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Manon Mercader

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Manon Mercader. Rôle des infrastructures portuaires dans le maintien des populations de poissons côtiers : apports de la restauration écologique. Océan, Atmosphère. Université de Perpignan, 2018. Français. NNT : 2018PERP0027 . tel-01955161

HAL Id: tel-01955161

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THÈSE

Pour obtenir le grade de
Docteur

Délivré par
UNIVERSITE DE PERPIGNAN VIA DOMITIA

Préparée au sein de l'école doctorale Energie
Environnement
Et de l'unité de recherche CEFREM (UMR 5110)

Spécialité : **Océanologie**

Présentée par **Manon Mercader**

**Rôle des infrastructures portuaires dans le
maintien des populations de poissons côtiers
Apports de la restauration écologique**

Soutenue le 26 Avril 2018 devant le jury composé de

Rachid Amara, Professeur, Université de Côte d'Opale	Rapporteur
Pierre Boissery, Chargé de Mission, AERMC	Membre invité
Thierry Dutoit, Directeur de Recherche, IMBE	Rapporteur
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Marion Verdoit-Jarraya, Maitre de Conférence, Université de Perpignan	Co-directrice

L'homme et la mer

Homme libre, toujours tu chériras la mer !
La mer est ton miroir ; tu contemples ton âme
Dans le déroulement infini de sa lame,
Et ton esprit n'est pas un gouffre moins amer.

Tu te plais à plonger au sein de ton image ;
Tu l'embrasses des yeux et des bras, et ton coeur
Se distrait quelquefois de sa propre rumeur
Au bruit de cette plainte indomptable et sauvage.

Vous êtes tous les deux ténébreux et discrets :
Homme, nul n'a sondé le fond de tes abîmes ;
Ô mer, nul ne connaît tes richesses intimes,
Tant vous êtes jaloux de garder vos secrets !

Et cependant voilà des siècles innombrables
Que vous vous combattez sans pitié ni remord,
Tellement vous aimez le carnage et la mort,
Ô lutteurs éternels, ô frères implacables !

Charles Baudelaire



*The ocean deserve our respect and care,
but you have to know something before you can care about it.*

Sylvia Earle

Remerciements

*T*oute aventure a une fin et c'est ici que se termine celle de cette thèse.

Comme dans toute aventure le voyage n'a pas été paisible, mais c'est cela qui le rend intéressant, qui nous fait grandir et nous enrichit et quand le voyage touche à sa fin on regarde en arrière avec nostalgie et finalement ce sont des bons moments dont on se souvient. Le trajet parcouru durant ces années de doctorat, je le dois en grande partie à toutes les personnes, qui de près ou de loin, pour quelques heures ou plusieurs années ont partagé mon voyage, sans vous, rien n'aurait été possible. Aussi je tiens à tous vous remercier du fond du coeur. Il y a de fortes chances que j'oublie certains d'entre vous, j'espère que vous ne m'en tiendrez pas rigueur, je vais faire de mon mieux pour être la plus exhaustive possible.

Je tiens tout d'abord à remercier Philippe Lenfant, mon directeur de thèse, pour m'avoir donné l'opportunité de réaliser ce travail, mais surtout pour la confiance que tu m'as accordée. Il y a plusieurs années en arrière, alors que je ne trouvais pas de stage de Master 1 et ne souhaitais en aucun cas m'engager sur la voie de la recherche, tu as cru en moi et m'as poussé sur cette voie qui aujourd'hui est devenue la mienne. Un passage par Paris et les cocotiers de Nouvelle-Calédonie plus tard, tu m'as à nouveau fait confiance et cette thèse a commencé. Le chemin a été jalonné d'embuches, il est peut être même plus accidenté que je ne le pensais, mais il m'a rendu plus forte et les obstacles ont renforcé ma volonté à persévérer, je te suis vraiment reconnaissante de m'avoir conduit à m'y engager. Je remercie également Marion Jarraya, ma co-directrice, d'avoir rendu ce travail possible et de m'avoir accompagnée pendant ces quelques années.

Je souhaite tout particulièrement à remercier les membres du jury d'avoir accepté de prendre de leur temps pour évaluer ce travail de thèse et pour l'intérêt porté à mon sujet.

Je remercie également l'actuel directeur du CEFREM, Wolfgang Ludwig, ainsi que son prédécesseur, Serge Heussner, de m'avoir accueillie dans leur laboratoire et de m'avoir fait confiance pour mener à bien ce travail de thèse.

Je remercie aussi l'Agence de l'Eau Rhône Méditerranée Corse pour le soutien financier, et plus particulièrement Pierre Boissery pour son implication dans la thématique de la restauration écologique en zone portuaire. Mes remerciements vont également à la société Écocean, notamment à son fondateur et président Gilles Lecaillon. C'est en grande partie de la collaboration entre ces deux entités et le CEFREM qu'est né ce travail de thèse. Je vous remercie donc d'être à l'origine de cette thématique qui pouvait sembler complètement saugrenue et qui aujourd'hui encore, soulève de nombreux débats. Ce n'est pas tout le monde qui aurait pensé à aller s'occuper des bébés poissons dans les ports !

J'adresse mes remerciements à Benjamin Gourbal et David Mouillot pour avoir participé à mes Comités de Suivi de Thèse, vos conseils et commentaires furent constructifs et m'ont aidé à rester sur le bon chemin.

Ce travail n'aurait pas été possible sans la collaboration avec les gestionnaires de ports qui m'ont accordé l'autorisation de m'immerger dans ces zones habituellement totalement interdites à la plongée. Merci d'avoir rendu possible cette étude et de m'avoir facilité ce travail d'échantillonnage s'avérant parfois difficile.

Ces années de thèse n'auraient pas été ce qu'elles ont été sans les membres de l'équipe du CREM, j'aurais peut-être abandonné mille fois si vous n'aviez pas été là, aussi je vous adresse à tous un grand merci ! Adrien et tes conseils avisés et ta gentillesse, Jérémy et tes remarques cinglantes mais ton grand cœur, Alex pour nos échanges sur tout et rien dans notre bureau tropical, Romain pour nos trajets mouvementés en voiture et ta rigueur sans égale pour vérifier les tableaux, Alan pour nos sessions courses à pieds, sans ta motivation je ne me serais jamais maintenue en forme ces dernières années, Nico pour l'initiation à l'apnée et pour m'avoir rappeler à l'ordre quand je devenais un « un vieux serran aigri », Gilles pour tes conseils de terrain et les sorties NEV au cours desquelles j'ai bien failli mourir gelée, merci à tous.

Je tiens également à remercier les membres de la « eel team » pour leur bonne humeur et leurs encouragements et tout particulièrement Betty pour m'avoir accompagné avec bienveillance sur toute la durée de cette thèse et même avant. Des échanges scientifiques, à nos soirées endiablées en concert, en passant par nos sessions de gainage et les heures que tu as pu passer à m'écouter m'apitoyer, merci d'avoir été présente dans tous ces moments et d'avoir su trouver les mots pour me reconforter.

Je remercie les nombreux stagiaires que j'ai vu passer durant ces années, je ne vous citerai pas tous mais tout de même quelques mots pour ceux que j'ai encadré. Camille et Remy vous étiez les premiers et j'espère que cette expérience « professionnelle » a été enrichissante, merci pour votre bonne humeur, Julien merci pour la quantité et la qualité du travail que tu as fourni, de même pour Christophe et en plus un grand merci pour ta zenitude presque désarçonnante qui a su contrebalancer mon humeur parfois massacrant. Je remercie aussi Mary pour nos bons moments entre filles et la qualité de son travail ainsi que Quentin pour m'avoir si souvent accompagné durant ma première année de terrain et tant fait rire dans ces moments souvent éprouvants.

Merci aussi à Laurent ; bientôt 7 ans qu'on se supporte maintenant, de binome de TP à thésards dépravés, je me serais sacrément ennuyée sans toi ! Merci à Mohsen de « m'avoir sauvé » en m'expliquant de nouvelles méthodes statistiques et pour son enthousiasme. Ainsi « qu'aux filles », Éléonore, Marjorie et Mégane, bien que vous soyez arrivées il y a seulement quelques mois, votre présence féminine dans ces bureaux jusqu'à présent quasi exclusivement masculin et vos encouragements sur ces derniers mois ont été très appréciés.

Merci à " el magnifico artista " Cyril Girard de m'avoir gentiment fourni certains de ses dessins pour illustrer ce manuscrit et à Didier Fioramenti pour les photos. Merci aussi à tous ceux que j'ai rencontré et avec qui j'ai échangé sur mon sujet me permettant de mieux l'appréhender et de l'enrichir. Je pense à Marc et Pierre, aux membres de l'équipe d'Écocéan, de la Réserve marine de Cerbères-Banyuls et du Parc marin du Golfe du Lion, ou encore à Fabien, Mathieu, Didier, ainsi qu'à tous les autres que je ne citerais pas sous peine de ne jamais terminer ces remerciements !

Enfin merci à mes amis, de m'avoir encouragé même si vous ne comprenez pas toujours ce que fait réellement « la fille qui compte les poissons » !!!

Et surtout à ma famille de m'avoir depuis toujours, et quelques soient mes choix, soutenue, encouragée, accompagnée et aidée (et supportée malgré mon horrible caractère !). Je vous suis reconnaissante d'avoir fait de moi la femme que je suis aujourd'hui. Un remerciement particulier à mon compagnon Olivier pour avoir fait certaines de mes figures ainsi qu'à ma grand-mère Daniele qui relit depuis des années tous mes documents, corrigeant les milliers de fautes que j'ai pu faire, cette thèse ne dérogeant pas à la règle.

La fin d'une aventure n'est que le commencement des prochaines...

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Chapitre 1 :

Introduction générale



1- Les petits fonds côtiers, des écosystèmes à forts enjeux

1.1 Le milieu marin : importance et menaces

Les océans recouvrent plus de 70% du globe et, bien que remarquable, ce chiffre ne reflète pas toute la réalité de leur importance. En effet, cette vision en deux dimensions néglige un aspect essentiel, le volume en trois dimensions occupé par la biosphère. Sur terre ce volume est relativement restreint, s'étendant de la cime de la canopée à quelques mètres sous terre où pénètrent les racines et vivent les vers et micro-organismes. Dans l'océan, il en est tout autrement, avec une profondeur moyenne d'environ 3 km, ils représentent quelques 99% de la biosphère totale de la planète (Dawson, 2012). Dans les mers et océans du globe chaque goutte d'eau contient la vie qu'ils ont d'ailleurs vu apparaître. Dans tous les phylum connus à l'heure actuelle (à l'exception des Onychophores), il existe des espèces marines ayant vu le jour bien avant les espèces terrestres (May, 1994). Les océans fournissent approximativement la moitié de l'oxygène de notre atmosphère (via le phytoplancton) et ils jouent également un rôle crucial dans la régulation du climat ce qui en fait un élément central du fonctionnement de la planète. Chaque être vivant dépend directement ou indirectement des océans et cela est particulièrement le cas pour l'Homme, pour qui ils procurent en outre de nombreux biens et services. Les écosystèmes marins jouent un rôle dans la purification de l'eau et la protection des côtes, ils sont source d'une grande variété de molécules d'intérêt pharmaceutique et fournissent également des bénéfices culturels et récréatifs (plongée, pêche de loisir, aquariophilie...) dont les retombées économiques sont capitales pour de nombreuses régions. Ils approvisionnent surtout plusieurs millions de personnes en leur procurant leur ressource alimentaire principale (notamment via la pêche et l'aquaculture) (Holmlund and Hammer, 1999; Liqueste et al., 2013; Sumaila et al., 2011). Aujourd'hui, les poissons représentent 17% des apports en protéines animales de la population mondiale et leur consommation ne cesse d'augmenter depuis les 50 dernières années passant de 9.9 kg par capita dans les années 1960 à 19.7 kg en 2013 (FAO, 2016). Avec l'augmentation de la population humaine, prédite pour atteindre 9 milliards de personnes d'ici 2050, une augmentation de la demande alimentaire est attendue, notamment en poisson (environ 75 million de tonnes pour les 2 milliards de personnes supplémentaires prédits (Rice and Garcia, 2011)).

