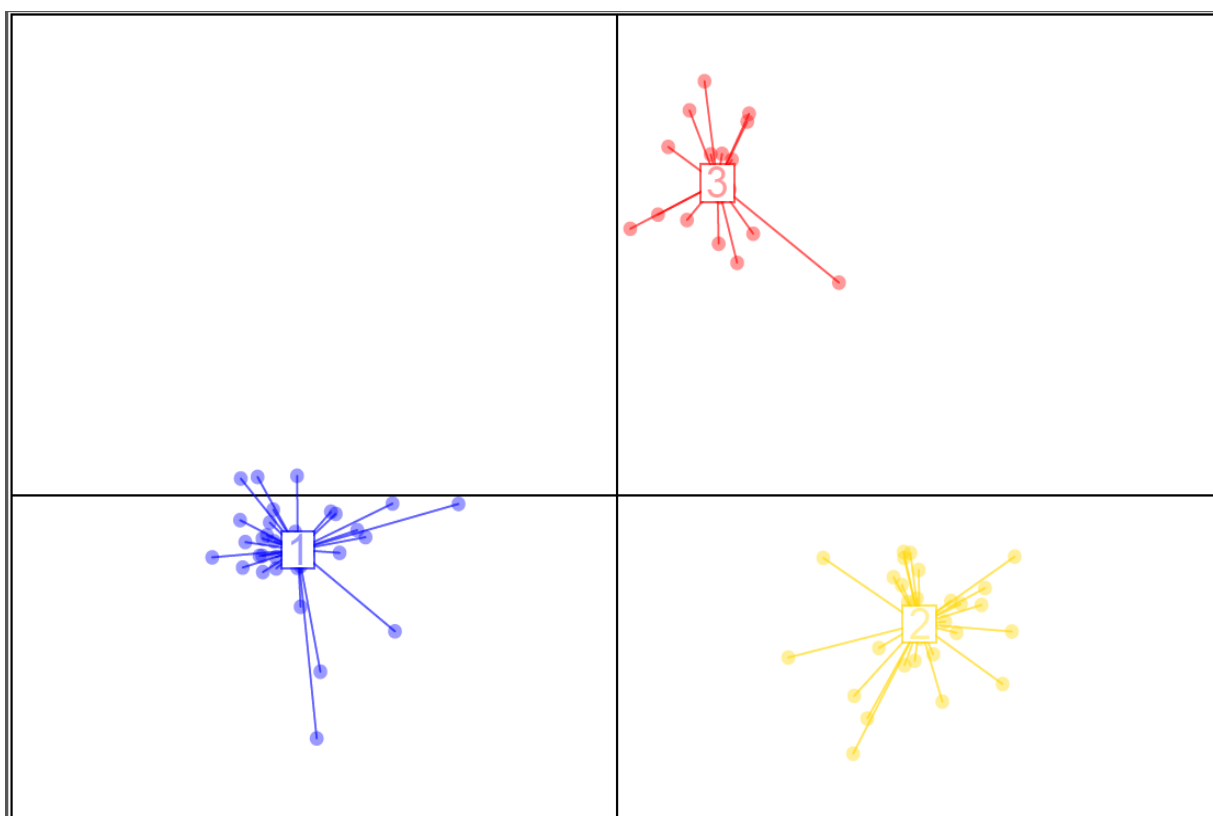


Fig.3 Scatterplots of DAPC for *Dentex dentex* sampled in Corsica Island, clusters are shown by different colours, while dots represent individuals, the lines connect individuals to the cluster center of gravity which they belong.

A high percentage of individuals from Ajaccio, Bonifacio and Cap Corse are assigned to the cluster 1 (66%, 52%, 45%, respectively) (Table 4). The cluster 2 comprised 50% of the individuals from Galeria and only 17%, 30%, 33% of the individuals from Ajaccio, Bonifacio and Cap Corse, respectively. The clusters 3 cannot be clearly associated with one or more localities. No significant correlation between genetic differentiation and geographic distance was revealed by a Mantel test ($P>0.05$) in the sampled locations.

Table 4 Classification success (%) of *Dentex dentex* specimens from Corsica Island based on microsatellites data used in DAPC. The percentage of individuals classified in each stock and the number of samples (in parentheses) are shown.

Zones\ Cluster	Cluster 1	Cluster 2	Cluster 3
Ajaccio	66% (4)	17% (1)	17% (1)
Bonifacio	52% (14)	30% (8)	18% (5)
Cap Corse	45% (8)	33% (6)	22% (4)
Galeria	23% (6)	50% (13)	27% (7)

VI.3.2 Otolith shape

The first two discriminant functions of the multivariate QDFA, explained 99% of the total variance. A significant overall group effect was observed ($Wilks \lambda = 8.11 \times 10^{-10}$, $p\text{-value} < 0.0001$). The corresponding confusion matrix is provided in Table 5 and exhibited an overall high (60%) probability of correct classification. The highest classification success was found for Bonifacio, 100% of samples were classified in the proper group. The proportions were lower for the others areas: 50%, 33%, 31% for Cap Corse, Ajaccio, Galeria, respectively. While individuals collected in Ajaccio and Cap Corse were generally misclassified to neighboring or proximate locations, those from the Galeria were classified as originating from the most distant locations. For example, 50% of the misclassified individuals collected in Galeria were classified as originating from the Bonifacio.

Table 5 Cross validation classification matrix of *Dentex dentex* specimens from Corsica Island based on otoliths shape used in Quadratic Discriminant Function Analyses. The percentage of individuals assigned to each locality and the number of samples (in parentheses) are shown.

Originated\ classified	Ajaccio	Bonifacio	Cap Corse	Galeria	% correct
Ajaccio	33% (2)	67% (4)	0% (0)	0% (0)	33%
Bonifacio	0% (0)	100% (27)	0% (0)	0% (0)	100%
Cap Corse	5% (1)	17% (3)	50% (9)	28% (5)	50%
Galeria	0% (0)	50% (13)	19% (5)	31% (8)	30%
Total	3	47	14	13	60%

The first two canonical axes of the CVA combined explained 77% of total variation (45%, 32%, respectively). To find the otolith morphotypes, samples were arranged according to their morphological similarity in a morphospace using the mean canonical scores of the two first CVA axes (Fig.4). All samples were classified correctly using the classification functions based on geometric morphometrics. The CVA scatter plot showed a differentiation associated with the origin of the individuals; supporting the existence at four morphotypes. However, Procrustes distances range from 0.023 (Cap Corse vs. Galeria) to 0.048 (Bonifacio vs. Ajaccio), and all permutation tests indicate that mean shapes did not differ significantly among areas (all $P > 0.05$ in pairwise permutation tests between areas). The consensus shape (average shape) and deformation grids obtained using the coordinates of the 50 (semi-)landmarks from each area are given in Fig. 4. There was some concordance in the morphological variation with respect to the origin of the group: the otoliths were arranged according to their zones for Cap Corse and Ajaccio.

A morphological convergence with some degree of similarity was observed in otoliths shape between Bonifacio and Galeria samples. The Bonifacio specimens share part of the morphospace with Galeria specimens as CVs slightly overlap. No significant correlation between otoliths shape and geographic distance was revealed by a Mantel test ($P > 0.05$) in the sampled locations.

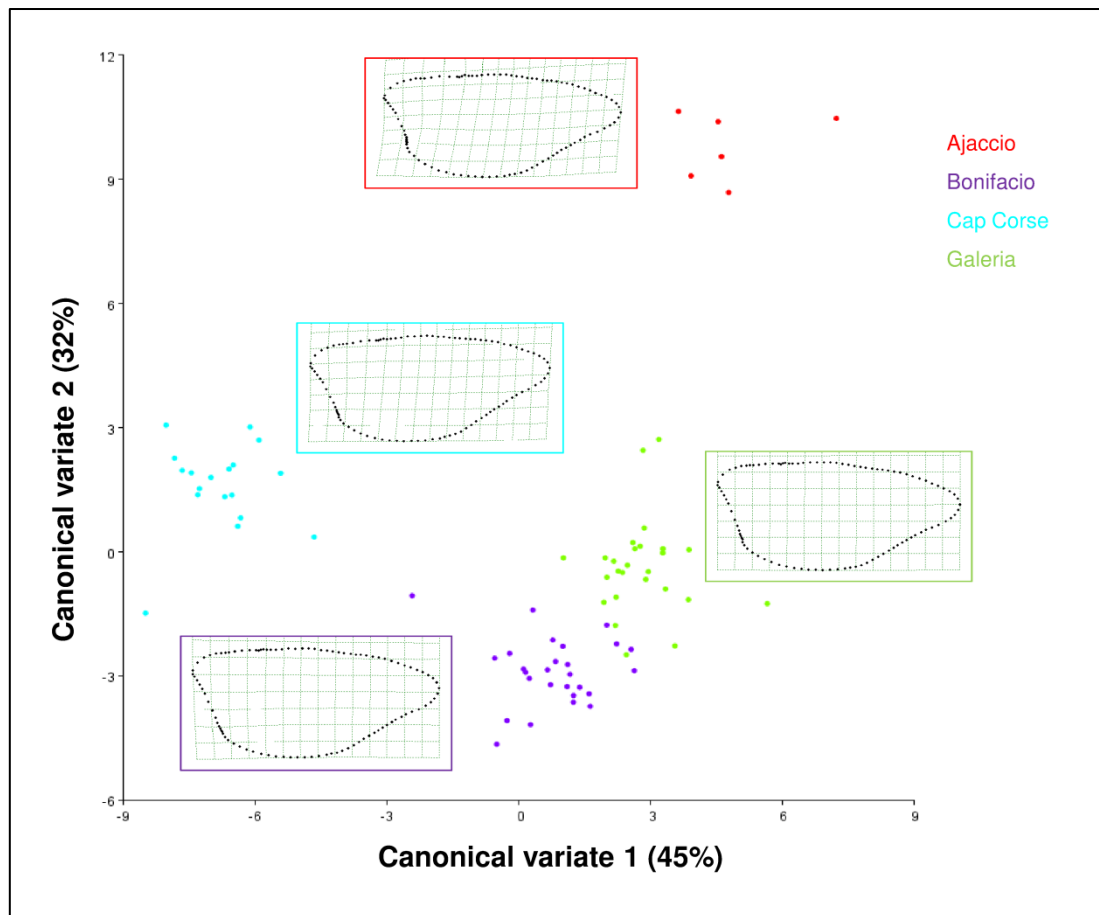


Fig.4 Canonical variate analysis on otoliths shape variables of specimens of *Dentex dentex* from Corsica Island. The transformation grids (thin-plate) show the shape changes from four localities (Ajaccio, Bonifacio, Cap Corse, Galeria) in Corsica Island.

VI.3.3 Parasite communities

4968 parasites were found in the total sample. No significant differences were found for *LT* between locations (Mann–Whitney U-test, $P > 0.05$). Parasite fauna diversity as well as prevalence, mean abundance and mean intensity values detected at each of the four localities, are given in Table 6.