Si l'aquaculture, en constant développement depuis les années 1970 (dont la part représentait 7% du total de poissons consommés en 1974 contre 39% en 2004) pourrait en partie répondre à cette demande, les captures par pêche stagnent depuis le début des années 1990

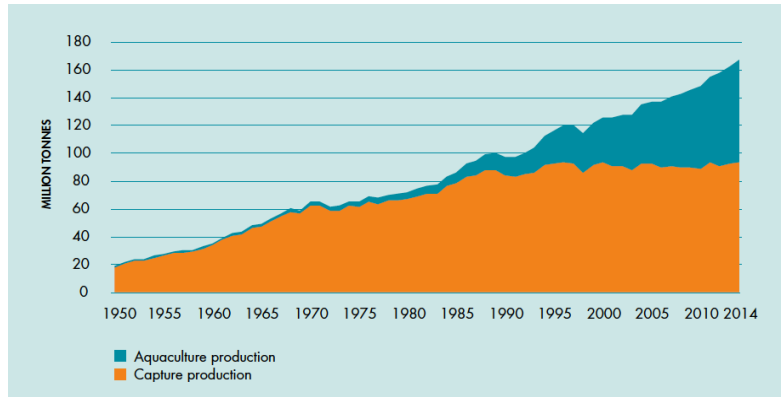


Figure 1 : Production mondiale des pêches de capture et de l'aquaculture (FAO, 2016)

(FAO, 2016) (Figure 1) malgré l'intensification des efforts de pêche, témoignant de l'épuisement des stocks de poissons à l'échelle mondiale (Blasiak, 2015; Pauly et al., 2002). En effet, la surpêche est responsable de la majorité des déclin de populations marines (Dulvy et al., 2003), avec 20 à 25% d'espèces menacées d'extinction (Webb and Mindel, 2015).

Outre la surpêche, les activités humaines sont une source d'autres pressions sur les milieux marins comme la pollution, la destruction d'habitat, l'introduction d'espèces exotiques (Figure 2) (Airoldi and Beck, 2007; Crain et al., 2009; Dugan et al., 2011; Halpern et al., 2008, 2015).

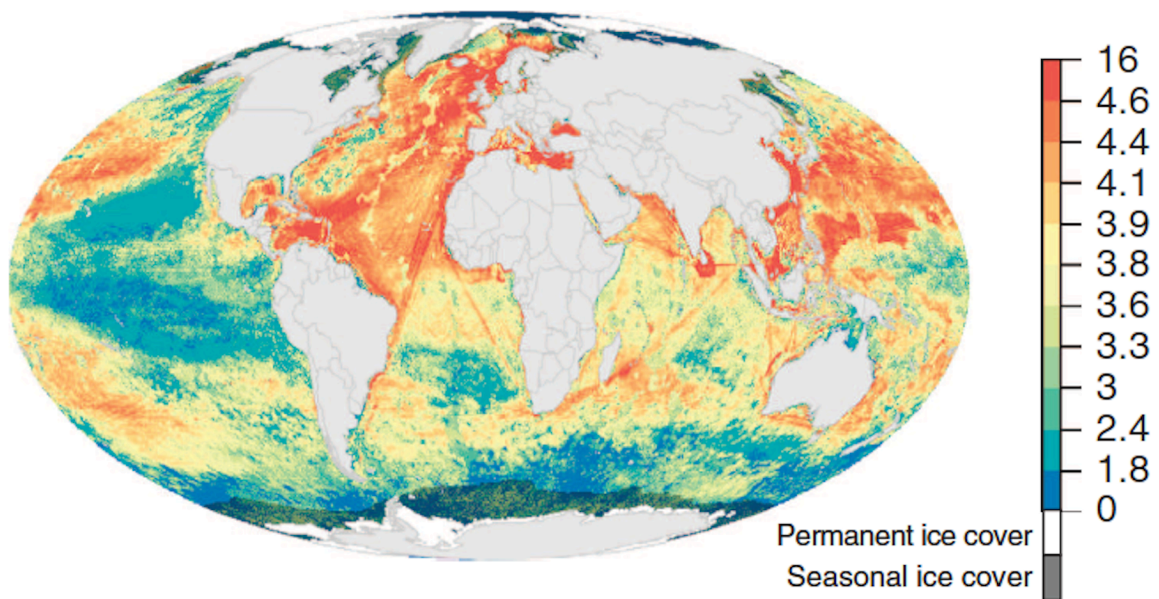


Figure 2 : Impacts cumulés des activités humaines sur les écosystèmes marins en 2013. Le score d'impact est calculé sur 19 pressions anthropiques associées à la pêche, la destruction d'habitat, la pollution et au réchauffement climatique (Halpern et al., 2015).

Les effets globaux du changement climatique, bien que difficilement quantifiables, menacent aussi le milieu marin. Par exemple, l'aire de répartition de nombreuses espèces se décale (García Molinos et al., 2015; Poloczanska et al., 2013), les épisodes de blanchissement des coraux sont de plus en plus réguliers et intenses (Hughes et al., 2017). Ainsi, ces pressions anthropiques, en constante augmentation (Halpern et al., 2015), sont la cause d'une continuelle perte de biodiversité (Worm et al., 2006) (Figure 3).

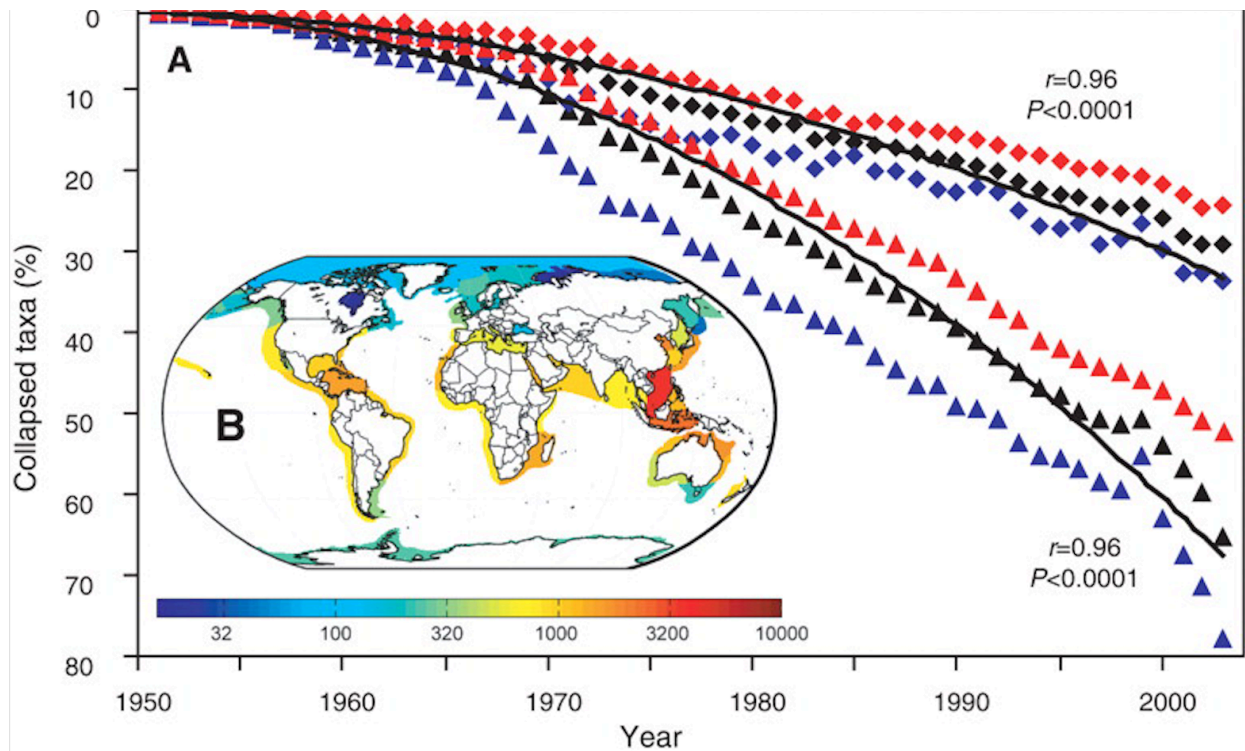


Figure 3 : Perte globale d'espèces pour les grands écosystèmes marins. (A) Trajectoires d'effondrement pour les poissons et invertébrés (losange : effondrements par année, triangle : effondrement cumulés), pour tous les grands écosystèmes ensemble (noir), les écosystèmes avec moins de 500 espèces (bleu), et ceux avec plus de 500 espèces (rouge). (B) Carte des 64 grands écosystèmes marins utilisés pour l'étude colorés en fonction de leur nombre d'espèces de poissons (Worm et al., 2006).

1.2 Le dilemme des zones côtières

Les zones côtières représentent moins de 15% de la surface de terre de la planète, mais concentrent plus de 60% de la population humaine (EEA, 1999) et cette proportion devrait atteindre les 75% d'ici 2025 (Airoldi and Beck, 2007; Crain et al., 2009; Dugan et al., 2011). Par conséquent le niveau d'activité humaine (pêche, transport, industrie, activités récréatives...) y est considérable entraînant des impacts particulièrement élevés sur les écosystèmes côtiers. A l'interface terre-mer, le développement urbain, commercial, industriel et touristique, ainsi que le besoin de protéger les côtes de l'érosion et des

inondations ont renforcé l'essor des infrastructures littorales (ports, marinas, brise-lames, épis, digues...). Il en résulte une artificialisation croissante du littoral à l'échelle mondiale. En Méditerranée française par exemple, le taux d'occupation des fonds entre 0 et -10m a été multiplié par trois depuis 1975, et celui de linéaire artificialisé est passé de moins d'1% à plus de 10% (Figure 4). En Californie, en Virginie ou encore dans le Maryland plus de 50% des fonds meubles naturels ont été remplacés par des structures artificielles (Hardaway and Duhring, 2010), avec pour conséquence majeure la destruction de l'habitat (McKinney, 2006) causant de sévères dommages aux environnements côtiers (Bulleri and Chapman, 2010; Gerland et al., 2014; Halpern et al., 2008; Scyphers et al., 2015).

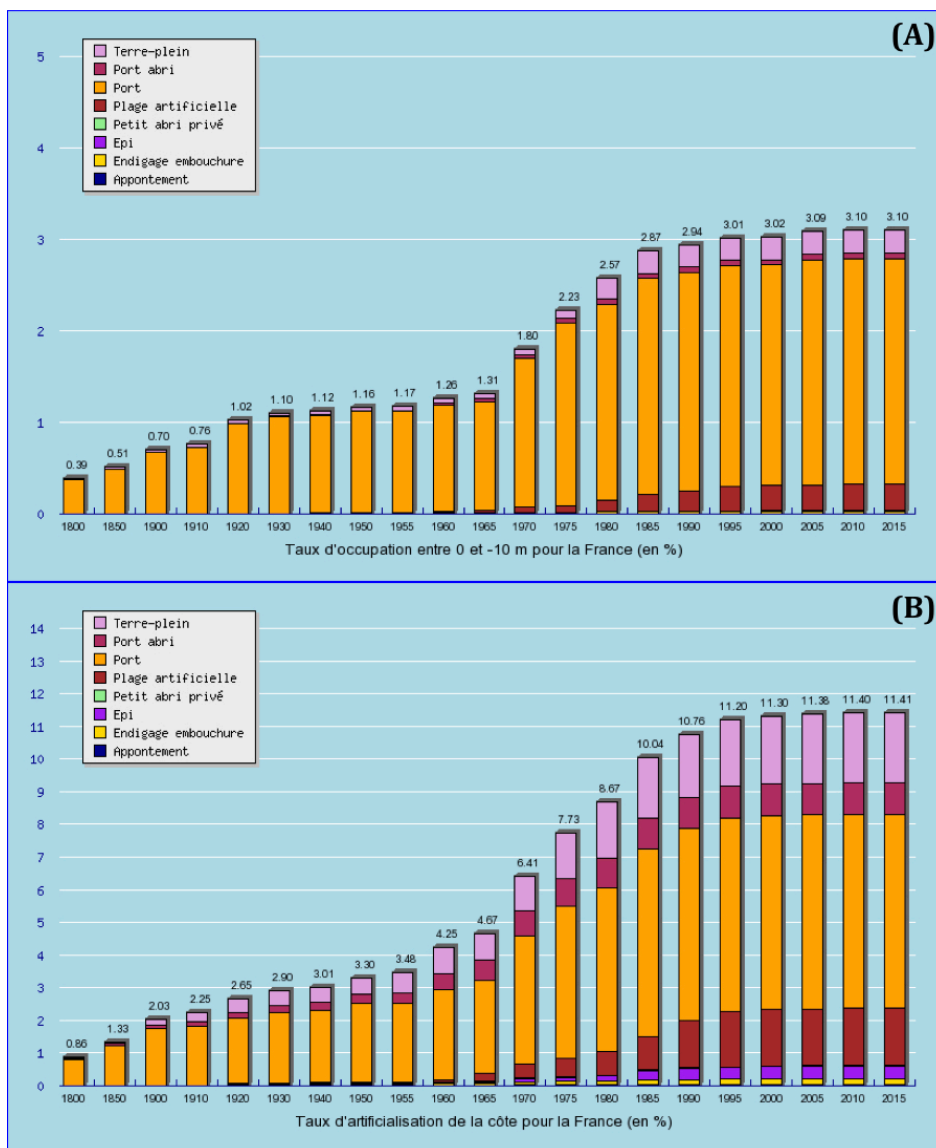


Figure 4 : Évolution du taux (A) d'occupation des fonds de 0 à -10m et (B) d'artificialisation de linéaire côtier en Méditerranée française entre 1800 et 2015 (MEDAM, 2015)