Table 6 Prevalence (P) mean abundance (A) and mean intensity (I) of parasites (\pm SE) in samples of *Dentex dentex* in four zones of the Corsica Island.

Species	Ajaccio			Bonifacio			Cap Corse			Galeria		
	P (%)	A	I	P (%)	A	I	P (%)	A	I	P (%)	A	I
<i>Metadena depressa</i>	42.85	10.85 (\pm 8.20)	25.33 (\pm 16.97)	44.82	3.34 (\pm 1.43)	8.08 (\pm 3.01)	18.18	0,45 (\pm 0.23)	2.50 (\pm 0.64)	20	2,4 (\pm 1.86)	12 (\pm 8.83)
<i>Aphallus tubarium</i>	85.71	32.71 (\pm 12,47)	38.16 (\pm 13.27)	79.31	18.27 (\pm 4.84)	23.04 (\pm 7.60)	86.36	51.59 (\pm 16.3 5)	59.73 (\pm 18.2 7)	90	40.26 (\pm 8.90)	44.74 (\pm 9.51)
<i>Allopodocotyle Jaffensis</i>	71.42	7.42 (\pm 4,03)	10.4 (\pm 5.14)	10.34	0.31 (\pm 0.21)	3 (\pm 1.52)	31.81	2.27 (\pm 1.32)	7.14 (\pm 3.68)	10	0.26 (\pm 0.15)	2.66 (\pm 0.66)
<i>Cainocreadium dentecis</i>	85.71	25.28 (\pm 11.67)	29.5 (\pm 13.14)	72.41	16.62 (\pm 7.37)	27.09 (\pm 9.74)	50	12.54 (\pm 7.30)	25.09 (\pm 13.8 7)	53. 33	10.8 (\pm 4.67)	20.25 (\pm 7.75)
<i>Hemiurus communis</i>	0	0	0	6.89	0.13 (\pm 0.10)	2 (\pm 1)	4.54	0.04 (\pm 0.04)	1 (\pm 1)	20	0.66 (\pm 0.33)	3.33 (\pm 1.20)
<i>Pachycreadium carnosum</i>	57.14	21.57 (\pm 14.00)	30.2 (\pm 18.62)	20.68	1.20 (\pm 0.62)	5.83 (\pm 2.27)	40.90	6.63 (\pm 3.28)	16.22 (\pm 7.05)	36. 66	4.7 (\pm 2.12)	12.81 (\pm 1.86)
<i>Timoniella imbutiforme</i>	0	0	0	10.34	0.68 (\pm 0.50)	6.66 (\pm 3.84)	31.81	4.27 (\pm 2.57)	13.42 (\pm 7.23)	23. 33	1.96 (\pm 1.03)	8.42 (\pm 5.01)
<i>Nematoda</i>	28.57	0.42 (\pm 0.29)	1.5 (\pm 0.5)	24.13	0.68 (\pm 0.31)	2.85 (\pm 0.91)	13.63	0.95 (\pm 0.56)	7 (\pm 1.65)	16. 66	0.20 (\pm 0.08)	1.2 (\pm 0.20)

The parasite population descriptors varied significantly among locations (Table 7). The highest prevalences were obtained for *Aphallus tubarium* (Rudolphi, 1819) at all the studied localities. Comparisons of prevalence and abundance between areas showed that on the eight parasite species recorded, only three species *Allopodocotyle jaffensis* (Fischthal, 1980), *Cainocreadium dentecis* (Jousson & Bartoli, 2001) and *Pachycreadium carnosum* (Rudolphi, 1819) varied significantly comparing the four regions. *A. jaffensis* was significantly more prevalent in the Ajaccio samples than in the Bonifacio and Galeria samples. Chi-square tests indicated significant differences in parasites prevalence (*Allopodocotyle jaffensis*) between Cap Corse and Galeria areas. *C. dentecis* was significantly more prevalent in the Ajaccio samples than in the other zones. Considering prevalence, *P. carnosum* showed higher values in Ajaccio and Bonifacio than in Galeria and Cap Corse, respectively. Regarding the comparisons of abundance (Table 7), *A. jaffensis*, showed significant higher values in Ajaccio than in the other three zones. *P. carnosum* was significantly more abundant in the Ajaccio samples than in Bonifacio samples. For the remaining species, abundances were more homogeneous across samples and no significant differences were observed among areas. Parasites showed differential distributions essentially with hosts from Ajaccio zone, as evidenced by comparisons of prevalence and abundance of component species (Table 7). However, these results may be due to the small sample sizes in this area.

Table 7 Chi-squared (χ^2 test) and Kruskal–Wallis ANOVA (H) comparisons of prevalence and abundance (respectively) of component parasite species of *Dentex dentex* in four zones of the Corsica Island (see Table 6), NS (Not significant), asterisks refer to values that were significant (*p < 0.05).

Parasite taxa	test	P	AJA - BON	AJA - CAP	AJA - GAL	BON - CAP	BON - GAL	CAP - GAL
<i>Metadena depressa</i>	χ^2	NS	NS	NS	NS	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS
<i>Aphallus tubarium</i>	χ^2	NS	NS	NS	NS	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS
<i>Allopodocotyle Jaffensis</i>	χ^2	*	AJA > BON	NS	AJA > GAL	NS	NS	CAP > GAL
	KW	*	AJA > BON	AJA > CAP	AJA > GAL	NS	NS	NS
<i>Cainocreadium dentecis</i>	χ^2	*	AJA > BON	AJA > CAP	AJA > GAL	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS
<i>Hemiurus communis</i>	χ^2	NS	NS	NS	NS	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS
<i>Pachycreadium carnosum</i>	χ^2	*	AJA > BON	NS	NS	BON < CAP	NS	NS
	KW	*	AJA > BON	NS	NS	NS	NS	NS
<i>Timoniella imbutiforme</i>	χ^2	NS	NS	NS	NS	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS
Nematoda	χ^2	NS	NS	NS	NS	NS	NS	NS
	KW	NS	NS	NS	NS	NS	NS	NS

L DFA of the entire parasite assemblage data detected significant variations in abundance between sites. The first two discriminant functions of the multivariate L DFA contributing to 59% (eigenvalue = 0.654) and 35% (eigenvalue = 0.387), respectively, explained 94% of the total variance. A significant overall group effect was observed (Wilks λ = 0.411, p-value < 0.0001). The L DFA showed that the parasite species presented a moderate power of discrimination among locations, with on average 45% of correct allocation (Table 8). The

analysis gave a classification success range from 11% for Cap Corse to 59% for Bonifacio. The level of classification of individuals to the site from which they originated was 59, 58, 33 and 11% for Bonifacio, Galeria, Ajaccio and Cap Corse, respectively (Table 8).

Table 8 Cross validation classification matrix of *Dentex dentex* specimens from Corsica Island based on parasites communities (abundance) used in Linear Discriminant Function Analysis. The percentage of individuals assigned to each locality and the number of samples (in parentheses) are shown.

Originated\ classified	Ajaccio	Bonifacio	Cap Corse	Galeria	% correct
Ajaccio	33 % (2)	50% (3)	17% (1)	0% (0)	33%
Bonifacio	4% (1)	59% (16)	11% (3)	26% (7)	59%
Cap Corse	11% (2)	22% (4)	11% (2)	56% (10)	11%
Galeria	4% (1)	27% (7)	12% (3)	58% (15)	58%
Total	6	30	9	32	45%

The distribution of individuals along the discriminant functions evidenced a high overlap for all samples. Nevertheless, some differentiation between Bonifacio and Galeria samples could be noticed, with the highest rate of correct classification. These samples forming a group generally located more up along the first discriminant function axis (y-axis) for Bonifacio, and a group generally located more down (y-axis) for Galeria (Fig. 5).

A significant correlation between parasites abundance and geographic distance was revealed by a Mantel test ($P < 0.05$) in the sampled locations (same results with Euclidean distance).

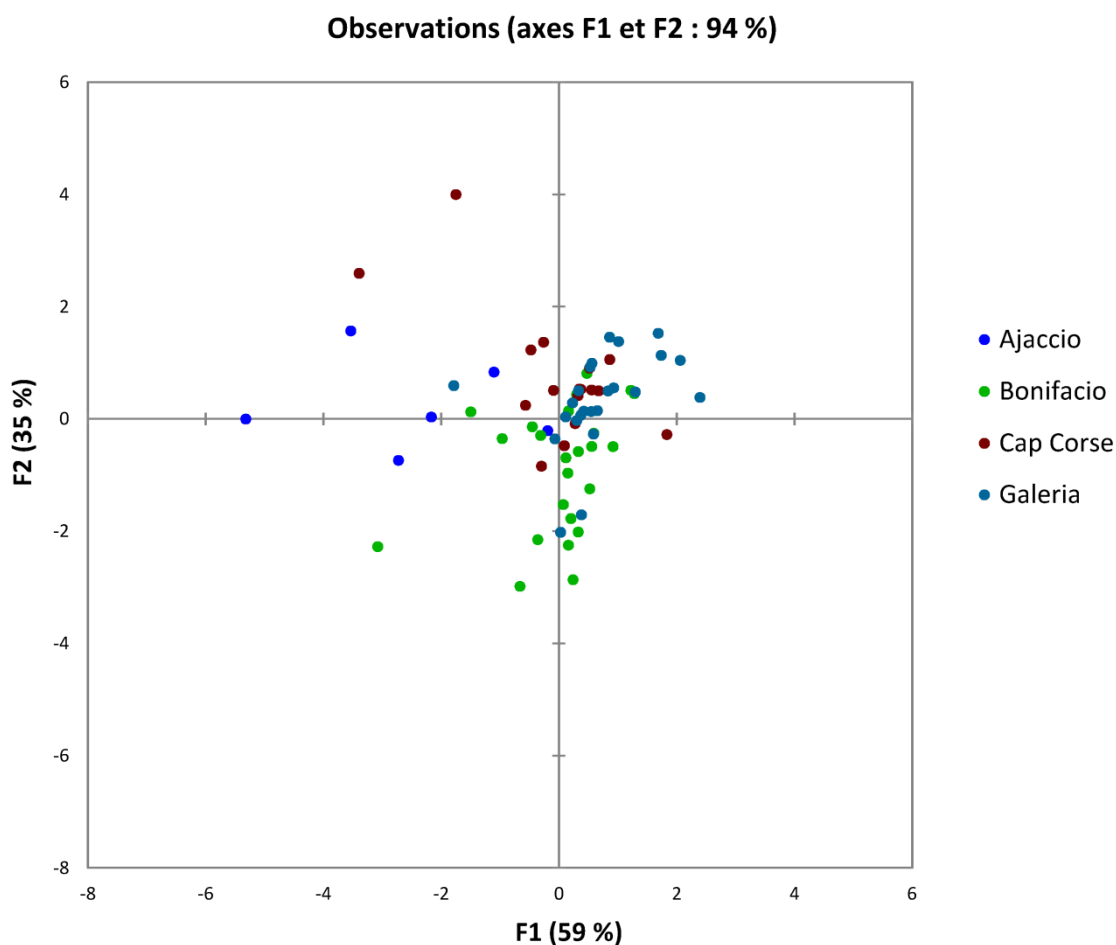


Fig.5 Discriminant function scores for parasites communities of *Dentex dentex* from four localities (Ajaccio, Bonifacio, Cap Corse, Galeria) in Corsica Island.

VI.3.4 Combination of microsatellites, otoliths shape and parasites communities markers

Mantel tests indicate no significant correlation ($P > 0.05$) between all the combinations tested between: genetic and otoliths, genetic and parasites, otoliths and parasites and the three markers combined. The nMDS analysis, showed a principal clustering of samples around the intercept and no geographically meaningful associations among samples (stress factor > 0.40 ; poor) (Fig. 6).

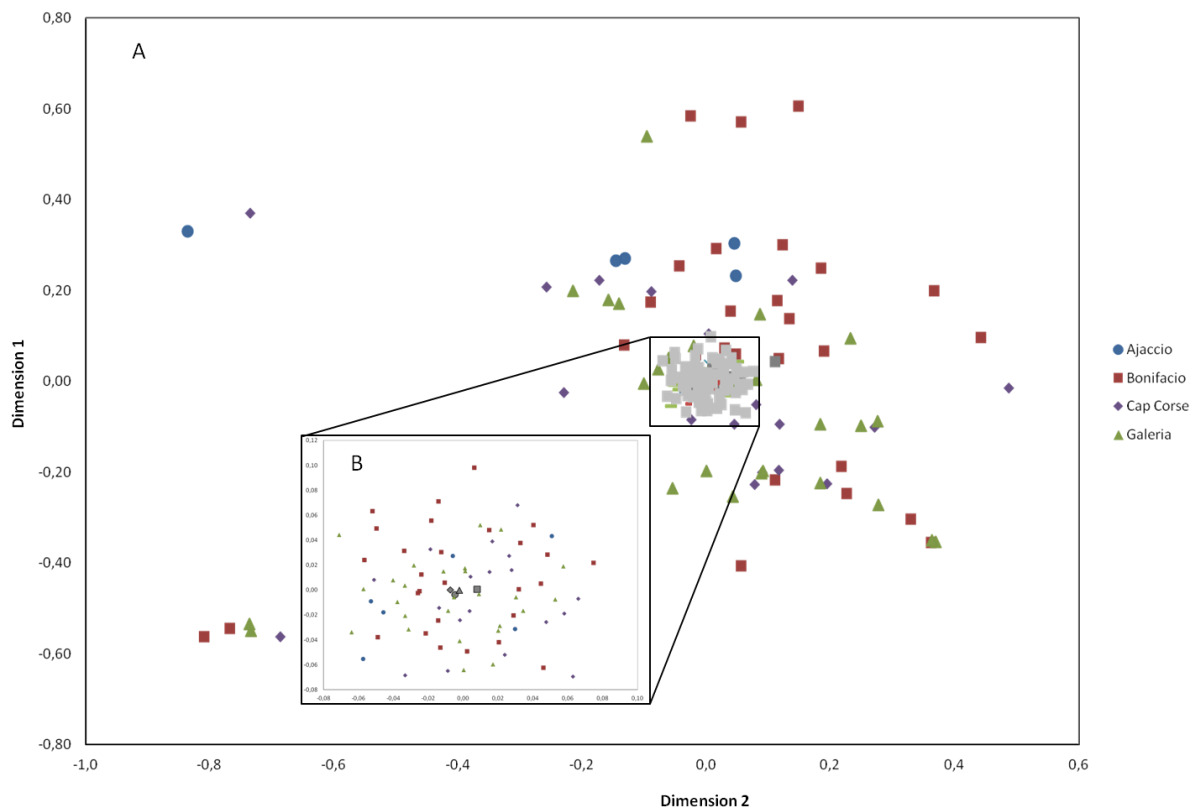


Fig. 6 Non metric Multidimensional scaling plots of the parasite data (Bray-Curtis distances) (A), inset displays (B) genetic markers (Cavalli-Sforza chord distances) and otoliths shape (Procrustes distances) centroids only (grey color) of *Dentex dentex* from four localities (Ajaccio, Bonifacio, Cap Corse, Galeria) in Corsica Island.

VI.4 Discussion

VI.4.1 Microsatellites

The delimitation of population groups is important for stock assessment and becomes a powerful tool when combined with the understanding of population dynamics and the ecological niche occupation of species, both in evolutionary and ecological time (Begg and Waldman 1999; Gauldie and Crampton 2002). Microsatellite analysis indicated that there was no significant genetic differentiation in *D. dentex* between Corsican sampling sites. The apparent genetic homogeneity of many marine species is thought commonly to be due to two factors that minimize accumulation of genetic differences among populations: large effective population sizes that limit genetic drift and life history characteristics that favor dispersal in continuous dynamic oceanic environments (Ward et al. 1994; Waples 1998). The dispersal of marine fish can take place via three mechanisms; larval drift (Cowen et al. 2000), trophic or reproductive migrations of adults and home range (Russ and Alcala 1996; Kramer and

Chapman 1999). However, genetic homogeneity does not necessarily imply panmixia and low F_{st} values may provide information about the recent history or present levels of gene flow. Low F_{st} values could mean: 1) ongoing panmixia among locations, 2) distinct lineages exist but have diverged too recently to be detected despite no current gene flow or 3) just enough gene flow exists to homogenize neutral markers despite extremely limited exchange of individuals on average among sites (e.g. an occasional long-distance dispersal event) (Conover et al. 2006). Only a small amount of gene flow is necessary to homogenize genetic variation that is neutral to selection (Vucetich and Waite 2000; Palumbi 2003). Gene flow rates of 1% would give genetic homogeneity among samples (Ward 2000a). Because neutral markers are more easily homogenized by low levels of gene flow, F_{st} is not very sensitive to the difference between relatively low gene flow and panmixia (Conover et al. 2006). For example, even a small number of migrant fish per generation can be sufficient to prevent detectable heterogeneity in neutral genetic markers (Waples 1998). While such low migration rates are generally sufficient to guarantee population connectivity over evolutionary timescales, they are a negligible force for rebuilding depleted stocks over a timescale of interest to fisheries (Mariani et al. 2005). The difference between restricted gene flow and panmixia may be very important in structuring adaptive genetic variation or in the identification of management units for fisheries (Conover et al. 2006). The findings of sample homogeneity are of little assistance to fisheries managers, who still need information to define stocks (Abaunza et al. 2008). In this sense, the holistic approximation to stocks identification is more efficient (Waldman 1999), as information with multiple perspectives can be obtained following the application of different techniques (Cadrin et al. 2005).

Deficits of heterozygotes were detected in Bonifacio and Galeria samples (measured as F_{is}). Four main factors could explain this observed imbalance. The locus can be under selection, at least through “genetic hitchhiking effect”, being close to some morphological or productive trait of selective interest (Braverman et al. 1995). The “null alleles” (non amplifying alleles) may be present and lead to a false observation of homozygotes (Fairbrother and Beaumont 1993). The consanguinity, produced by mating between relatives (between an individual and his ascendants, collateral and/or its descendants), the result is a loss of genetic variability over generations (Schaal 1975). The presence of population substructure may lead to Wahlund’s effect (Sinnock 1975). If the population is divided into partially isolated subpopulations, individuals from the same subpopulation have an increased probability of sharing a common ancestor and hence an increased probability of homozygosity (Overall and Nichols 2001). The most plausible explanation for our case could be population subdivision by the existence of diverse gene pools. The geographical distance was not correlated significantly with the genetic distances, which data may indicate that geographical distance is not a limiting factor for movements between common dentex populations.

VI.4.2 Otoliths shape

Although most genetic studies showed that gene flow between populations of marine fish is high, environmental heterogeneity has recently been suggested as an important driving force of divergent selection among populations (Bradbury et al. 2010).

Otolith shape analysis showed significant variation among the collection locations around Corsica Island. The result of DFA suggests one potential distinct population unit of *D. dentex* from Bonifacio varying in their degree of differentiation from those in the other areas (100% correct reclassification). These results agree with previous studies where classification values above 75% are generally considered acceptable in a stock discrimination context (Friedland and Reddin 1994; Stransky et al. 2008). Moreover, some specimens from Galeria, Cap Corse and Ajaccio were reclassified by the DFA in the Bonifacio area. These results may indicate a relative connectivity among the Bonifacio fish with the other sampling sites. Because studying the otolith of wild-collected specimens integrates all past ontogenetic and environmental variations, such pattern may result from the coexistence of migratory and residential behaviours (Secor 1999b). Some overlap between the study areas was also observed by the CVA, namely between Bonifacio and Galeria samples. This could also indicate that some specimens from these two areas are subject to similar environmental pressure that have shaped otoliths in a consistent manner (Farias et al. 2009).

To use the otolith shape variability appropriately as a natural marker in stock identification studies, it is important to consider the factors that may affect the shape variability (Cañás et al. 2012). This observed variation in otolith shape of common dentex between Bonifacio samples and the others localities may have different basis. Genetic dissimilarities, ontogeny, environmental factors and food supply can influence the shape of the sagittal otoliths (Cardinale et al. 2004; Galley et al. 2006; Vignon and Morat 2010). General otolith shape can be determined genetically (Vignon and Morat 2010). Experiments carried out by Cardinale et al. (2004) revealed that fish belonging to different stocks but growing under the same temperature and feeding conditions can have similar growth rates but significantly different otolith shapes. This indicates that genetic differences between populations can influence the shape of otoliths in the absence of any growth related differences (Galley et al. 2006). Moreover, substantial otolith shape differences have also been observed between groups of fish that are close in terms of geographical distribution (Pothin et al. 2006; Vignon et al. 2008) and for stocks that could not be separated using genetic techniques (DeVries et al. 2002). Otolith shape does not necessarily reflect genetic differences (Stransky 2005). Environmental factors that affect somatic and therefore otolith growth also have an effect on the otolith's final shape (Agüera and Brophy 2011). Generally, these variations are related to phenotypic plasticity as a result of different environmental conditions (Cadrin 2000). For

instance, feeding influences otolith shape, to the point that even recent feeding history creates discernable differences in otolith shape (Gagliano and McCormick 2004). In field studies, otolith shape variation appears to coincide with geographical differences in temperature (Bolles and Begg 2000), water depth (Lombarte and Leonart 1993), salinity (Capoccioni et al. 2011) and substrate type (Mérigot et al. 2007).