L'augmentation constante des pressions anthropiques sur la bande littorale est inquiétante car, bien que n'occupant que 0.5% du volume des océans, les eaux côtières sont d'une grande importance fonctionnelle. Leur production est équivalente à celle des forêts tropicales (Odum and Barrett, 1971) et représente 30% de la production totale des océans (Liu et al., 2010; Mantoura et al., 1991). Cette forte productivité ainsi que la diversité d'habitats qu'elles fournissent en font des zones particulièrement riches et indispensables à de nombreuses espèces, par exemple 50% des espèces de poissons sont inféodées aux zones côtières (Mora et al., 2008). Par ailleurs, les atteintes à l'intégrité de l'habitat (modification, fragmentation, destruction) sont considérées comme une des plus grande menace pour les écosystèmes marins et leur biodiversité (Airoldi and Beck, 2007; Coll et al., 2010; Dafforn et al., 2015; Gray, 1997; Halpern et al., 2008; Lotze et al., 2006; Seaman; 2007).

1.3 Importance de l'intégrité du paysage sous-marin

Par analogie avec le milieu terrestre, un paysage sous-marin est un ensemble hétérogène d'unités paysagères submergées. Pour les petits fonds côtiers (frange littorale comprenant l'infralittoral ainsi que les milieux de transition tels que les estuaires ou les lagunes), ces unités ou patches de nature géomorphologique et biologique différentes forment une mosaïque (Boström et al., 2011; Chapman, 1995) caractérisée par sa composition en terme de type de patch et d'arrangement spatial de ces patches (Wedding et al., 2011). Ces unités sont généralement définies suivant leur fonctionnement écologique et correspondent à des habitats benthiques aux caractéristiques environnementales propres (type de substrat, profondeur, disponibilité en nourriture et refuge) (Chapman, 1995; Fraschetti et al., 2008). Le paysage sous-marin est alors la somme de tous les habitats qui le composent dont le fonctionnement écologique en tant qu'ensemble diffère de la simple addition des propriétés de chaque habitat pris séparément, les interactions entre habitats générant de nouvelles propriétés (Boström et al., 2011; Macreadie et al., 2010). La complémentarité entre habitats implique les échanges d'énergie et de matière (effets directs) mais également des effets indirects (Alsterberg et al., 2017). Par exemple dans les écosystèmes marins tropicaux, mangroves et récifs coralliens interagissent, les mangroves servant de nurseries pour de nombreuses espèces, influencent ainsi la biomasse et la structure des communautés des récifs adjacents, qui à leur tour protègent les mangroves

en faisant office de brise-lames (Ferrario et al., 2014; Harborne et al., 2006; Mumby et al., 2004). Différentes unités paysagères peuvent également avoir différentes fonctions écologiques indispensables au renouvellement des populations (zones de frayères, de nurseries...). Les échanges entre habitats dépendent de la connectivité du paysage c'est-à-dire du « degré avec lequel le paysage facilite ou entrave les mouvements des individus entre les parcelles de ressources » (Taylor et al., 1993). La connectivité dépend ainsi des facteurs environnementaux, de l'agencement paysager et des caractéristiques des espèces et repose sur la notion clé d'hétérogénéité spatiale et temporelle. La connectivité biologique peut se diviser en deux composantes :

- la connectivité structurelle, qui correspond à la structure du paysage (*i.e.* l'agencement spatial des différentes unités paysagères) ; elle équivaut donc à la connectivité potentielle offerte par le paysage (Fischer and Lindenmayer, 2007; Tischendorf and Fahrig, 2000) ;
- la connectivité fonctionnelle qui dépend des traits de vie des espèces, en particulier de leurs capacités dispersives mais également de leur comportement et de leur préférence d'habitat ; elle correspond donc à la réponse des organismes à la structure du paysage (Auffret et al., 2015; Baguette and Van Dyck, 2007; Watts and Handley, 2010).

La fragmentation de l'habitat tend à réduire la connectivité, alors que l'homogénéisation du paysage tend à réduire la fonctionnalité qui sont toutes deux des composantes majeures du maintien de la biodiversité (Alsterberg et al., 2017; Crooks and Sanjayan, 2006; Taylor et al., 1993).

1.4 Importance de l'habitat pour le cycle de vie des poissons marins côtiers

L'hétérogénéité et la complexité offerte par la mosaïque du paysage sous-marin des petits fonds côtiers procure une grande diversité d'habitats fournissant refuge et nourriture pour les juvéniles de nombreuses espèces (Beck et al., 2001; Nagelkerken et al., 2000; Shulman, 1985). Tous les éléments composant le paysage des zones côtières ne sont pas équivalents en terme de productivité pour les juvéniles. En effet, certains habitats comme les mangroves ou les herbiers par exemple, abritent de fortes densités en juvéniles alors que des habitats adjacents sans couvert végétal présentent des densités bien moindres (Hutchings and Recher, 1974; Orth et al., 1984; Williams, 1955). Cela a mené à définir un cadre standardisé permettant d'évaluer l'importance relative des habitats juvéniles dont les plus productifs (en terme de juvéniles) sont considérés comme nurserie.

Dans ce cadre, une nurserie est définie comme un habitat dont la contribution moyenne par unité de surface à la population adulte est plus élevée que celle fournie par d'autres habitats dans lesquels se trouvent également des juvéniles. Cette meilleure contribution au recrutement peut résulter de toutes les combinaisons de quatre facteurs : des densités plus élevées, un meilleur taux de croissance, un taux de survie plus élevé et des déplacements vers les habitats adultes plus importants (connectivité)(Beck et al., 2001). Suivant cette définition un habitat n'abritant que de faibles densités en juvéniles mais occupant une large proportion du paysage sous-marin n'est pas considéré comme une nurserie, pourtant sa contribution à la population adulte peut être importante. Par exemple, pour deux habitats, l'un d'une surface de 100 m² dont la contribution à la population adulte est de 15 individus / m² et l'autre d'une surface de 1000 m² mais ne contribuant que pour 5 individus / m², le premier sera considéré comme une nurserie et pas le second, et ce, même si leur contribution totale respective est de 1500 contre 5000 individus. Afin de prendre en compte tous les habitats dont le rôle peut être crucial pour le maintien des populations, Dahlgren et al. (2006) ont introduit le concept « d'habitat juvénile effectif » pour désigner ces habitats dont la contribution totale est potentiellement élevée mais dont la contribution par unité de surface est faible. Ces habitats sont donc d'importants habitats juvéniles mais ne sont pas des nurseries. Ces deux concepts sont complémentaires, mais leur distinction est importante, notamment dans une optique de conservation, restauration ou gestion où des financements limités nécessitent d'établir des priorités (Beck et al., 2001).

Les nurseries font partie des « habitats essentiels » c'est-à-dire des habitats indispensables à l'accomplissement du cycle biologique d'une espèce. Pour les poissons, il s'agit « des eaux et du substrat nécessaires pour frayer, se nourrir et croître jusqu'à maturité » (Benaka, 1999). La majorité des poissons côtiers ont un cycle de vie complexe composé de deux phases, une pélagique et l'autre benthique (Armsworth, 2002; Jones, 1988; Mora and Sale, 2002; Öhman et al., 1998). La première est dite dispersive, les œufs puis les larves sont transportés au gré des courants ; son issue est marquée par une métamorphose des larves que l'on appelle alors post-larves (ou larves « compétentes »). Ces post-larves sont capables de nager activement afin de coloniser les côtes (Hindell et al., 2003). Après quelques heures, les survivantes se métamorphosent en juvéniles qui doivent faire face à un nouvel environnement benthique (Balon, 1999; Planes and Lecaillon, 2001). Ils sont en effet exposés à un substrat hétérogène abritant d'éventuels prédateurs et compétiteurs intra- ou interspécifiques et doivent alors faire un choix d'habitat leur garantissant la

meilleure probabilité de survie (compromis entre dépenses énergétiques et risques associés à l'habitat le plus proche) (Gibson et al., 2002). Cette phase de transition entre les milieux pélagique et benthique est appelée installation (Adams et al., 2004; Andrews and Anderson, 2004; Carr and Hixon, 1995; Caselle and Warner, 1996; Risk, 1997). Au bout d'une période variant de quelques mois à plusieurs années suivant l'espèce, les juvéniles intègrent la population adulte, c'est la phase de recrutement (McCormick and Kerrigan, 1996; Shapiro, 1987) (Figure 5). La réalisation du cycle biologique et donc le renouvellement et le maintien des populations, dépend du succès de chacune de ces étapes du cycle de vie (reproduction, dispersion, colonisation, installation et recrutement) (Doherty, 1991; Doherty and Williams, 1988) et donc en grande partie de la disponibilité et de la qualité des habitats essentiels. Les variations de l'intensité du recrutement dépendent de processus pré- et post- installation. Les premiers déterminent la quantité initiale de larves arrivant sur la côte (hypothèse du recrutement limitant (Doherty, 1991)). Il peut s'agir de mécanismes influençant la reproduction, la survie larvaire ou la dispersion, comme les conditions hydrologiques, la température ou encore la disponibilité en nourriture (Asplin et al., 1999; Pineda et al., 2010; Watson and Munro, 2004; Zhang et al., 2014). Si l'approvisionnement larvaire est un facteur important dans la régulation du recrutement, il n'est pas rare que la quantité de nouvelles recrues ne soit pas corrélée à celle de larves étant arrivées sur la côte (Bradford and Cabana, 1997; Pineda et al., 2010; Rooper et al., 2004). Cela souligne l'importance des processus post-installation, c'est-à-dire de la survie et de la croissance des juvéniles qui dépendent directement de la disponibilité et de la qualité des habitats juvéniles (Beck et al., 2001; Cheminée et al., 2014; Nagelkerken et al., 2015; Parsons et al., 2014, 2015). La notion d'habitat essentiel à l'installation conditionne ainsi pour une grande part la réussite du recrutement qui lui-même conditionne la pérennité des ressources (Bellwood and Hughes, 2001; Schmitt, 1999). Les atteintes à ces habitats juvéniles sont ainsi l'une des principales causes de diminution ou d'extinction des poissons marins côtiers (Able et al., 1998; Gibson, 1994).

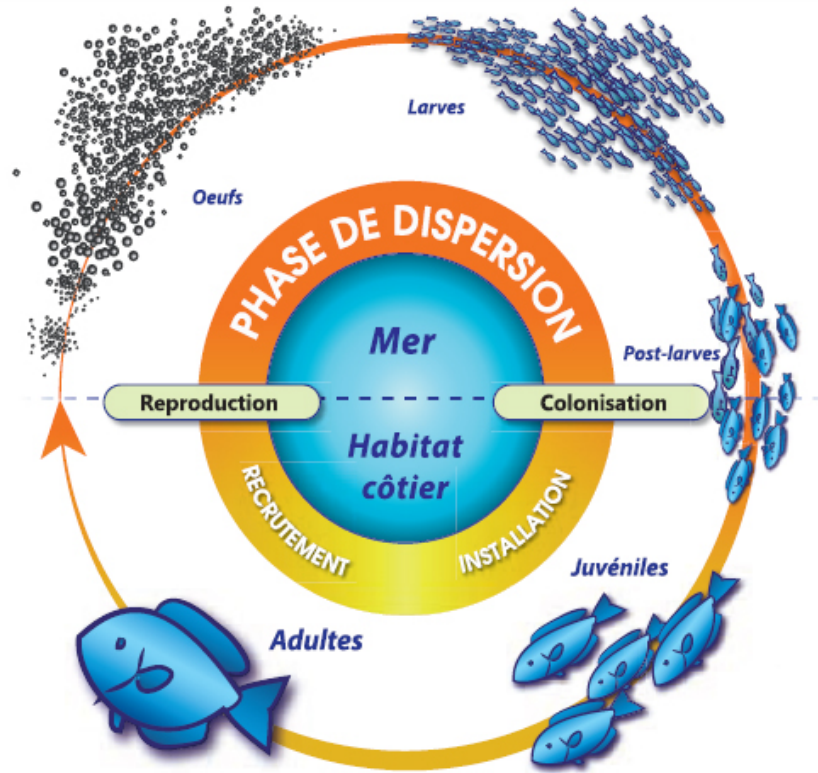


Figure 5 : Cycle de vie des poissons marins côtiers (benthiques et necto-benthiques), modifié par Cyril Frédéric© d'après Pastor (2008).

2- La science au service du maintien des écosystèmes littoraux

De tout temps l'Homme a pratiqué certaines formes de conservation ou préservation de son environnement, que ce soit à des fins alimentaires ou sacrées. Toutefois, en réponse à l'augmentation incessante des impacts humains, ces actions se sont développées et diversifiées donnant naissance à des disciplines scientifiques à part entière, généralement regroupées sous l'appellation d'écologie appliquée (Hunter and Gibbs, 2007). Parmi ces disciplines, deux sont d'un intérêt particulier dans ce travail de thèse, la biologie de la conservation et l'écologie de la restauration.

La biologie de la conservation est la science du maintien de la diversité biologique de la planète. Si ces racines sont vastes et anciennes, la discipline n'a réellement émergé qu'en 1978 suite à la Première Conférence Internationale sur la Biologie de la Conservation. D'abord centrée sur la sauvegarde d'animaux menacés (particulièrement d'espèces emblématiques ou d'intérêt commercial), elle s'est petit à petit développée avec l'idée que la diversité biologique n'inclut pas seulement les espèces mais s'étend des gènes aux

écosystèmes, la menant à être aujourd'hui une discipline phare (CBD, 1992; Hunter and Gibbs, 2007).

Tout aussi ancienne mais peut-être un peu moins répandue, l'écologie de la restauration a pour objet d'étude les mécanismes de réparation des écosystèmes. L'action de réparation en elle-même étant appelée restauration écologique (Galatowitsch, 2012; 2012). Etant au centre de cette thèse, les définitions et concepts liés à cette discipline sont plus amplement détaillés dans les sections 2.3 et 2.4.

Par ailleurs, ces deux disciplines portent sur des approches transdisciplinaires faisant appel à de nombreux domaines comme par exemple la sociologie, la philosophie, l'économie ou encore le droit et l'éducation (Figure 6), mais trouvent essentiellement leurs fondements dans l'écologie dont certains principes sont rappelés dans la section 2.2. Ces sciences « au service d'une mission » (conserver ou restaurer la biodiversité) sont parfois désignées comme des disciplines de crise car les mécanismes qu'elles visent à décrire doivent être rapidement compris afin d'intervenir dans les plus brefs délais (DeSalle and Amato, 2004; Soulé, 1985). Ce besoin d'action dans l'urgence nécessite parfois d'agir sans l'entière connaissance de la totalité des mécanismes impliqués, ce qui leur vaut parfois la critique d'autres domaines scientifiques. Toutefois, cela engendre aussi un développement rapide et important d'outils permettant de répondre aux problèmes posés par ces crises (par exemple les avancées technologiques en génomique ou encore le développement de modèles statistiques de plus en plus performants), qui bénéficient également aux autres sciences (DeSalle and Amato, 2004; Hunter and Gibbs, 2007). Ces deux disciplines représentent deux approches distinctes qui servent finalement un intérêt commun, maintenir la biodiversité de notre planète en faisant le lien entre Science, Politique et aspects pratiques. Malgré ces finalités partagées, leurs approches et buts spécifiques divergent entraînant une réelle dichotomie entre elles. Pourtant, intégrer conservation et restauration en combinant leurs méthodes respectives aux services d'aboutissants communs permettrait certainement des gains considérables d'efficacité (Wiens and Hobbs, 2015; Young, 2000).

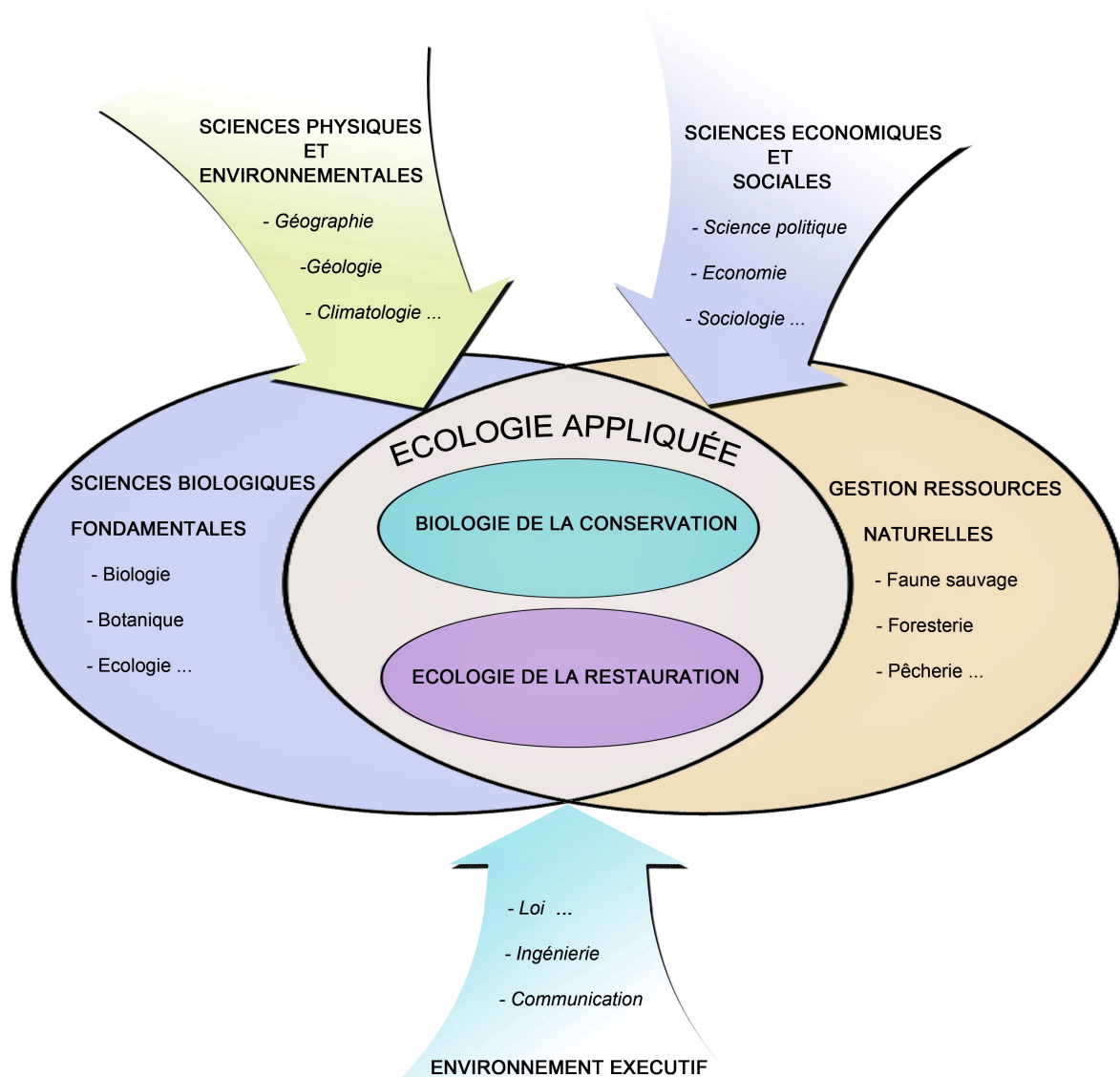


Figure 6 : Représentation schématique de la relation entre l'écologie appliquée (et notamment la restauration écologique) et les autres disciplines , modifié d'après Jacobson (1990).

2.1 Objectifs et outils de conservation en milieu marin

Le maintien des écosystèmes marins associé à l'exploitation durable des ressources marines est une problématique globale de plus en plus préoccupante (cf. section 1.1). Ainsi, les efforts de conservation se multiplient dans de nombreuses zones géographiques afin de répondre aux objectifs fixés par les politiques globales (Watson et al., 2014). La mise en place de gestions des pêches (quotas/taille minimale de captures...) représente une des premières mesures de conservation utilisée afin de garantir une exploitation durable des stocks. Ces mesures ne sont toutefois bénéfiques qu'à certaines espèces et sont souvent insuffisantes pour garantir le maintien de certains stocks. Par suite, la gestion du milieu

marin s'est diversifiée avec notamment la création d'un outil majeur et maintenant largement répandu, les Aires Marines Protégées (AMP) (Cochrane, 2002). Aujourd'hui, la Convention pour la Diversité Biologique préconise par exemple la protection d'au moins 10% de la surface des océans d'ici 2020 (CBD, 2011) et plus récemment le Congrès Mondial des Parcs de l' Union internationale pour la conservation de la nature (IUCN) demande une protection d'au moins 30% de chaque habitat marin (World Parks Congress, 2014). Il est avéré que les AMP sont un outil efficace de conservation de la biodiversité marine (Pauly et al., 2002) avec toutefois de grandes variations de cette efficacité suivant leurs caractéristiques (taille, âge, niveaux de protection et de gestion...) (Edgar et al., 2014). De plus, seulement 3% des 10% recommandés sont aujourd'hui protégés avec de grosses disparités géographiques et des niveaux de protection restant faibles dans la majorité des cas (autorisation de la pêche, peu de contrôle...) (Costello and Ballantine, 2015). Une des limites majeures des AMP réside dans la difficulté d'implémentation de cet outil du fait des enjeux économiques et sociétaux (Charles and Wilson, 2008; Jones, 2001) De plus, leur mise en place ne concerne que des zones relativement préservées, les zones déjà très dégradées, bien que nombreuses, bénéficient peu de ce type de mesure. Souvent considérées comme « perdues » pour la biodiversité elles sont généralement laissées à l'abandon. Toutefois, depuis quelques années, l'idée de restaurer une partie des habitats dégradés s'installe comme mesure complémentaire de la conservation afin de garantir le maintien des écosystèmes et de la biodiversité marine. Au niveau européen, la Directive Cadre Stratégie pour le Milieu Marin (DCSMM) dont l'objectif global est le maintien ou le retour au bon état écologique du milieu marin d'ici 2020, préconise non seulement de conserver des écosystèmes marins mais également de rétablir le fonctionnement des écosystèmes ayant subi de fortes dégradations (European Parliament, 2008). La transposition française de cette directive, le Plan d'Action pour le Milieu Marin (PAM), propose par exemple l'initiation d'opérations pilotes de restauration et la définition d'un cadre stratégique de restauration écologique des habitats naturels en Méditerranée (DIRMM, 2016). A l'international, les initiatives de restauration écologique en milieu marin se multiplient. En milieu tropical, cela se traduit essentiellement par la transplantation de coraux afin de restaurer les récifs ou encore par la restauration des mangroves (Epstein and Rinkevich, 2001; Goreau and Hilbertz, 2005; Kamali and Hashim, 2011; Lewis, 2005; Rinkevich, 1995, 2008; Shaish et al., 2008). En milieu tempéré, quelques programmes de restauration émergent également mais restent pour l'instant majoritairement axés sur de

l'éco-conception en zones urbaines avec pour objectif de favoriser la biodiversité ou certaines fonctions (Elmqvist et al., 2015; Shu-Yang et al., 2004). Toutefois, les programmes de restauration écologique en milieu marin sont bien plus récents et surtout bien moins nombreux qu'en milieux terrestre ou dulçaquicole. Aussi, un large travail aussi bien sur les concepts et fondations écologiques de la discipline, que sur les moyens techniques de mise en œuvre est nécessaire pour développer cette approche en mer et tendre vers une gestion intégrée et adaptative du milieu marin.