For example temperature is proven to change the rate and pattern of deposition during otolith growth producing changes in the otoliths length and overall shape (Lombarte and Leonart 1993; Suyama et al. 2009). Vignon and Morat (2010) confirm the hypothesis that otolith shape in fish occurs under dual regulation: environmental variation influencing overall change in the otolith shape, and genetic variation affecting the otolith shape locally. Campana and Casselman 1993 suggested that environmental factors are generally more influential determinants of otoliths shapes than genetic ones. It remains still difficult to establish which between these two determinants contributes the most to otolith shape, this feature representing a constraint for the method (Calò et al. 2013).

Nevertheless, otolith shape differences observed in the present study are most likely due to environmental conditions, in the absence of any genetic variation between samples. Geographic variations in environmental conditions such as temperature or/and salinity may have influenced otolith shape. In particular the Bonifacio area is a strait, strong and highly variable currents are known to occur in strait configurations (Astraldi et al. 1999; Dumas et al. 2009). Due to its geomorphological configuration, bathymetry and the presence of numerous islands and islets, the strait of Bonifacio is a complex area in term of currents (Gerigny et al. 2011), so giving this site particular oceanographic characteristics. The oceanographic conditions in the study are not homogeneous, which can be the primary cause of the otoliths shape differences. The geographical distance was not correlated significantly with otolith shape distances.

VI.4.3 Parasites communities

Parasite abundance data suggests that common dentex of Corsica Island belong to different population units. Univariate analyses revealed that some parasites species significantly differed in abundance between regions, multivariate analysis detected also a significant difference in the overall parasite assemblages of fish from the two regions. Thus, results of discriminant analysis suggested there could be at least two discrete populations of fish; one in Bonifacio and another in Galeria.

It has been established that 59% of dentex from Bonifacio and 58% from Galeria could be correctly classified based on their relative abundance of parasites. These differences between zones demonstrate the potential for discriminating discrete common dentex stocks

by their parasites. In fact, fish populations are often discriminated by their parasites, which have been recorded for numerous host species (Marques et al. 2006; Alarcos and Timi 2013; Pereira et al. 2014). Moreover, parasites discriminant analysis also seems to indicate that a mixing, migratory behavior or connections of common dentex populations also occurs between the different components. Several factors may contribute to the apparent isolation of stocks of common dentex, indicated by parasite markers in the present study. Variation in endoparasite fauna may be a consequence of different biotic and abiotic features of the immediate environment and corresponding availability of infected prey items (González et al. 2006). Parasites are specific to certain geographical areas and their distributions are mainly determined by temperature and salinity profiles and association with specific masses of water (Timi 2007). Environmental conditions have an influence on the distribution of endoparasites, either directly, or via their effects on other host species (MacKenzie and Abaunza 1998). Hosts may acquire parasites with direct life cycles during quick, occasional or temporary incursions in a particular locality (Vignon et al. 2008). Furthermore, the parasites used in this study have complex life cycles, their distribution patterns are not only dependent on environmental conditions but also on the distribution and population density of all hosts involved in their life cycles (Timi 2007). Local environmental factors can regulate the survival and transmission success of infective stages causing interpopulation variations of parasite burdens (Pietroock and Marcogliese 2003). Indeed, the observed differences in parasites communities of *D. dentex* between zones may reflect contrasting oceanographic and biological characteristics. The structure of the food web has also strong effect on transmission rates of some parasite species (Marcogliese 2002). Therefore, host feeding habits can influence the number of parasite species exploiting a host species (Boje et al. 1997; Luque et al. 2004). Accordingly, differential prey availability and its impact on diet composition have been highlighted as causes of spatial changes in parasite burden at a regional scale for other fish species (Sardella and Timi 2004). In fact, ecological factors are known to be key determinants of parasite communities in hosts inhabiting the boundaries of their geographical distribution (Kennedy and Bush 1994).

One possible explanation for the formation of localized populations of common dentex in these two areas (Bonifacio and Galeria) may be explained by the implement of protection measures. The two sites sampling were located near or inside of two Marine Protected Areas (MPAs: “la Réserve Naturelle des Bouches de Bonifacio” and “la Réserve Naturelle de Scandola”). Refuge areas usually have more favourable biotic and abiotic conditions, such as those found near Bonifacio and Galeria sites. One of the most important benefits to marine coastal species is that MPAs can act as refuges into which fish move to escape fishing (Lester et al. 2009). The common dentex is one of those species that benefit from this protection measure, as it is especially threatened by both recreational and artisanal fishing.

Cascade processes concern interconnected changes in predation interactions involving keystone species at different trophic levels (Francour et al. 2001). The replenishment of their stocks in protected areas may thus trigger cascade processes (Steneck 1998), and also influence the availability and composition of these potential preys (Rocklin 2010).

The use of parasites as biological indicators can be regarded as a valuable tool to evaluate population structuring, as it reflects the biology, habitat use and the different environmental pressures to which the host is subjected during its lifetime (Marques et al. 2005). Mantel tests indicate a significant correlation between geographic and parasite distances. Several mechanisms can produce a decrease of the similarity in species composition between two communities with an increase of the distance between them (Poulin and Kamiya 2013). These fall into three general classes of mechanisms: 1) species turnover along environmental gradients, 2) dispersal constraints imposed by the environment and 3) species differences in dispersal, probably always combine to various degrees to generate observed patterns of distance decay in similarity (Poulin and Kamiya 2013). It may be that at finer spatial scales, parasites are better to discriminate among stocks than genetic and otoliths markers.

VI.4.4 Combined use of markers

In the present study using more than one marker data set to define population structure of *D. dentex* highlights the potential value of using a multidisciplinary approach. The combination of these markers provides complementary insights and an opportunity to compare their utility and potential to understand population interactions. Genetic, otoliths shape and parasitological markers provide complementary information about population structure of common dentex around Corsica Island. Some techniques showed differences between areas while others did not. In order to conduct a suitable analysis of the various results, the nature and time scale of the techniques must be taken into account (Abaunza et al. 2008). Moreover, when differences were detected with any technique, the reasons underlying the differences were explained. The otoliths and parasite divergences are in contrast with the processus of genetic differentiation. Microsatellite DNA markers showed genetic homogeneity among the four localities. However, a high degree of variation in otoliths shape and parasites assemblages was demonstrated around Corsica Island, suggesting that population units exist for the species at this spatial scale.

The result of otoliths shape suggests one potential population unit of *D. dentex* from Bonifacio varying in their degree of differentiation from those in the other areas. The results of parasites communities suggested there could be at least two population units (Bonifacio and Galeria). In spite of the differences found among approaches, the results obtained from

otoliths and parasites allow an interpretation relatively similar suggesting that a population unit occurs in Bonifacio. The spatial differences for these two markers provide evidence for the existence of at least one (maybe two) local population units spatially separated in the common dentex population.

Several possible reasons exist for the varying results between the methods. Stock segregation levels indicated by microsatellite DNA markers relate to variation over an evolutionary time scale therefore act at broad spatio-temporal resolutions (Tanner et al. 2014). It concerns multi generations lineages. On the other hand, otoliths shape and parasitological tags were relevant to an ecological timescale on finer temporal and spatial scale. Thus, results reported here are not necessarily inconsistent with genetics evidence that would fail to show discrimination between sampled zones. Genetic segregation results from processes occurring at evolutionary time-scales and requires nearly full isolation to yield significant levels of discrimination between groups (Niklitschek et al. 2010).

Indeed, these population units, although not genetically differentiated, may be more or less isolated from each other, and thus react independently to environmental changes and exploitation (Jemaa et al. 2015). Neglecting to account for a population structure, as suggested for *D. dentex* increases the risk of localized depletion. High exploitation, combined with ineffective fisheries management, can result in loss of stock richness, which in turn may lead to declines in genetic diversity and reproductive potential of the fish stock (Hutson et al. 2011; Ferguson et al. 2011). Such diversity may also contribute to the resilience of fish populations to the impacts of climate change (Brander 2010). Therefore, accurate stock identification is essential information for fisheries managers in ensuring the sustainability of a resource, as well as the biodiversity of an ecosystem (Zischke et al. 2009).

VI.5 Conclusion

This information has shed light on a species where little information was known regarding population structure. A complex population structure around Corsican coasts has been reported, providing a new perspective on common dentex fishery stock conservation and management strategies. Further studies on the estimates of gene flow over global geographical range of common dentex (using microsatellites markers) are needed to understand the metapopulation connectivity. Studies on the biology of common dentex (especially larval behaviour) and alternative approaches such as larval dispersal modelling are also needed to better understand the observed differences. Determining the nature and the directional dispersal patterns of such spatial connections is essential to understanding resilience of each local fishery to fishing pressure (Schunter et al. 2011; Correia et al. 2012). Further research is also necessary to assess movement patterns of juveniles and adults *D.*

dentex at a smaller spatio-temporal scale, with methods such as electronic tagging with acoustic tracking. These methods may elucidate potential geographical movements and clarify their stock structure around Corsica Island.

Chapitre VII

Synthèse générale, Conclusion et perspectives

VII.1 Synthèse générale

Ce travail (Chapitre II) compile l'ensemble des données parcellaires existantes sur la biologie, l'exploitation, et la structure de population du denti sur son aire de répartition. À travers les axes développés, ce document de synthèse fournit une vision claire de l'état des connaissances actuelles sur le denti et des lacunes qu'il reste à combler.

Un inventaire précis a été effectué pour caractériser l'exploitation du denti par la pêche artisanale, notamment en rassemblant des travaux qui n'avaient jamais été publiés ou à diffusion réduite issues de la « littérature grise ». Le denti est ciblé par la pêche artisanale tout au long de l'année par l'utilisation combinée de trois principaux engins de pêche (palangre, filet trémail, filet maillant), qui varient suivant la saison et les zones géographiques.

Les données sur les captures mondiales du denti suggèrent une possible fluctuation cyclique des populations, avec l'apparition de pics d'activités pluriannuels. Il semblerait que les captures de denti aient fluctué au cours de ces 60 dernières années, avec un fort déclin depuis les années 1990. Plusieurs hypothèses sont possibles pour expliquer ces variations cycliques de la production, la première peut être due à une fluctuation de l'effort de pêche au cours du temps (ex : des améliorations technologiques, la mise en place de mesures de gestion). Ensuite, trois principales hypothèses écologiques peuvent être aussi avancées comme : (i) des changements dans les interactions entre espèces, telles que les interactions « prédateur-proie », (ii) des processus non-linéaires qui influencent la dynamique de la population, (iii) et/ou des variations environnementales (e.g Shelton and Mangel 2011). Un message qu'il faudrait retenir est qu'il n'y a pas qu'un seul mécanisme qui soit entièrement responsable de ces fluctuations. Ainsi, il serait nécessaire de mieux comprendre comment ces facteurs interagissent entre eux et affectent la variabilité des populations naturelles (Shelton and Mangel 2011).