2.2 Perturbations et stabilité des écosystèmes

Afin de conserver ou restaurer un paysage, un écosystème ou une espèce, il est fondamental d'avoir une bonne compréhension de son fonctionnement. Ainsi, la notion de stabilité d'un écosystème ou de persistance d'une population est centrale dans la pratique de ces sciences. Au cours de son évolution tout système vivant (quel que soit son échelle : individu, communauté, paysage...) est soumis à des facteurs de perturbations qui peuvent être naturels, comme les tempêtes, les feux ou les maladies, ou anthropiques tels que la pollution, l'exploitation ou la destruction d'habitat. Ces perturbations peuvent entraîner des transformations dans l'état d'équilibre du système qui se traduisent par des changements de biomasse, de diversité ou de fonctionnement (productivité, flux...). Face aux perturbations, la stabilité du système est maintenue par la résistance et la résilience de ce dernier. La résistance correspond à sa capacité à garder son état d'équilibre, ou autrement dit, à l'intensité, la nature et la fréquence des perturbations que le système peut tolérer sans modification majeure de sa structure et de son fonctionnement (Connell and Sousa, 1983; Folke et al., 2004; GESAMP, 1995). La résilience est quant à elle une mesure de la capacité du système à revenir à son état d'équilibre après avoir subi des modifications suite aux perturbations. Elle est ainsi inversement proportionnelle au temps mis par l'écosystème pour revenir à son état initial (GESAMP, 1995; Holling, 1973; Lockwood, 2000). Si les perturbations sont trop intenses ou trop répétées, il est possible que l'écosystème ne puisse « récupérer », les modifications subies sont trop importantes pour qu'il revienne à son état d'équilibre initial, on considère alors qu'il a franchi un seuil d'irréversibilité. Le nouvel état dans lequel se retrouve alors l'écosystème est appelé état d'équilibre alternatif. Le chemin évolutif d'un écosystème au cours du temps, c'est-à-dire la succession de ses différents états ainsi que les itinéraires suivis suite aux perturbations est

appelé trajectoire (Figure 7). La stabilité d'un écosystème est généralement mesurée en terme de fonctions écologiques, ces fonctions diverses et variées englobent des processus écologiques allant du taux de production primaire à la dispersion de graines en passant par le taux de recyclage des nutriments ou encore l'épuration de l'eau pour ne citer que quelques exemples. Ces fonctions sont profondément liées à la diversité des communautés qui le composent, celle-ci pouvant, suivant l'échelle spatio-temporelle considérée et la nature des perturbations, augmenter ou au contraire réduire la stabilité d'un écosystème (ses capacités de résistance et résilience) (Dayton et al., 1992; Folke et al., 2004; Lavorel, 1999; Tegner et al., 1997).

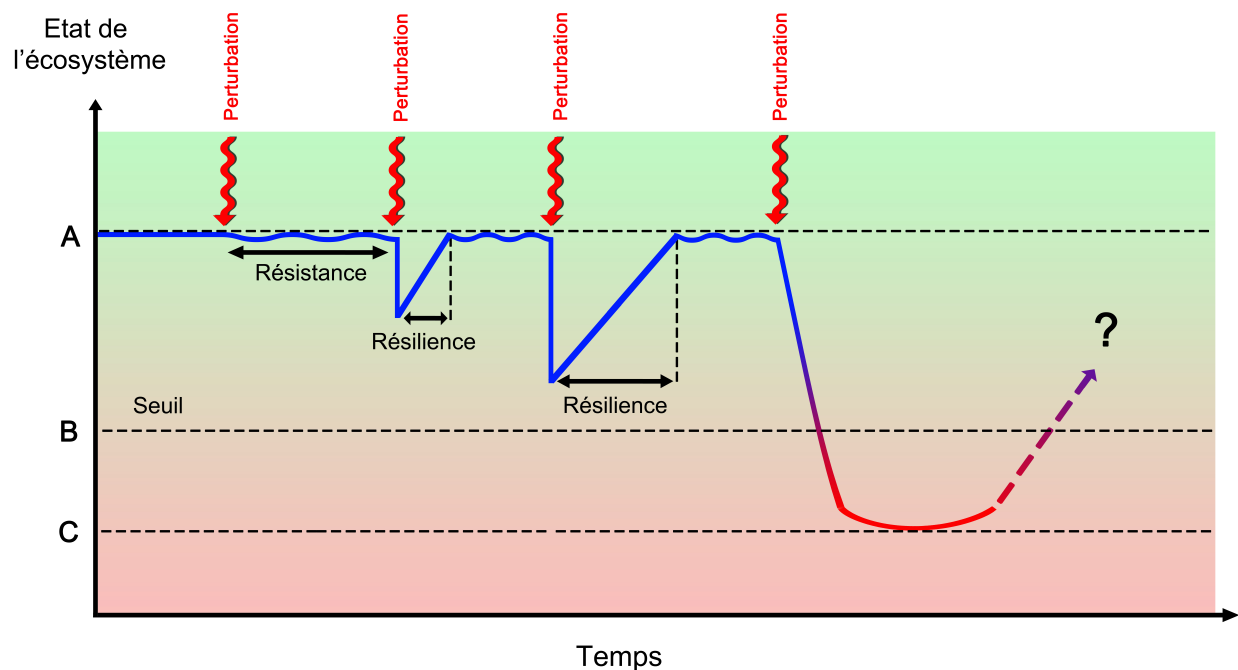


Figure 7 : Chemin évolutif d'un écosystème (trajectoire) illustrant les concepts d'état d'équilibre initial (A), de résistance (capacité à résister aux perturbations sans changement majeur), résilience (capacité à revenir à l'état stable initial suite à des modifications engendrées par les perturbations), de seuil d'irréversibilité (B) et d'état stable alternatif (C). Modifié d'après (Andel and Aronson, 2012).

2.3 Qu'est-ce que la restauration écologique ?

Il y a une cinquantaine d'années Aldo Leopold et ses collègues commencèrent à reconstruire un écosystème à l'arboretum de l'université du Wisconsin. Parmi ces scientifiques, Jordan William inventa alors le terme d'écologie de la restauration pour désigner la compréhension des processus écologiques et de l'écologie des communautés qu'il leur avait fallu acquérir afin de reproduire ce qu'ils observaient dans la nature. En collaboration avec Anthony Bradshaws, ces scientifiques axèrent leurs travaux sur les mécanismes de

réparation des écosystèmes et comment les mettre en application. Depuis, la discipline ne cesse de se développer, avec notamment la création de la Society for Ecological Restoration (SER) à la fin des 1980. La SER définit la restauration écologique comme « l'activité intentionnelle d'initier ou d'accélérer le rétablissement d'un écosystème ayant été endommagé, dégradé ou détruit, en prenant en compte son intégrité, ses fonctionnalités et sa pérennité » (SER, 2004) ; la science derrière cette pratique étant appelée écologie de la restauration. Les perturbations humaines étant de plus en plus intenses, répétées et de nature différente des perturbations naturelles, la stabilité des écosystèmes est affectée (Turner et al., 1993). Les zones fortement altérées ou dégradées, pour lesquelles le système a franchi le seuil d'irréversibilité et ne peut revenir de lui-même à son état initial se multiplient, et c'est dans ces zones que la restauration est donc souvent initiée. Le but de la restauration est alors de remettre ce système sur une trajectoire acceptable, afin qu'il atteigne un état de référence. Suivant les motivations à l'origine du programme de restauration, souvent anthropo-centrées et d'ordre utilitaire comme la capacité à pourvoir des services écosystémiques, l'état du système, et les objectifs souhaités, on distingue différentes options de restauration.

- La restauration au sens strict qui vise le retour à un état fonctionnel et capable de s'auto-maintenir, c'est-à-dire à un rétablissement de la biodiversité, de la structure et des fonctions de l'écosystème ; l'objectif étant d'être identique à la référence. Cependant, cette approche n'est envisageable que pour des écosystèmes dont le niveau de résilience est encore suffisant pour qu'une intervention restreinte de l'Homme suffise à les replacer sur une trajectoire souhaitable (Aronson et al., 1995).

- La réhabilitation qui s'applique lorsque les milieux sont trop dégradés pour faire l'objet de restauration et qui nécessite des actions lourdes pour rétablir certaines fonctions et replacer ces systèmes sur une trajectoire favorable (qui peut être différente de la trajectoire naturelle du milieu). L'objectif est de faire récupérer au système certaines caractéristiques de la référence comme la présence de certaines espèces, fonctions ou encore services. Ce type d'action concerne en général des milieux pour lesquels il est impossible de supprimer toutes les pressions ou de remédier à toutes les dégradations. C'est donc un bon compromis pour les milieux trop dégradés pour lesquels la restauration serait impossible. Toutefois une gestion et une intervention régulière de l'Homme sont souvent nécessaires.

- La réaffectation, qui concerne la transformation d'un milieu afin de lui assigner un nouvel usage. Elle est indépendante de l'état de dégradation du milieu et le nouvel état qui en résulte peut être sans relation avec l'écosystème original, l'utilisation d'une référence n'étant alors plus indispensable. En général, la réaffectation nécessite des actions et une gestion constantes afin de maintenir le nouvel écosystème ou de privilégier les fonctions ou éléments souhaités (Andel and Aronson, 2012).

2.4 La restauration écologique, comment ?

Un programme de restauration écologique émerge lorsque l'Homme décide délibérément de changer son environnement dans l'optique de bénéfices mutuels pour lui-même et la nature. Cette décision peut être motivée par de nombreux facteurs qui bien souvent agissent de concert. La motivation première peut être principalement pragmatique, fondée sur le fait que l'Homme dépend de la nature. La restauration est alors un moyen de maintenir ou de rétablir certains services à des fins socio-économiques. Néanmoins, des facteurs culturels, comme par exemple l'attachement d'une société à un écosystème ou à une parcelle de terre en particulier, peuvent également initier certains projets, la restauration étant alors motivée par ce que l'Homme chérit et estime et plus uniquement par ce qu'il peut tirer de la nature (Clewel and Aronson, 2006; Galatowitsch, 2012).

Ainsi, suivant les raisons à l'origine de la restauration d'un système, l'ampleur et la nature des dégradations, et les moyens disponibles (technologiques, financiers, humains...), les objectifs seront différents. Cependant, quels que soient ces objectifs, il devront être clairement établis en amont de tout projet et définis en concertation avec tous les acteurs (politiques, gestionnaires, scientifiques, usagers...)(SER, 2004). Il pourra alors être choisi de restaurer une espèce, une fonction ou un service particulier. Toutefois, pour une meilleure efficacité il est préférable, dans la mesure du possible, de considérer l'écosystème dans sa totalité et d'avoir pour objectif de le rendre auto-suffisant (Ehrenfeld, 2000). Ainsi, la volonté de réintroduire une espèce particulière devra passer par la restauration de son habitat, mais également des interactions que celle-ci entretient avec ce dernier ainsi qu'avec les autres espèces vivant dans le système. Un bel exemple de ce type de restauration est celui du grand papillon bleu (*Maculinea arion*) dont la réintroduction en Angleterre fut fructueuse grâce à la restauration de son habitat et des interactions qu'il entretient avec une espèce particulière de fourmis (Thomas et al., 2009). En fonction des

objectifs et de leurs motivations, le projet s'inscrira dans une des trois démarches décrites dans la section précédente : restauration, réhabilitation, ou réaffectation. Ainsi, certains viseront la restauration dans son sens le plus strict, d'autres tenteront de réhabiliter certaines fonctions, et enfin d'autres encore se contenteront d'améliorer l'état de sites dégradés afin de leur rendre une utilité pour l'Homme (Andel and Aronson, 2012). Une fois les objectifs bien définis, deux étapes successives devront alors être envisagées pour finaliser le projet de restauration écologique : l'évaluation de l'état du système (étape de diagnostic) et la définition d'un plan d'action (étape de planification).