La surexploitation et l'eutrophisation sont parmi les menaces majeures relevées par l'UICN pour le denti dans certaines parties de son aire de répartition (Carpenter and Russell, 2014). Cependant, il n'existe que peu de mesures de gestion pour cette espèce à des niveaux nationaux, seules quelques unes sont mises en place à des échelles locales principalement au sein d'AMP. La mise en œuvre de mesures pour protéger le potentiel reproducteur du denti semble nécessaire. Ainsi, au cours des différents chapitres des mesures spécifiques sont proposées pour favoriser la gestion durable de cette espèce.

Il a été montré dans le chapitre précédent que le denti est d'importance écologique, économique et une espèce emblématique en Méditerranée. Malgré ce statut, les données disponibles sur les rendements, les engins de pêche utilisés, la saisonnalité des captures ou

encore les zones exploitées par la pêche professionnelle, sont rares. En raison de la complexité de cette activité, très peu d'études ont quantifié l'effort et les captures de la pêche artisanale (Maynou *et al.* 2011a). Le manque de données quantitatives à des échelles spatiales et temporelles réduit fortement la possibilité de développer des méthodes de pêche durable et des mesures de gestion efficaces (Colloca *et al.* 2004). Par conséquent, comprendre la dynamique spatio-temporelle de la pêche artisanale et identifier la distribution de l'exploitation sont des éléments essentiels. L'objectif du chapitre III était de fournir de nouvelles informations sur la pêche artisanale du denti à l'échelle de la Corse, au cours de cinq années de suivi halieutique. Les Captures Par Unités d'Efforts (CPUE) du denti par la pêche artisanale ont varié dans l'espace et dans le temps, mais ont montré une stabilité annuelle au cours de la période d'échantillonnage. La variabilité mensuelle a montré qu'il existe un pic d'exploitation qui est atteint au mois de mai, avec des taux plus faibles pendant le reste de l'année (de juin à septembre). Il faut noter que la palangre est utilisée en Corse pour l'exploitation du denti, mais cette activité est pratiquée principalement entre septembre et avril, ces données n'étaient pas disponibles et n'ont donc pas été prises en compte dans cette étude. L'augmentation saisonnière des captures observée au printemps était probablement liée à la stratégie de reproduction de cette espèce qui se déroule entre mars et juin (Morales-Nin & Moranta 1997).

Les résultats ont montré que la composition en classe de taille des individus capturés au cours de la période de frai représentait principalement des individus matures (classe de taille Moyen et Grand). La mortalité par la pêche tend à soustraire de la population les individus grands et âgés en particulier les femelles fécondes (the BOFFFF concept) (Field *et al.* 2008, Hixon *et al.* 2014). Il est possible que l'augmentation de la pression de pêche sur ces espèces au cours de cette période ait un impact négatif sur les stocks (Tzanatos *et al.* 2008). De tels effets peuvent sérieusement endommager la résilience des populations et accroître la variabilité de la population et le risque d'extinction, sans pour autant donner un signal clair de baisse de la biomasse totale de la population dans les données de la pêche (Hsieh *et al.* 2010). Des preuves récentes ont montré que les captures durant la période de reproduction pouvaient présenter des phénomènes d'hyperstabilités. Ainsi les CPUE peuvent être relativement stables pendant plusieurs années, mais l'abondance totale diminue progressivement au cours du temps pouvant arriver à des niveaux critiques et provoquer un effondrement brutal des captures lorsque le point de rupture est atteint (Sadovy & Domeier 2005). Ces scénarios ont déjà été signalés pour d'autres espèces de poissons comme chez la morue, *Gadus morhua*, L., 1759 ou le serran farlot, *Paralabrax nebulifer* (Girard, 1854) (e.g, Shelton and Mangel 2011 ; Erisman *et al.* 2011). Cependant nous ne disposons pas encore d'information sur l'état du stock de denti en Corse, c'est-à-dire le niveau de la

biomasse de reproducteurs et de sa dynamique de population, qui conditionne la capacité de cette population à se renouveler.

Les histogrammes de taille et d'âge ont montré qu'après cette période de frai (de juin à septembre) les captures sont constituées le plus souvent de petits et jeunes individus immatures. Ne pas permettre à ces individus d'arriver à maturité et qu'ils aient la possibilité de se reproduire au moins une fois peut provoquer une troncation de la structure de population exploitée. Ces phénomènes ont été précédemment montrés dans des cas de pêcheries industrielles comme chez les sébastes par exemple (e.g. Berkeley *et al.* 2004). Cette exploitation menace le potentiel de reproduction de l'espèce et peut contribuer au déclin des stocks et altérer la dynamique de la population (Hupfeld & Phelps 2014). L'approche spatiale utilisée révèle une distribution hétérogène de l'effort et des captures de denti et a identifié des zones importantes d'exploitation. L'identification de ces zones de pêche exploitées indique clairement l'existence de «hot spots», qui représentent probablement des habitats essentiels dans l'histoire de vie de cette espèce et/ou des espèces associées, comme des zones de frai ou de nurserie. Cette étude a fourni les premières cartes à fine échelle de l'exploitation au niveau spatial du denti avec la distribution et l'intensité de l'effort de pêche associé autour de la Corse. La présente étude apporte une contribution significative aux connaissances sur l'exploitation du denti commun (au niveau spatial, temporel et démographique) par une pêche artisanale méditerranéenne. De futures recherches doivent être poursuivies pour mieux comprendre la dynamique de population du denti notamment pendant la période de reproduction. Au vue des résultats obtenus, une combinaison d'outils de gestion et des mesures spécifiques pour protéger le potentiel reproducteur de cette espèce devraient être encouragées comme : (i) une période de « repos biologique » en fermant temporairement la pêche du denti pendant la période de reproduction, (ii) une taille minimale de débarquement qui soit supérieure à la taille à 50 % de maturité (iii) réduire les prises accessoires (rejets morts) dans les filets à langoustes, et/ou (iv) la création d'aires marines protégées pour ces habitats clés identifiés comme des « hot spots » (Nemeth *et al.* 2007, Matić-Skoko *et al.* 2015). Il serait souhaitable d'engager les pêcheurs artisanaux dans un partenariat avec les scientifiques et les gestionnaires. Plus les pêcheurs sont engagés dans le processus de gestion, et plus les chances de succès d'une gestion durable sont grandes (Di Franco *et al.* 2014b).

Il y a peu de données sur l'effort et/ou les captures totales pour la pêche récréative en générale toutes espèces confondues, et la pêche récréative du denti souffre des mêmes carences. Il est nécessaire de disposer de données biologiques, sociales et économiques précises à court terme pour évaluer l'impact de cette activité. Ces données seront essentielles pour estimer la mortalité totale par pêche pour une évaluation plus fiable des

stocks halieutiques, surtout lorsque ces captures sont potentiellement élevées par rapport à la pêche commerciale, ce qui est supposé pour le denti. On a vu que ce poisson est considéré comme une espèce d'intérêt, par ce fait il est ciblé aussi bien par la pêche artisanale que la pêche récréative. L'objectif du Chapitre IV a été de caractériser l'exploitation du denti pour ces deux activités au sein d'une aire marine protégée (la Réserve Naturelle des Bouches de Bonifacio). Il est montré de manière quantitative et qualitative l'impact de ces pêcheries sur ces ressources mais aussi l'influence des mesures de gestion mises en place sur les niveaux de captures. Les résultats de l'analyse de la série temporelle pour la pêche artisanale, malgré de fortes variations interannuelles, ont montré deux périodes importantes : (i) une augmentation progressive des rendements entre 2000 et 2006 et (ii) une relative stabilité entre 2007 à 2012. Une des raisons possibles qui pourrait expliquer l'augmentation du rendement entre 2000 et 2006 serait l'effet direct des mesures de protection mise en place dans la RNBB. Depuis sa création en 1999, au sein de la RNBB, des dispositions restrictives ont été appliquées sur les activités de pêche professionnelle : régulation du nombre de licences, interdiction d'engins de pêche et tailles de mailles spécifiques, instauration de réserves intégrales interdites à toutes activités (Albouy et al. 2010). Ces restrictions ont tendance à diminuer la pression de pêche sur les parties protégées et à augmenter les captures dans les zones adjacentes (Mouillot *et al.* 2008).

La stabilisation observée des rendements entre 2007 et 2012 pourrait s'expliquer par l'augmentation et l'effet combiné de la pêche récréative et du tourisme nautique. Des avancées technologiques majeures au cours de ces dernières années, ont conduit à une plus grande capacité en termes de capturabilité pour la pêche récréative (Cooke & Cowx 2006). Des progrès ont également été accomplis dans la localisation des bancs de poissons avec la démocratisation d'outils de pointe comme les GPS, sondeurs et sonars (see Cooke & Cowx 2006). Ces investissements se traduisent généralement par une augmentation accrue de l'efficacité de l'effort de pêche (Torres-Irineo *et al.* 2014). De plus, le nombre en augmentation des bateaux de plaisance qui fréquentent la RNBB peut avoir un certain nombre d'effets sur l'environnement côtier marin. Ainsi en 2006, 14 003 bateaux ont visité les deux principaux ports touristiques de la RNBB (Bonifacio, Porto-Vecchio) au cours de la saison estivale. La croissance rapide de ce nombre de bateaux de plaisance peut être à l'origine de stress et perturber de nombreux aspects de la biologie et l'écologie des poissons marins. Ces stress comprennent la pollution (accumulation d'éléments traces métalliques), l'altération de l'habitat (augmentation de la turbidité de l'eau, dommages dus aux ancrages), le changement comportemental dû aux vagues produites et aux perturbations sonores (évitement des zones de trafic par les poissons), et/ou la propagation d'espèces invasives (Whitfield & Becker 2014).

Le denti est ciblé par la pêche artisanale et récréative dans la RNBB par une grande variété d'engins. Pour la pêche professionnelle, la palangre capture essentiellement de grands individus, alors que le « filet à poisson » et le « filet à langouste » ont un large spectre de capture en termes de classes de taille. Comme cela a été montré dans le Chapitre III pour l'ensemble de la Corse, les prises au filet à poisson dans la RNBB sont les plus fortes au mois de mai, pendant la période de reproduction. Les captures au filet à langouste correspondent essentiellement à des prises accessoires, et bon nombre des individus sont rejetés morts (mangés par les « puces de mer », qui sont principalement des Amphipodes) et constituent une perte non commercialisable. Les engins les plus utilisés pour la pêche récréative sont respectivement la pêche à la traîne en bateau, la chasse sous-marine suivie de la palangrotte. La traîne est l'engin de pêche le plus efficace en termes de nombre et de biomasse prélevée, il représente 90 % des captures réalisées, en ciblant essentiellement de grands individus. La chasse sous-marine semble avoir un impact relativement mineur par rapport à la traîne dans la zone d'étude. Ces résultats ne sont pas en accord avec ceux d'Abdul Malak et al. (2011), qui ont identifié la chasse sous-marine comme la principale menace pour l'exploitation du denti en Méditerranée. L'effet combiné de la pêche artisanale et de loisir (ex : palangre et traîne) sur les grands individus peut avoir de graves conséquences sur l'état des stocks de *D. dentex*. Comme on l'a vu dans le Chapitre III cette sélectivité peut non seulement réduire la biomasse, mais aussi provoquer une troncature de la structure en taille et en âge, une perte de la diversité génétique, et des changements évolutifs. Cela peut *in fine* induire des mécanismes « dépensatoires » où la population décroît en deçà d'un certain seuil et celle-ci ne peut plus assurer son renouvellement (Lewin et al. 2006).