Évaluer l'état du système à restaurer est une étape primordiale de tout projet de restauration. Cette évaluation a pour but d'identifier les sources de dégradation ainsi que l'ampleur et la nature de ces dernières, mais également les niveaux structurel et fonctionnel maintenus par le système (*i.e.* son potentiel de récupération). Cette étape de diagnostic peut parfois être un défi. Tout d'abord, il est souvent difficile de distinguer les changements liés à l'activité humaine de ceux résultant de l'évolution naturelle du système. L'identification des différents facteurs de perturbations ainsi que la détermination de l'effet de chacun d'eux peut également être un challenge (Galatowitsch, 2012). C'est lors de ces étapes de caractérisation et d'évaluation que doit également être définie la référence, celle-ci servant de modèle pour la planification du projet. Suite au diagnostic et à la définition de la référence, les objectifs peuvent être ajustés et redéfinis afin d'être les plus précis possible (SER, 2004).

La définition d'un plan d'action du projet est une étape qui est parfois négligée, notamment dans les petits projets, pourtant celle-ci est un élément essentiel de communication, permettant la coordination des différents membres du projet et la formalisation des différentes étapes de la restauration. A l'image du plan de gestion d'une réserve, ce plan d'action (i) résume l'évaluation environnementale et récapitule les objectifs, (ii) décrit les mesures prévues pour les atteindre ainsi que les protocoles de suivi et d'évaluation de ces mesures et, (iii) énonce également les moyens nécessaires pour mettre en place les différentes mesures, ainsi que les potentielles actions de communication et de sensibilisation prévues (Galatowitsch, 2012).

Enfin, la restauration écologique à proprement parler vient, une fois ces étapes préalables achevées. Les méthodes et technologies pouvant alors être implémentées sont aussi diverses que les systèmes pouvant être restaurés. Elles sont choisies en fonction de la nature, de la taille et de l'état du site à restaurer, des objectifs et des moyens disponibles.

Ces interventions peuvent être relativement simples et peu coûteuses comme complexes, lourdes et très chères. Par exemple, la restauration des dunes littorales peut ne consister qu'en la simple mise en place de ganivelles afin de retenir le sable et protéger du piétinement, ou également inclure la transplantation de plantes stabilisatrices (Gomez-Pina et al., 2002; Huang and Yim, 2014; van der Meulen and Salman, 1996), ces mesures restant faciles à mettre en œuvre et peu onéreuses. À l'inverse, la restauration de la rivière Skjern (Danemark) et de ces lacs et zones humides associés, a nécessité la reconfiguration du lit de la rivière. Des digues ont été déplacées, des méandres ajoutés, des rapides créés, soit au total 2.7 millions de mètres cubes de sol qui ont été déplacés pour un coût supérieur à 37 million d'euros (Pedersen et al., 2007).

Une fois les actions de restauration implémentées, des étapes de surveillance et d'évaluation doivent être mises en place. Historiquement, peu de projets ont bénéficié d'une réelle évaluation (Bernhardt, 2005), le personnel impliqué dans la restauration préférant souvent investir les ressources financières et humaines dans les actions même de restauration plutôt que dans la collecte de données. Pourtant l'évaluation doit faire partie intégrante d'une restauration avisée car elle permet d'une part, d'adapter les actions de restauration en fonction de leur efficacité dans un processus itératif de gestion adaptative (Bearlin et al., 2002; Runge, 2011) et d'autre part, d'évaluer si les objectifs sont atteints permettant la justification de l'utilisation de la restauration écologique dans les stratégies de gestion de l'environnement (Wortley et al., 2013) (Figure 8). Ces dernières années, le nombre d'évaluations de projets de restauration a largement augmenté et ces évaluations sont de plus en plus complètes, incluant non seulement des mesures d'abondance et de diversité mais également de fonction écologique. Cependant, les attributs socio-économiques restent encore quant à eux trop rarement pris en compte (Wortley et al., 2013). Toutefois, ces méthodes de monitoring et d'évaluation sont essentiellement empruntées aux champs plus larges de l'écologie en général et plus particulièrement à la conservation et aux études d'impacts environnementaux dans la mesure où les méthodes propres à l'écologie de la restauration sont encore trop peu développées (Galatowitsch, 2012). Ainsi, encore aujourd'hui, beaucoup d'évaluations n'utilisent par exemple pas la comparaison avec une référence alors que le succès de la restauration se définit pourtant plus comme un changement vers un état fonctionnel (référence) qu'un simple éloignement d'un état dégradé (témoin).

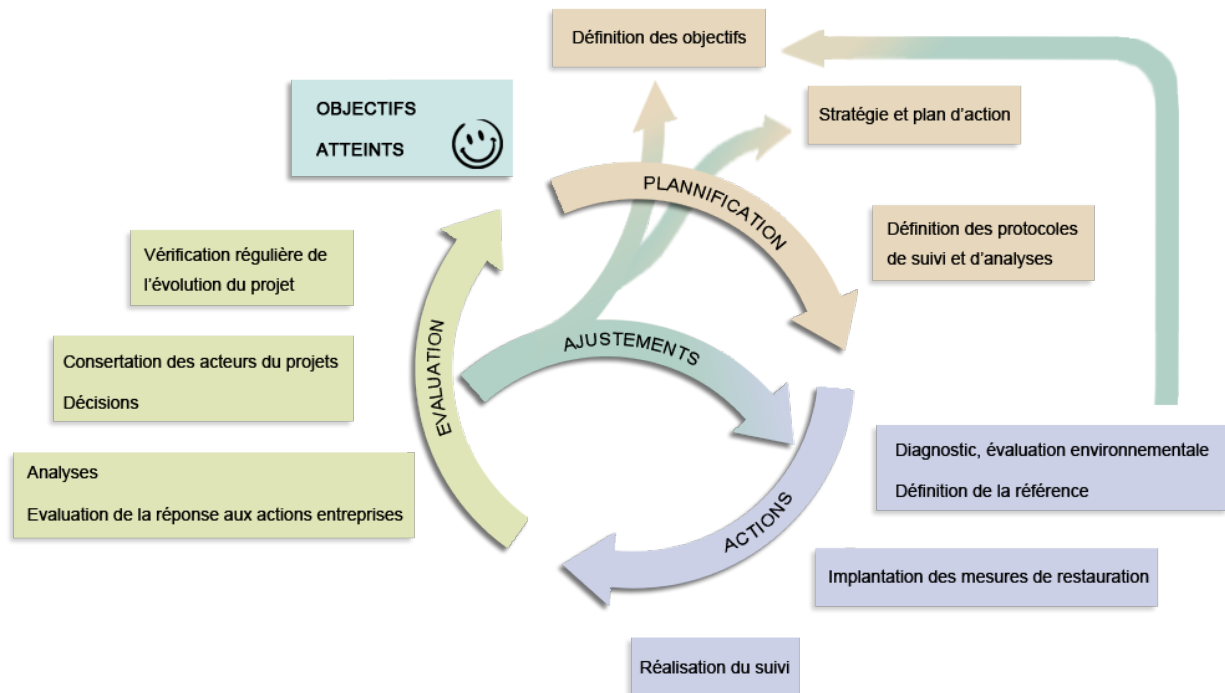


Figure 8 : Cycle de la gestion adaptative appliqué à un projet de restauration écologique. Les décisions sont prises sur la base de données acquises lors de suivis réguliers, des ajustements peuvent être entrepris à différentes étapes du projet afin d'adapter les mesures de restaurations pour atteindre les objectifs. Modifié d'après Bearlin et al., (2002).

3- Les ports, des zones côtières à l'abandon ?

3.1 Infrastructures anthropiques côtières, impacts et rôles potentiels

Comme nous l'avons vu dans la section 1.2, les zones côtières sont particulièrement soumises aux pressions anthropiques du fait de la forte concentration humaine sur le littoral. Les structures artificielles deviennent une composante ubiquiste du littoral allant même jusqu'à représenter l'élément majeur du paysage dans certaines zones urbaines (Airoldi and Beck, 2007; Airoldi et al., 2005; Chapman and Bulleri, 2003; Russell et al., 1983, 1983). Pourtant, les effets écologiques liés à l'implantation de ces infrastructures n'ont reçu que peu d'attention de la part de la communauté scientifique. Cela est certainement lié au fait que contrairement aux récifs artificiels, leur vocation première ne vise ni la réduction d'impacts liés à l'activité humaine, ni l'augmentation ou le maintien de la biodiversité, ni même le renforcement d'une population ou d'un stock donné. En outre, les changements environnementaux causés sont souvent considérés comme des effets secondaires (Bulleri, 2005; Bulleri and Chapman, 2010). Toutefois, les quelques études menées sur ces structures ont déjà permis de mettre en lumière nombre de changements

induits par leur mise en place, qui sont détaillés et discutés dans la revue de Bulleri and Chapman, (2010). Ces infrastructures peuvent, entre autre, avoir des effets à grande échelle spatiale. Il est par exemple possible qu'elles modifient la connectivité en bouleversant les courants et donc les flux larvaires, ou en faisant office de corridors ou de relais (Kinlan and Gaines, 2003; 2007). Elles peuvent aussi favoriser le maintien de certaines espèces ou populations (Barwick et al., 2004; Guidetti, 2004) mais également l'homogénéisation biotique (Branch et al., 2008; McKinney, 2006; McKinney and Lockwood, 1999). Elles sont particulièrement sensibles à l'établissement d'espèces invasives, le ratio espèces exotiques/espèces natives étant plus élevé que dans les habitats naturels adjacents (Glasby et al., 2007; Tyrrell and Byers, 2007; Vaselli et al., 2008). La présence de digues a par exemple favorisé la propagation de l'algue verte invasive *Caulerpa racemosa* en permettant l'établissement de populations viables (Vaselli et al., 2008). A l'échelle de la structure en elle-même, il a été démontré que l'impact dépend fortement de la nature des habitats environnants (Bulleri, 2005). Sur une côte rocheuse, l'introduction de substrats artificiels est considérée comme n'entraînant que peu de changements, la structure des assemblages qu'ils soutiennent étant assimilable à celle des habitats naturels qui les entourent (Branch et al., 2008; Southward and Orton, 1954; Thompson et al., 2002). Par contre, pour des structures introduites sur substrat meuble (comme par exemple les digues, les épis, les pontons flottants...), les assemblages sont très différents de ceux des zones rocheuses de proximité (Clynick et al., 2008; Fowler and Booth, 2013; Lam et al., 2009; Moschella et al., 2005; Perkol-Finkel and Benayahu, 2004; Rilov and Benayahu, 2000). Ces différences concernent de nombreux facteurs et paramètres comme la pente (plus abrupte voire verticale) et l'hétérogénéité du substrat (Chapman, 2003; Lam et al., 2009; Moschella et al., 2005; Perkol-Finkel and Benayahu, 2004), la nature des matériaux de construction, surtout lorsque celle-ci est artificielle (béton, géotextile, métal, plastique (Attrill et al., 2000; Edwards and Smith, 2005), l'exposition amoindrie aux vagues et courants (Bulleri and Chapman, 2004; Clynick, 2006; Vaselli et al., 2008), la mobilité (pour les structures flottantes) (Connell, 2000; Dafforn et al., 2009; Glasby, 2001; Holloway and Connell, 2002; Perkol-Finkel et al., 2008) ou encore la différence d'ensoleillement causée par l'ombre des structures (Able et al., 1998; Sanger et al., 2004). Ainsi, bien que pouvant abriter une certaine biodiversité et assurer certaines fonctions, ces structures ne peuvent être considérées comme des substituts aux habitats naturels et sont inévitablement une source de perturbations pour le paysage sous-marin côtier. Leur mise en place résultant d'une

réponse aux besoins humains leur prolifération est inévitable, en particulier dans le contexte actuel d'intensification des événements météorologiques extrêmes, de montée des eaux et de croissance démographique constante (Gerland et al., 2014; Halpern et al., 2008; Scyphers et al., 2015). Pour les structures déjà en place, leur caractère indispensable pour l'Homme rend difficile voire impossible d'envisager leur retrait, sauf dans certains cas bien particuliers où le réalignement du trait de côte et la restauration de zones humides associés peuvent être envisagés (French, 2008; Hughes and Paramor, 2004; Townend and Pethick, 2002). Par suite, dans la plupart des cas la restauration au sens strict n'est pas envisageable, même s'il est toutefois possible de considérer de limiter l'impact des structures ou même de réhabiliter certaines fonctions et services pouvant y être associés. Il est par exemple possible de créer de l'habitat pour de nombreuses espèces (Baine, 2001; Firth et al., 2014; Sella and Perkol-Finkel, 2015) qui pourront potentiellement contribuer à la pêche (professionnelle et de loisir) ou à d'autres activités récréatives ou éducatives comme l'observation des oiseaux ou la plongée (Burcharth, 2007; Zedler and Leach, 1998). Depuis une dizaine d'années des efforts considérables sont faits pour minimiser l'impact de l'artificialisation du littoral (Hardaway and Duhring, 2010; Scape / Landscape architecture, 2014). Toutefois, les collaborations entre gestionnaires, scientifiques et ingénieurs devraient être plus fréquentes afin de développer des solutions de génie écologique permettant la mise en place de structures alliant des critères indispensables à leur solidité et durabilité à des critères écologiques (permettant le développement de plus d'espèces, ou favorisant certaines fonctions par exemple) (Chapman and Blockley, 2009; Chapman and Clynick, 2006; Sella and Perkol-Finkel, 2015).

3.2 La place particulière des ports dans le paysage côtier

Très tôt dans l'histoire l'Homme a utilisé le transport maritime. Au départ, des baies naturelles étaient utilisées pour abriter les bateaux, mais rapidement ces sites naturels ont été aménagés afin de faciliter l'embarquement et le débarquement des personnes et des marchandises. Les ports étaient nés. Les sources dans le domaine de l'histoire du développement portuaire restent rares et peu documentées, toutefois elles paraissent s'accorder sur le fait que toute civilisation ancienne ayant développé le commerce maritime a également aménagé des ports. Il apparaîtrait ainsi que les premiers ports aient vu le jour dès l'Age de bronze (soit environ 3700 ans avant J.C.) à Lothal en Inde, où la civilisation

Harappéenne avait établi l'une de ces plus grandes villes. Des ports ont également été aménagés très tôt au Liban, plus précisément à Sidon et Tyr dès 2750 ans avant J.C., mais également en Chine où le port de Guangzhou remonterait à la dynastie Qin (221 à 206 avant J.C.), en Egypte où le port de Canopus servait déjà pour le commerce avant même la fondation d'Alexandrie (331 avant J.C.), ou encore à Athènes où le port de Piraeus servait de base à une flotte militaire 480 ans avant J.C. Ainsi, les ports représentent la plus ancienne forme de modification de la côte et encore aujourd'hui la plus répandue et certainement celle ayant le plus d'impacts (Morgan, 1988). Ils sont responsables de la majorité de l'artificialisation du littoral, par exemple en Méditerranée française, 90% de l'occupation des fonds de 0 à - 10 m reviennent aux ports (Figure 9)(MEDAM, 2015). Cette occupation peut résulter d'une réelle propagation sur le domaine marin, qui auquel cas engendre la destruction de l'habitat naturel ou tout du moins sa forte modification, ou d'une trouée dans le cordon littoral, ce qui a pour résultat une extension du trait de côte (Figure 9). La construction des ports n'engendre pas seulement une indéniable perte d'habitat, mais également nombre de dommages indirects comme des changements dans les courants et l'accumulation de sédiments pouvant influencer la composition des communautés benthiques ainsi que la dispersion et l'installation des larves (Martin et al., 2005; Meinesz et al., 1991; Roberts, 1997).

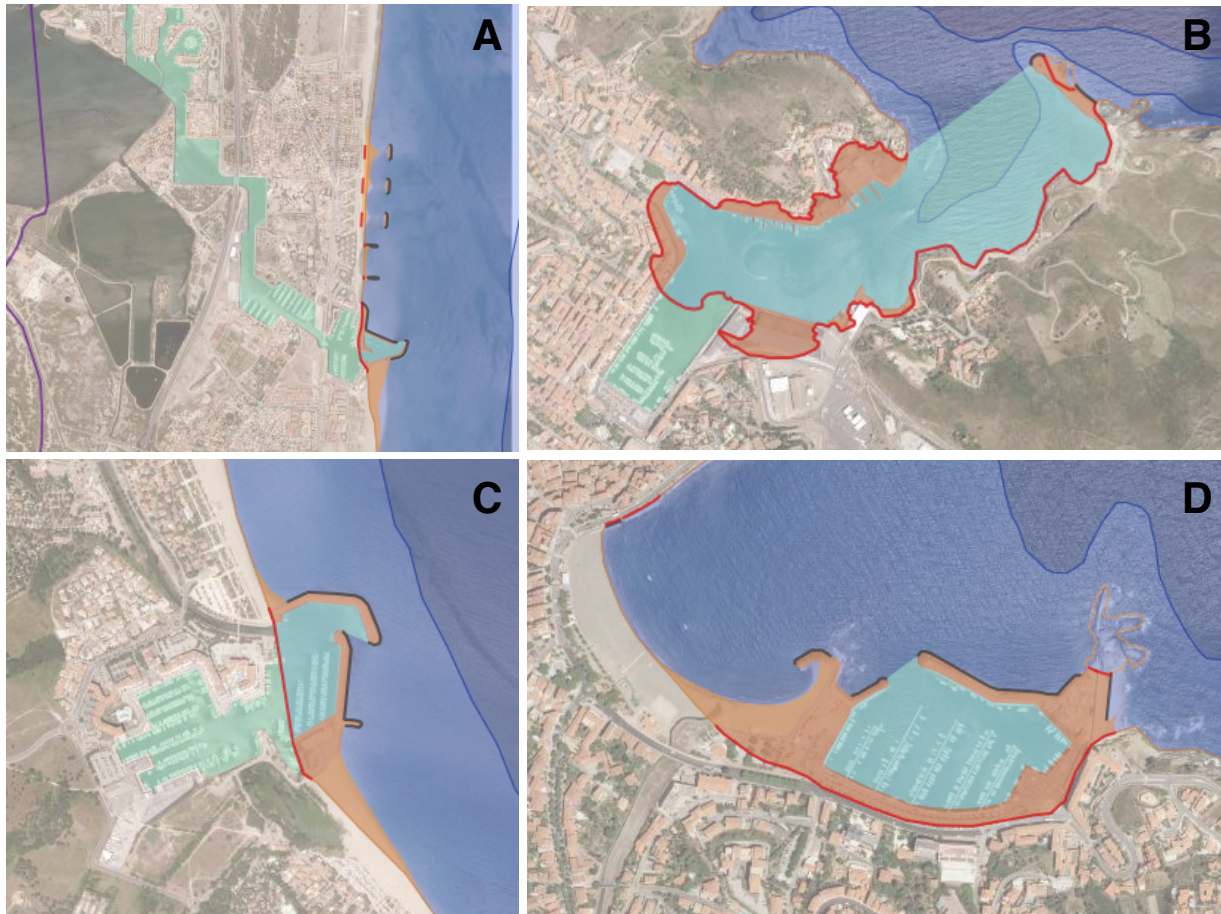


Figure 9 : Impact des ports sur la zone côtière en Méditerranée française ; en rouge littoral artificialisé, en noir enrochements artificiels extérieurs au port, en orange surface construite sur la mer et accumulation de sédiment, en turquoise plan d'eau naturel ayant été artificialisé, en vert plan d'eau créé artificiellement (creusé dans le lido). (A) Le Barcarès, exemple de port en bordure de zone lagunaire dont la construction engendre une modification de la connexion mer-lagune, (B) Port-Vendres, exemple de grand port construit essentiellement sur une zone naturelle, (C) Argelès, exemple de grand port essentiellement creusé dans le lido, (D) Banyuls, exemple de petit port entièrement gagné sur la mer. Cartes MEDAM, septembre 2015.

Les activités associées aux ports, telles l'industrie, la pêche, les activités récréatives (plongée, jet ski...) ou encore la plaisance sont également sources de multiples impacts. Le plus évident est la pollution (biologique et chimique) chronique de l'eau et du sédiment dans l'enceinte mais également à proximité du port (Darbra et al., 2004, 2005), qui peut gravement nuire aux organismes marins (Falandysz et al., 2002; Neira et al., 2011) dont les poissons et plus particulièrement les jeunes stades de vie (Able et al., 1999; Amara et al., 2007; Kerambrun et al., 2012, 2013).

Le passage des bateaux est aussi une source de fortes nuisances, la pollution sonore qu'ils engendrent pouvant avoir un effet néfaste sur de nombreux organismes marins (Ferrari et al., 2018; Popper et al., 2003). Le trafic maritime est également le vecteur principal de transport d'espèces invasives (Bax et al., 2003). À tout moment, les eaux de ballast

transportent à elles seules plus de 10 000 espèces différentes entre les régions biogéographiques (Carlton, 1999) et elles ne sont qu'un vecteur parmi d'autres. En effet, la navigation de plaisance représente également un autre vecteur non négligeable, notamment du fait de l'absence totale de régulation de cette activité (Clarke Murray et al., 2011). Ainsi, les ports sont le premier site d'établissement pour de nombreuses espèces non-indigènes voire invasives. Tous ces facteurs modifient fortement le fonctionnement écologique des zones sur lesquelles les ports sont implantés (Airoldi and Beck, 2007). Néanmoins, ces nouveaux « écosystèmes urbains » peuvent potentiellement soutenir de nouvelles fonctions écologiques et même jouer un rôle dans le maintien de la biodiversité marine (Clynick et al., 2008).

3.3 Pourquoi la réhabilitation de la fonction de nurserie en zones portuaires ?

Le fait que les structures artificielles puissent jouer un rôle dans le maintien de la biodiversité est un concept ayant émergé assez récemment (Savard et al., 2000). L'utilisation des paysages urbains comme habitats est particulièrement bien étudiée pour les oiseaux, de nombreuses espèces utilisant ces nouveaux écosystèmes, certaines présentant même des abondances plus élevées que dans les écosystèmes naturels, d'autres au contraire étant incapables de s'y maintenir (Burton et al., 2002; Malpass et al., 2018; Parsons et al., 2003; Turner, 2003). En milieu marin, les zones urbanisées ne reçoivent encore que peu d'attention, seules les communautés benthiques associées aux infrastructures de défense des côtes ont jusqu'à présent bénéficié d'un certain nombre d'études (cf. section 3.1). L'utilisation des structures urbaines par les poissons reste peu étudiée, pourtant les quelques études portant sur le sujet ont montré leur potentiel d'attraction pour de nombreuses espèces typiques des zones rocheuses adjacentes et bien souvent d'intérêt commercial ou récréatif important (Carr and Hixon, 1997; Granneman and Steele, 2015; Guidetti, 2004; Rilov and Benayahu, 2000). Parmi les structures urbaines marines, les ports restent les moins étudiés alors qu'ils sont les plus répandus (cf. section 3.2). Les quelques études concernant l'utilisation des ports par les poissons montrent que ces écosystèmes urbains abritent des assemblages pouvant différer de ceux présents dans les habitats naturels de proximité, et que les jetées supportent de fortes abondances de juvéniles de certaines espèces (Clynick, 2006, 2008; Clynick et al., 2008; Sella and Perkol-Finkel, 2015). Il avait déjà été montré que les brises lames peuvent soutenir des densités de

juvéniles pouvant être supérieures à celles des habitats naturels (Pastor et al., 2013). En outre, Pastor (2008) avait également identifié une forte diminution des densités en juvéniles le long d'un gradient mer / lagune passant par un port, suggérant à l'évidence une forte utilisation des ports par ces jeunes poissons. Enfin, des études récentes ont montré que la mise en place d'habitats artificiels paraît faciliter l'installation et le développement des juvéniles de poissons (Bouchoucha et al., 2016; Mercader et al., 2017a; Patranella et al., 2017), et pourrait également favoriser des espèces menacées comme l'hippocampe du Cap (*Hippocampus capensis*) ou le mérrou brun (*Epinephelus marginatus*) (Claassens et al., 2018; Mercader et al., 2017b). Les caractéristiques physiques des ports, zones semi-fermées, calmes, protégées et souvent à forte production primaire, fournissent des conditions favorables à la survie et à la croissance des juvéniles (Beck et al., 2001; Harmelin-Vivien et al., 1995). Par ailleurs, très peu de nurseries naturelles se trouvent en zones protégées (Cheminée et al., 2017; Roberts et al., 2001). Jusqu'à présent, les jeunes stades de vie n'étaient que très peu pris en compte lors de la mise en place des AMP. De plus, la localisation des nurseries sur des zones à forts enjeux socio-économiques (plages, fond de baie...) rend particulièrement difficile l'implémentation de mesure de protection de ces habitats. Ainsi, réhabiliter la fonction de nurserie au sein des infrastructures portuaires peut représenter un outil complémentaire aux mesures de conservation afin de favoriser le développement et la survie des juvéniles de poissons et ainsi le maintien des populations adultes.