Au niveau spatial, les captures des deux activités (pêche professionnelle et pêche récréative) étaient quantitativement maximales dans les zones de protection renforcée (ZPR). Le denti semble particulièrement sensible et réagir positivement aux mesures de protection mise en place dans l'AMP. Dans ce cas, deux hypothèses principales peuvent expliquer les taux de capture élevés de denti dans les ZPR: (i) l'interdiction de la chasse sous-marine dans ces zones et (ii) l'effet de refuge. Enfin les estimations de production annuelle moyenne sont de 5,8 t pour la pêche professionnelle et de 3,4 t pour la pêche récréative (à la traîne), soit un total de 9,2 t. Ainsi, la pêche récréative représente 37 % de l'ensemble des captures de denti sur la zone de la RNBB. Cependant, il est à noter que la production rapportée pour ces deux activités est probablement sous-estimée. Pour la pêche récréative, les données récoltées ont un degré d'imprécision dû principalement aux contraintes associées à la stratégie d'échantillonnage (e.g. Lockwood, 2000). De plus, les activités de braconnage et notamment de pêche illicite non déclarée, qui sont manifestement existantes, en attestent plusieurs constats et interpellations, n'ont pas pu être prises en

compte dans l'étude car étant à l'heure actuelle difficilement quantifiables. Pour la pêche artisanale, ce sont les rejets qui n'ont pas été estimés dans cette étude. Les résultats indiquent que la pêche récréative contribue significativement à la mortalité par la pêche de cette espèce. Elle peut générer une pression combinée et amplifier les effets négatifs de la pêche artisanale sur la population de denti. Ainsi cette activité peut mettre en danger la durabilité de la pêche artisanale en exploitant les mêmes zones et les mêmes ressources (Rocklin *et al.* 2011).

Les résultats de cette étude apportent de nouvelles connaissances sur l'état de l'exploitation du denti par la pêche artisanale et récréative dans une AMP en Méditerranée, donnant un aperçu des niveaux de captures et des pressions résultant de ces activités. Cette étude montre bien que *D. dentex* est ciblé par les deux activités de pêche et que la proportion des captures réalisées par la pêche récréative, plus particulièrement la pêche en bateau à la traine lente, est alors très significative. Au cours des prochaines années, les gestionnaires de la RNBB prévoient une augmentation des activités de pêche récréative alors que l'effort de pêche de la pêche artisanale se stabiliserait (Albouy *et al.* 2010). Il semble donc important d'appliquer de nouvelles mesures de gestion pour les activités récréatives. Pour le denti dans le RNBB, les gestionnaires pourraient envisager la mise en œuvre de mesures spécifiques pour protéger son potentiel reproducteur, comme l'établissement de tailles minimales de capture. Il est essentiel que cette taille soit plus grande que la taille à maturité, surtout pour les espèces les plus vulnérables (Font & Lloret 2014). Sur la base de la taille à la première maturité et les traits d'histoire de vie du denti (Morales-Nin & Moranta 1997), il serait conseillé d'établir une taille minimale de capture à 40 cm.

Les chapitres précédents ont montré que certains engins de pêche peuvent avoir un impact particulier sur ces populations, notamment dans les zones de nurseries (juvéniles) ou dans les zones de frai (adultes matures). *Dentex dentex* est fortement vulnérable à la pêche de part ses traits d'histoire de vie incluant sa longévité, sa grande taille et sa croissance faible (Carpenter and Russell, 2014). Certaines recherches ont déjà étudié la croissance du denti en utilisant comme méthode d'estimation d'âge des lectures sur écailles ou otolithes entiers (Chemmam-Abdelkader *et al.*, 2004; Culioli, 1986; Morales-Nin and Moranta, 1997). Cependant, aucune de ces études n'a vraiment évalué et comparé la précision de l'estimation d'âge entre ces structures. L'âge est un élément clé car il constitue la base pour les calculs de croissance, de mortalité et les estimations de productivité. Une des étapes clés dans les procédures d'estimations d'âge et de croissance est de choisir la structure la plus appropriée et précise pour déterminer l'âge des poissons (Cazorla & Sidorkewicj 2008). L'utilisation d'âges erronés a causé de graves problèmes dans la gestion et la compréhension des populations de poissons (Alves & Vasconcelos 2013). Le Chapitre V

constitue la première étude qui a comparé des méthodes différentes (écaille, otolithe entier et sectionné coloré) pour évaluer la qualité des estimations d'âges des structures calcifiées chez le denti, puis définir ces paramètres de croissance en Corse.

A partir des résultats obtenus, la lecture sur écaille apparaît comme fiable seulement jusqu'à cinq ans, au-delà de cet âge, les otolithes entiers peuvent être utilisés jusqu'à 12 ans. Enfin, les otolithes sectionnés peuvent être employés pour toutes les classes d'âges. Ces résultats montrent les limites d'utilisation des lectures sur écailles et otolithes entiers, et mettent en évidence la fiabilité des otolithes sectionnés pour estimer l'âge de denté commun tout au long de sa vie. L'âge maximum estimé dans cette étude est de 36 ans basé sur un otolithe sectionné, ce qui constitue l'âge maximal reporté pour cette espèce. Cette donnée prolonge la durée de vie estimée de l'espèce au-delà de son maximum précédemment reporté dans la littérature qui était de 33 ans à partir d'écailles (Chemmam-Abdelkader 2004), et confirme que le denti peut être considéré comme une espèce longévive.

Le taux de croissance du denti dans l'étude est relativement élevé et semble assez rapide par rapport à des études antérieures en Méditerranée. Ce résultat pourrait s'expliquer par un environnement particulièrement propice en Corse pour la croissance du denté commun. Cependant, il est encore faible par rapport au potentiel maximum atteint par l'espèce en aquaculture ($k = 0.507$, Machias et al., 2002). Les différences observées entre les paramètres estimés pourraient être attribuées à plusieurs facteurs comme : (i) le type d'engin de pêche utilisé, (ii) les structures utilisées pour ajuster la courbe de croissance, (iii) une variabilité génétique, (iv) des variations environnementales (température, salinité), (v) l'alimentation et/ou des maladies (parasites) (Pauly, 1994; Duan et al., 2014). Dans l'ensemble, cette étude a fourni de nouvelles informations essentielles sur l'âge et la croissance du denti qui ont permis de mieux caractériser ses traits biologiques et pourraient contribuer à une meilleure évaluation de la dynamique de ses populations.

Très peu de recherches ont étudié la structure de la population du denti. Les résultats révèlent un haut degré de différenciation entre les populations d'Atlantique et de Méditerranée à partir de marqueurs génétiques (ADN mitochondrial et allozyme) et morphologiques (forme du corps) (Bargelloni *et al.* 2003, Palma & Andrade 2004). Il semble y avoir une barrière effective qui sépare ces deux populations. On peut supposer que des phénomènes passés qui ont fait l'histoire de la mer Méditerranée, combinés à des modèles hydrographiques présents, peuvent avoir favorisé et maintenu la différenciation observée de la sous-population méditerranéenne (Bargelloni et al 2003; Palma et Andrade 2004). L'identification de la structure des stocks exploités est fondamentale pour une gestion durable des pêches en déterminant des unités spatiales appropriées (Begg & Waldman 1999). Le but du Chapitre VI était d'identifier la structure de population de denti autour de la

Corse, par une approche holistique, avec une combinaison de marqueurs qui ont différentes échelles spatiales et temporelles d'intégration: les microsatellites, l'analyse de la forme des otolithes et les communautés de parasites.

L'analyse des microsatellites a indiqué qu'il n'y avait pas une différenciation génétique significative entre les sites d'échantillonnage. L'homogénéité génétique apparente de nombreuses espèces marines est généralement due à deux facteurs qui réduisent l'accumulation de différences génétiques entre les populations: (i) une grande taille de la population qui limite la dérive génétique et (ii) des traits d'histoire de vie qui favorisent la dispersion dans un milieu marin continu et dynamique (Ward et al. 1994; Waples 1998).

Cependant, l'homogénéité génétique n'implique pas nécessairement la panmixie et des valeurs de F_{st} faibles peuvent fournir des informations sur l'histoire récente ou les niveaux actuels des flux géniques. Un flux de gènes faible (seulement 1%) peut donner une homogénéité génétique entre les échantillons (Ward 2000b). Par exemple, seul un petit nombre de poissons migrant par génération peut être suffisant pour empêcher l'hétérogénéité détectable dans les marqueurs génétiques neutres (Waples 1998).

Bien que ces faibles taux de migration soient généralement suffisants pour garantir la connectivité de la population sur des périodes évolutives, ce mécanisme reste négligeable pour la reconstitution des stocks exploités sur une échelle de temps plus réduite pour la gestion des pêches (Mariani et al. 2005). En ce sens, l'approche holistique avec l'application de différentes techniques qui donnent des informations avec des niveaux d'intégrations différents semble plus efficace (Cadrin et al 2005).

L'analyse de la forme des otolithes a montré une variation significative entre les sites autour de l'île. Le résultat de l'analyse discriminante suggère une potentielle unité populationnelle distincte à Bonifacio par rapport aux autres zones d'échantillonnage (100% de reclassement correct).

Cependant quelques individus de Galeria, Cap Corse et Ajaccio ont été reclassés par cette analyse dans la zone Bonifacio. Ces résultats peuvent indiquer une connectivité relative entre les différentes populations. Parce que l'étude des otolithes intègre toutes les variations ontogéniques et environnementales passées ; ainsi un tel modèle peut résulter de la coexistence de comportements migratoires et résidentiels (Secor 1999a). Cette variation observée dans la forme des otolithes du denti entre Bonifacio et les autres sites peuvent avoir différentes origines. Ainsi, des facteurs génétiques, ontogéniques, environnementaux, ou le régime alimentaire peuvent influencer la forme des otolithes (Cardinale *et al.* 2004, Galley *et al.* 2006, Vignon & Morat 2010). Néanmoins, les différences observées dans la présente étude sont probablement dues principalement aux conditions environnementales, en l'absence de toute variation génétique significative entre les individus.

L'analyse de la parasitofaune suggère aussi qu'il existe des unités de populations distinctes en Corse. Ainsi, les résultats de l'analyse discriminante indiquent qu'il pourrait y avoir au moins deux unités populationnelles distinctes de denti; une à Bonifacio et une autre à Galeria (59 % et 58% de reclassement correct, respectivement). Néanmoins, ces analyses semblent également indiquer qu'il existe des échanges et une certaine connectivité entre les différents sites. Les différences des communautés de parasites observées peuvent être la conséquence de facteurs biotiques et abiotiques comme des variations environnementales ou de la disponibilité des proies parasitées (González et al. 2006). Une autre hypothèse pouvant expliquer la formation de ces populations de denti à Bonifacio et Galeria serait la mise en place de mesures de protection spatiale. L'échantillonnage de ces sites est à proximité ou à l'intérieur de deux aires marines protégées (AMP: "la Réserve Naturelle des Bouches de Bonifacio» et «la Réserve Naturelle de Scandola"). La reconstruction de leurs stocks et du réseau trophique dans ces zones protégées peut ainsi déclencher des processus en cascade (Steneck 1998), et influencent également la disponibilité et la composition de leurs proies potentielles.

Il existe diverses raisons qui peuvent expliquer les différences de résultats entre les techniques. Le niveau de discrimination des stocks indiqué par les marqueurs microsatellites se rapporte à des processus évolutifs agissant à de larges résolutions spatio-temporelles (Tanneur et al. 2014). La forme des otolithes et les communautés de parasites sont, elles, appropriés à une échelle spatio-temporelle plus fine correspondant à des processus écologiques. Ainsi, les résultats obtenus avec les otolithes et parasites ne sont pas nécessairement incompatibles avec les résultats génétiques qui n'ont pas montré de discrimination entre les zones. En effet, ces unités de populations, bien que non génétiquement différenciées, peuvent être plus ou moins isolées les unes des autres et réagir différemment aux changements environnementaux et à l'exploitation (Jemaa et al. 2015).

Malgré les différences constatées entre les approches, les résultats obtenus à partir des otolithes et des parasites permettent une interprétation relativement similaire mettant en évidence une population distincte à Bonifacio. Ainsi ces deux marqueurs fournissent des preuves de l'existence d'au moins un (peut-être deux) groupes spatialement séparés au sein de la population de denti en Corse. Cette étude montre l'intérêt d'utiliser une approche holistique pour l'identification des stocks. La combinaison de ces marqueurs donne l'opportunité de tester leurs limites et de comparer leurs potentiels d'utilisation ainsi que leurs emprises spatiales et temporelles. Cette étude fournit de nouveaux éléments dans la compréhension de la structure de population du denti. Elle a mis en lumière une structuration spatiale complexe de la population, donnant de nouvelles perspectives pour la conservation et la gestion durable des stocks de denti en Corse.

VII.2 Conclusion et perspectives

Cette thèse fournit de nouvelles connaissances sur l'exploitation, la biologie et la structure de population du denti en Corse et contribue à l'amélioration de la compréhension générale de cette espèce où très peu d'informations étaient disponibles.

Cependant il existe des questions importantes qui restent encore sans réponses, notamment sur la connectivité des populations à fine et large échelle spatiale et les traits d'histoire de vie de ce poisson emblématique. Des études complémentaires seraient nécessaires pour résoudre ces questions fondamentales et combler les principales lacunes :

- Sur la biologie et le comportement du denti au stade larvaire. Par la modélisation de la dispersion larvaire grâce à l'utilisation d'un modèle océanique (ex : Mars 3D), combiné à un Individual Based Model (IBM, ex : Ichthyop) afin de suivre le déplacement des larves de différentes populations. Les informations recueillies par cette thèse (lieux potentiels de frayères, identification des stocks), pourraient servir de base pour alimenter et initier l'IBM. Il faut signaler que des travaux sont en cours et ont été effectués à l'Université de Corse sur cette thématique pour la région « Bonifacio » (Koeck et al 2015).

- Mieux comprendre les mécanismes de colonisation, quels sont les capacités natatoires et sensorielles des post-larves et l'impact des pressions environnementales sur le succès de cette phase d'installation. Actuellement, deux thèses sont en cours à l'Université de Corse travaillant sur ces thématiques (Laure-Hélène Garsi, Amélie Rossi).

- Déterminer la structure de la population de *Dentex dentex* en utilisant des marqueurs génétiques (microsatellites + ADNmt D-Loop) à travers son aire de répartition. Ce travail est en cours, dans le cadre du programme de recherche Denti à STELLA MARE (Responsable Dr Eric Durieux) à travers une collaboration scientifique avec Dr Patrick Berrebi (DR CNRS, Institut des Sciences de l'Evolution de Montpellier) et Dr Costas Tsigenopoulos (Hellenic Center of Marine Research, Heraklion).

- Etudier les capacités de mouvement et identifier à quelles échelles spatiales se déroulent les déplacements, à l'aide de techniques, tel que le marquage électronique avec un suivi acoustique. Une action commune entre le programme Denti et le programme Modélisation comportementale (responsable Dr Antoine Aiello) devrait démarrer prochainement sur le denti en télémétrie acoustique afin d'appréhender ces composantes de la dynamique spatiale. L'examen de ces mouvements à l'échelle individuelle, serait notamment important pour mieux connaître le comportement reproducteur de cette espèce lors de la période de

fraie. Il faut noter qu'une action pilote de marquage externe de type « spaghetti » dans le cadre du programme Denti (STELLA MARE) en collaboration avec un guide de pêche de loisir Francois-René Castellani a été menée dans la région de Scandola. Ces méthodes pourraient élucider les mouvements géographiques potentiels et compléter les résultats obtenus par la thèse en ce qui concerne la structure de la population de denti en Corse.

- Entreprendre l'étude du sexage du denti par identification visuelle. Il n'y a pas de dimorphisme primaire chez le denti, mais existe-t-il un caractère sexuel secondaire lié à la maturité sexuelle ? Pendant la période de ponte, la majorité des mâles de *Dentex dentex* présentent des opercules avec des couleurs attirantes (jaune vif) différentes de leur coloration habituelle (Chemmam-Abdelkader 2004). Est-ce que la présence de la coloration jaune est un caractère à suivre pour distinguer avec certitude les mâles ? Il serait intéressant de suivre l'évolution de la coloration de la « livrée nuptiale » du denti en bassin par un système de photo-acquisition journalier. De plus, le développement en parallèle des marqueurs génétiques « Bio-moléculaires » serait souhaitable. Au cours de cette thèse des individus ont pu être sexés avec certitude lors de dissection, à partir de ces échantillons, il s'agirait d'isoler et identifier les marqueurs génétiques potentiels pour le sexage. Par la suite, sur les individus en bassin tester la fiabilité de la méthode d'identification visuelle en comparant par une validation croisée les résultats obtenus par la génétique.

- Cette thèse en affinant la compréhension de la biologie, de l'exploitation et de la structure de population du denti en Corse, fournit des éléments essentiels pour la modélisation de la dynamique de la population. Ces données pourraient servir de base à l'évaluation de l'état du stock de denti en Corse, par exemple avec une méthode d'analyse de pseudo-cohorte. Compte tenu des résultats montrant le prélèvement significatif de la pêche récréative sur cette espèce, il faudrait aussi intégrer les données issues de cette activité, qui ne sont généralement pas incluses dans les modèles, pour avoir une évaluation complète de l'état du stock de denti exploité en Corse. Ces informations seraient utiles dans la conception de scénarios durables, notamment par le calcul d'un rendement maximal équilibré pour la pêche artisanale (Pascual et al. 2013).

Ces données acquises pourraient aussi bien être incluses au sein de modèles écosystémiques couramment utilisés, tels que Ecopath with Ecosim (EwE) et/ou EcoTroph (ET). Cela fournirait une meilleure compréhension du rôle de cette espèce au sein de l'écosystème et permettrait de prédire les possibles conséquences écologiques de certaines mesures de gestion ou l'impact des changements climatiques dans la région modélisée (Griffits et al. 2010).

Tout au long de ce manuscrit au cours des chapitres abordés, un certain nombre de recommandations et des mesures de gestion ont été préconisées pour promouvoir une gestion durable de cette espèce. Mais au-delà de l'approche mono-spécifique une réflexion plus globale peut être menée pour améliorer la qualité générale du milieu marin et l'exploitation des ressources halieutiques.

- Il est important de poursuivre la collecte des données de captures multi-spécifiques de la pêche artisanale autour de l'île pour actualiser et affiner l'évaluation des stocks exploités en Corse. Dans un même temps, récolter le Savoir Ecologique des Pêcheurs (SEP) et intégrer ces données comme source potentielle complémentaire de connaissances sur le fonctionnement des écosystèmes de la zone côtière.

- Pour la pêche récréative, une estimation du nombre de pêcheurs, un suivi et une surveillance à long termes de ces activités seraient recommandés sur l'ensemble de la Corse. Une approche à promouvoir serait la « science participative » par laquelle le citoyen est impliqué dans la collecte des données. Dans une société de plus en plus « connectée » et où les activités en ligne prennent de l'ampleur, cette méthode pourrait, elle aussi, être une source d'information complémentaire. Il est maintenant nécessaire de disposer de données biologiques, sociales et économiques précises pour évaluer son impact sur la zone côtière. Des moyens devraient aussi être mis en œuvre pour sensibiliser à la réglementation et éduquer les pêcheurs récréatifs à une pêche responsable et aux techniques de « bonnes pratiques ». La pêche « No kill » est un bon exemple, cette pratique est commune dans d'autres parties du monde (Cooke & Cowx 2004, 2006), mais n'est pas très répandue en Méditerranée. Ainsi, le trocardage est encore très peu utilisé même des guides de pêche en mer. En effet, cette technique ne fait actuellement pas partie du référentiel de la formation nationale des guides de pêche (Brevet Professionnel de Moniteur-Guide de Pêche de Loisirs), ce qui constitue une grande lacune. Lors de sorties en mer pour la constitution d'un stock de géniteurs pour l'aquaculture (STELLA MARE), les premiers résultats semblent indiquer que le denti réagit bien au trocardage de la vessie natatoire avec des taux de survie en bassin de plus de 80%. La mise en place de formation et l'instauration d'un permis de pêche récréatif en mer seraient peut être des outils adaptés. Cette démarche devrait être associée à des contrôles par les autorités compétentes ou la création de « brigade bleu » qui est l'une des revendications portée par les pêcheurs professionnels en Corse.

Plus largement, il serait souhaitable de développer des outils et une gestion concertée spatialisée des activités de pêches et nautiques en centralisant et mutualisant les données récoltées au sein d'un Système Information Géographique dynamique. Ces informations

serviraient d'outil d'aide à la décision pour appliquer les mesures de gestion les plus appropriées pour assurer la durabilité des ressources halieutiques, et permettre un partage équitable de l'espace et de la richesse entre les différents acteurs du milieu marin.

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Résumé

Le denté commun, plus couramment appelé denti, *Dentex dentex* (Linnaeus, 1758), est un poisson marin côtier (0-200m) emblématique et patrimonial en Méditerranée. Il représente un intérêt économique important pour la pêche artisanale et récréative, en Corse en particulier. En tant que prédateur supérieur, il occupe une position clé au sommet de la pyramide trophique. Il dispose un statut de conservation en étant classé comme « Vulnérable » par l’UICN. Malgré son importance écologique et économique, les données disponibles sur cette espèce sont encore limitées.

L’objectif de cette thèse vise à améliorer l’état des connaissances sur l’exploitation, la biologie et la structure de population du denti en Corse. En premier lieu, un travail de synthèse bibliographique a été effectué, qui compile toutes les informations parcellaires existantes sur la biologie, l’exploitation, et la structure de population du denti sur l’ensemble de son aire de répartition. De manière générale, il existe un manque d’information, mais à travers les axes développés, ce manuscrit fournit une vision claire de l’état des connaissances actuelles sur le denti et des lacunes qu’il reste à combler. Deuxièmement, une étude a été menée pour déterminer quels facteurs pouvaient influencer les variations spatio-temporelles des captures (CPUE) du denti par la pêche artisanale et décrire la structure démographique de la population exploitée à l’échelle de la Corse. Les CPUE ont varié dans l’espace (profondeur) et dans le temps (mois), mais ont montré une stabilité annuelle. Les résultats ont montré un pic d’exploitation (des individus grands/âgés) au mois de mai pendant la période de reproduction. Cette étude a fourni également les premières cartes à fine échelle de l’exploitation au niveau spatial du denti, avec l’identification de «hot spots», qui représentent probablement des habitats essentiels dans l’histoire de vie de cette espèce. Troisièmement, une étude a comparé l’exploitation du denti par la pêche artisanale et récréative au sein de la Réserve Naturelle des Bouches de Bonifacio. Le denti est ciblé par une grande variété d’engins, ce sont la palangre (pêche artisanale) et la traine (pêche récréative) qui présentent les taux d’exploitation les plus élevés. Au niveau spatial, les captures étaient quantitativement maximales dans les zones de protection renforcée. Les résultats indiquent que la pêche récréative contribue significativement à la mortalité par la pêche de cette espèce dans la zone d’étude (3.4 t/an soit 37 % de l’ensemble des captures). Ensuite, une comparaison de trois différentes méthodes d’estimation d’âge (écailles, otolithes entiers et sectionnés) a été effectuée pour évaluer quelle structure était la plus fiable et précise et définir les paramètres de croissance du denti en Corse. A partir des résultats obtenus, la lecture sur écaille apparaît comme fiable jusqu’à cinq ans, la lecture sur otolithe entier jusqu’à 12 ans et sur otolithe sectionné peut être employée sur toutes les tranches d’âges (âge record de 36 ans). Le taux de croissance dans l’étude est relativement élevé et semble assez rapide par rapport aux études antérieures en Méditerranée. Pour finir, le dernier chapitre avait pour but d’identifier la structure du stock de denti autour de la Corse, par une approche holistique, avec une combinaison de marqueurs : les microsatellites, l’analyse de la forme des otolithes et les communautés de parasites. L’étude a mis en lumière une structuration spatiale complexe de la population, donnant de nouvelles perspectives pour la conservation des stocks de denti en Corse. Cette thèse fournit de nouvelles connaissances sur l’exploitation, la biologie et la structure de population du denti en Corse et préconise des mesures de protection pour promouvoir une gestion durable de cette importante ressource halieutique en Corse.

Mots clés: Denti, Pêche artisanale/récréative, Age/croissance, Structure de population.

Abstract

The common dentex, *Dentex dentex* (Linnaeus, 1758), is an iconic marine coastal bony fish in the Mediterranean Sea. The common dentex, due to its large size, flesh quality, and high commercial value, is targeted by both artisanal and recreational fishing, especially in Corsica. As a top predator, it is a potential indicator species for the structure and functioning of the coastal ecosystems on which it depends. *D. dentex* is classified by the IUCN as «Vulnerable». Despite its economic and ecological importance, scientific data on this species in its natural environment are still very scant.

The aim of this thesis is to improve the state of knowledge on fisheries, biology and population structure of *D. dentex* in Corsica. First, a review evaluates the current literature on *D. dentex* biology, ecology, stock structure, fisheries on its global geographical range. In general, there is a lack of information, but across the developed axes, this manuscript provided a clear view of the current state of knowledge on *D. dentex* and suggests future research directions to fill important gaps. Secondly, a study was conducted to determine which factors could influence the spatial and temporal variations in catches (CPUE) by artisanal fisheries and describe the demographic structure of the population exploited in Corsica. The CPUE varies over spatial (depth) and temporal scales (month), but show annual stability. The results exhibits a peak of exploitation during May (large/old specimens), probably related to reproductive strategies,. This study generated the first fine scale maps showing the spatial exploitation of common dentex and the identification of exploited fishing grounds clearly indicates the existence of 'hot spots', which probably represent essential habitats, of the life history of this species. Third, a study compared the exploitation of common dentex by artisanal and recreational fishing in the Bonifacio Strait Natural Reserve. It is targeted by a wide variety of gears; longline (artisanal fishing) and trolling (recreational fishing) have the highest rate of exploitation. Spatially, catches were quantitatively maximal in partially protected areas. The results suggest also that recreational fishing contributes significantly to total fishing mortality of the common dentex in the study area (3.4 t/year or 37 % of the total catch). Then, a comparison of three methods of age estimation (scales, whole and sectioned otoliths) was performed to evaluate which structure was the most reliable and accurate and define the growth parameters in Corsica. The scales appear suitable for estimating age between 0 and 5 years old, whole otoliths can be used up to 12 years and sectioned otoliths are the most accurate and reliable structure for all age ranges (age record of 36 years). The growth rate of the Corsican common dentex seems very high and quite fast compared to previous studies in the Mediterranean Sea. Finally, the aim of the last chapter was to identify the stock structure of the common dentex around Corsica Island, using a combination of markers that have different spatial and temporal scales of integration: microsatellite DNA markers, otolith shape analysis and parasites communities. A complex population structure around Corsican coasts has been reported, providing a new perspective on common dentex fishery stock conservation and management strategies.

This thesis make a significant contribution to the knowledge of several aspects of the fisheries, biology and population structure of common dentex around Corsica Island and recommends protection measures to promote sustainable management of this important halieutic resource in Corsica.

Key Words: *Dentex dentex*, Artisansal/recreational Fishing, Age/growth, Population structure.

Riassuntu

U dentici, chjamatu spessu denti, *Dentex Dentex* (Linnaeus, 1758) hè un pesciu marinu custieru (0-200 meteri) emblimaticu è patrimoniali di u Maritarraniu. Rapisenta un intaressu icunomicu primurosù pà a pesca artigianali è ricriativa, soprattuttu in Corsica. Cum'è pridaghju superiori, u dentici si trova in una pusizioni cintrali in cima di a piramida tropica. Dispona d'un statutu di cunsirvazioni postu ch'eddu hè classificatu cum'è « vulnerabili » da l'UICN. Ancu ch'eddu sia impurtanti à liveddu iculogicu è icunomicu, i dati dispunivuli nantu à sta spezia sò pochi.

L'ughjettivu di 'ssa tesa hè d'amiliurà i cuniscenzi nantu à u sfruttu, a biulugia è a struttura di popolazioni di u dentici in Corsica. Prima, un travaddu di sintesi bibbiugraficu hè statu fattu, raccogliendu tutti l'infurmazioni parcillarii ch'è asistanti nantu à a biulugia, u sfruttu è a struttura di popolazioni di u dentici nantu à l'insemi di a so aghja di spartera. Di regula, ci hè un mancu d'infurmazioni ma pà via di l'assi sviluppati, stu manuscrittu parmetta d'avè una visioni chjara di i cuniscenzi attuali è di ciò ch'eddu ferma à fà. In un sicondu tempu, un studiu hè statu fattu pà circà à sapè ch'è sò i fattori ch'è poni influenzà i variazioni spaziotimpurali di i presi (CPUE) di u dentici da a pesca artigianali è discrive a struttura dimugrafica di a popolazioni sfruttata in Corsica. I CPUE sò svariati in u spaziu (profundezza) è in u tempu (mesi) ma ani musciatu una stabilità annuali. I risultati ani missu à palesu un sfruttu di primura (individui grandi / vechji) à u mesi di maghju mentri u piriudu di ripruduzioni. Stu studiu hà datu dinò i primi carti pricisi à liveddu spaziali di u dentici, cù l'identificazioni di « hot spots », ch'è raprisentanti di sicuru abitaculi di primura in a storia di a vita di sta spezia. In un terzu tempu, un studiu hà apparacunatu u sfruttu di u dentici da a pesca artigianali è ricriativa ind'è a riserva naturali di i bocchi di Bunifaziu. U Dentici hè toccu da una grandi varietà d'ardigni, sò u palamitu (pesca artigianali) è a canna (pesca ricriativa) ch'è prasintanti i parcentuali di sfruttu i più impurtanti. À liveddu spaziali, i presi erani quantitavamenti à u massimu in i zoni di prutezzioni rinfurzati. I risultati indettani ch'è a pesca ricriativa cuntribuiscia assai à a murtalità pà via di a pesca di sta spezia (3,4 tonnelli à l'annu voli di 37% di l'insemi di i presi). Eppo, un paraconi di i trè sfarenti metudi di stimazioni di l'età (scaglii, otoliti sani è ammuzzati) hè statu fattu pà valutà ch'è era a struttura a più sicura è a più pricisa è pà difiniscia i parametri di crescita di u dentici in Corsica. À partasi da i risultati uttenuti, a littura nantu à a scaglia pari a più sicura sin'à cinque anni, a littura nantu à otolitu sani sin'à dodeci anni è nantu à otolitu ammuzzatu pò essa aduprata pà ogni annu (età supranu di 36 anni). Pà compia, st'ultimu capitulu avia pà fini d'identificà a struttura di i riservi di u dentici ingiru à a Corsica, pà via d'un metudu otolisticu, cù una cumbinazioni di marcatori : i microsattelliti, l'analisi di a forma di l'otoliti è i cumunità di i parassiti. Hà missu in baddu una strutturazioni spaziali cumplessa di a popolazioni, dendu pruspettivi novi pà a cunservazioni di i riservi di u dentici in Corsica.

Sta tesa ci porta cuniscenzi novi nantu à u sfruttu, a biulugia è a struttura di a popolazioni di u dentici in Corsica è arricumanda misuri di prutezzioni pà prumova una gistioni durabili di sta risolza in Corsica.

Paroddi primurosi : dentici, pesca artigianali/ricriativa, età/crescita, struttura di popolazioni.