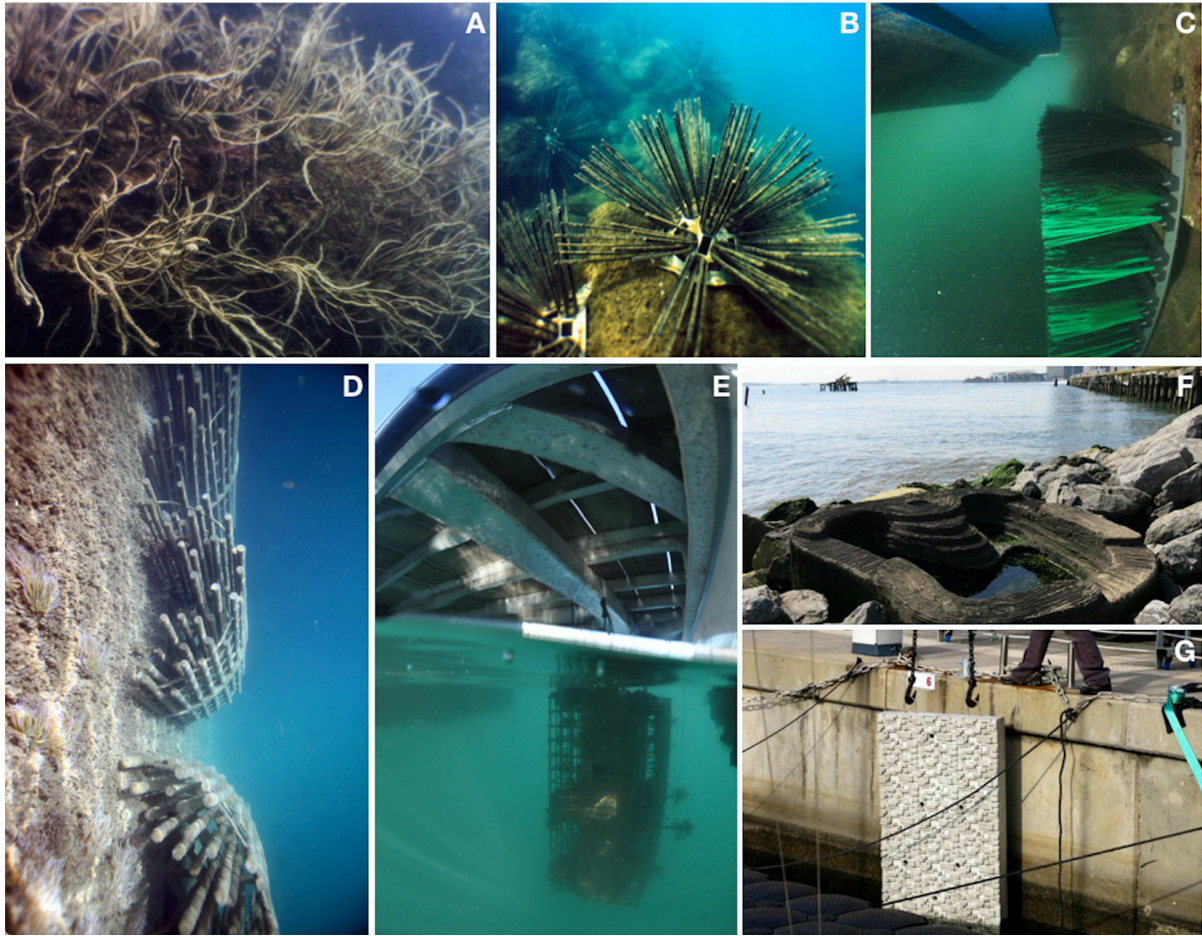


Figure 10 : Exemples d'habitats artificiels pouvant être installés en zones portuaires afin d'augmenter la complexité de l'habitat. Modules roselière (A) et oursin (B) développés par Seaboost, Egis eau, module ReFish (C) développé par Suez Consulting, modules Biohut kelp (D) et ponton (E) développés par Écocéan, Tide pool (F) et Enhanced seawall (G) développés par Econcrete.

4- Contexte, objectifs et structure de la thèse

4.1 Contexte et objectifs

L'objectif principal de cette thèse est de contribuer à mieux appréhender le rôle des infrastructures anthropiques, notamment portuaires, dans le cycle de vie des poissons côtiers ainsi que d'évaluer le potentiel de la réhabilitation de la fonction de nurserie dans ces zones comme outil pour le maintien des populations de poissons.

Ce travail fait suite aux programmes GIREL (2012-2015) et NAPPEX (Nurseries artificielles pour des ports exemplaires)(2013-2015) financés par l'Agence de l'eau Rhône Méditerranée Corse, dont l'objectif était de tester la faisabilité de solutions techniques d'ingénierie dans l'objectif de réhabiliter une fonction de nurserie en zones portuaires. Le principe de base consistait à fixer des habitats artificiels sur les ouvrages existants, avec

pour hypothèse que la structure tridimensionnelle complexe des modules puisse palier à la perte de complexité de l'habitat (Figure 10). Ces programmes pilotes ont donné des résultats encourageants, montrant des densités en juvéniles plus élevées sur les portions de quais ou de pontons équipées d'habitats artificiels que sur les portions témoins non équipées (Bouchoucha et al., 2016; Mercader et al., 2017a). Cela supporte l'idée selon laquelle des modifications structurelles des ouvrages portuaires existants paraissent augmenter leur valeur écologique en favorisant les juvéniles de poissons et participent ainsi au maintien de leurs populations. Toutefois, un manque d'état initial et de comparaison avec une référence naturelle a rendu difficile l'évaluation de l'efficacité de ces mesures. De plus, seule la densité en juvéniles a été étudiée dans ces études pilotes, ne répondant ainsi qu'à un seul des critères de Beck et al. (2001) définissant la valeur de nurserie d'un habitat. Enfin, ces travaux ont permis de soulever de nombreuses interrogations quant à la condition des juvéniles ayant grandi en zones portuaires, notamment du fait des potentielles contaminations chimiques et métalliques de tels milieux. Afin de répondre à une partie de ces interrogations une première thèse débuta en 2013, fruit d'une collaboration entre l'IFREMER de Toulon, le CEFREM de l'Université de Perpignan et l'unité MARBEC à Montpellier. Les travaux issus de cette thèse, menés par Marc Bouchoucha ont, entre autres, montré que les juvéniles ayant grandi en zones portuaires présentaient des niveaux de contaminations, un taux de croissance et des indices de condition comparables à ceux des juvéniles ayant grandi dans des nurseries naturelles. Ces résultats ont permis d'éloigner l'hypothèse du risque d'une éventuelle surmortalité liée à la pollution ou des risques sanitaires encourus ainsi que de répondre au critère du taux de croissance entrant dans la définition d'une nurserie (Bouchoucha, 2017). Cependant, la question portant sur l'évaluation de l'efficacité des mesures restait sans réponse et fait ainsi l'objet principal de cette deuxième thèse sur la thématique. Pour cela, trois objectifs principaux ont été définis.

Le premier objectif concerne l'estimation de l'effet refuge des habitats artificiels face à la prédation. En effet, les plus fortes abondances observées sur les habitats artificiels pourraient résulter d'un simple effet attracteur, d'une augmentation de « production » via un meilleur taux de survie, ou d'une combinaison des deux. Il est donc nécessaire de savoir si les modules sont en mesure de fournir un taux de survie comparable à celui observé sur d'autres types d'habitats afin de valider leur rôle de protection des juvéniles vis-à-vis de la prédation.

Le deuxième objectif de ce travail est d'évaluer à l'échelle d'un paysage sous-marin, les niveaux d'utilisation des ports par les juvéniles de poissons. En effet, la valeur de nurserie étant une mesure relative, il est nécessaire de travailler à une échelle englobant une multitude d'habitats afin de déterminer le rôle potentiel des infrastructures portuaires.

Le troisième objectif est d'estimer le gain potentiel lié à l'implémentation des actions de réhabilitation, non plus à l'échelle d'une portion de quai, équipée ou pas, mais à l'échelle du site dans sa globalité et surtout en comparaison avec des habitats naturels.

4.2 Structure de la thèse

Cette thèse se décline en quatre chapitres faisant suite à cette introduction et est complétée d'une synthèse, les résultats de certains chapitres étant présentés sous forme de publication.

Le chapitre 2 est dédié à un matériel et méthode général décrivant les approches retenues ainsi que la zone et les sites d'étude choisis.

Le chapitre 3 vise à estimer, *ex situ*, le taux de mortalité de deux espèces de Sparidés sur des habitats artificiels ainsi que sur des habitats naturels afin de déterminer le rôle refuge des premiers.

Le chapitre 4 est consacré à l'évaluation du rôle des infrastructures anthropiques en tant qu'habitats juvéniles pour les poissons côtiers. L'accent est notamment mis sur l'utilisation des ports et la répartition des juvéniles en fonction des différents types d'habitats composant les zones portuaires.

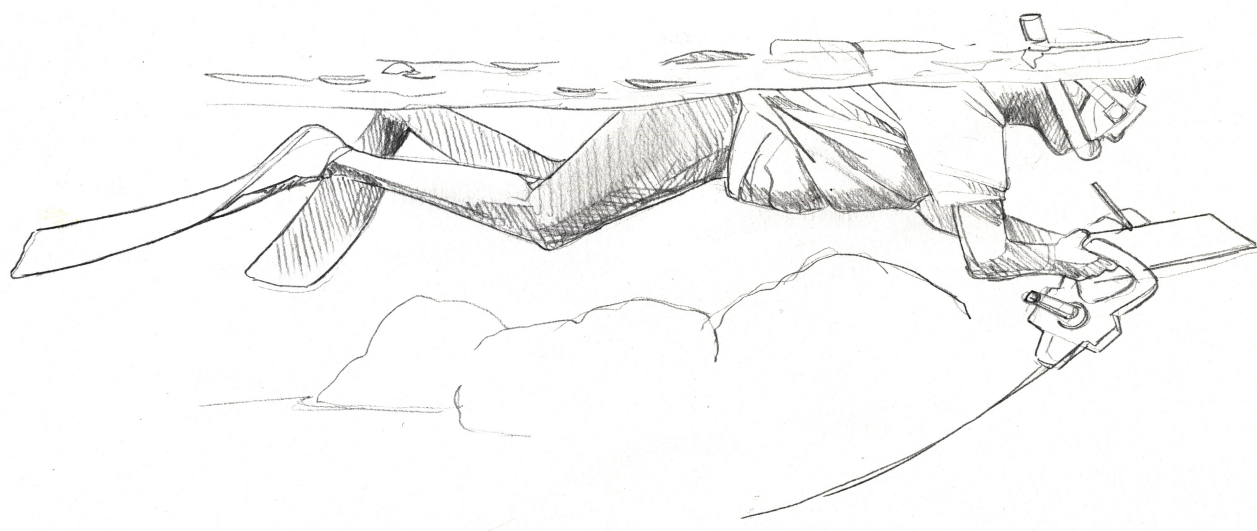
Le chapitre 5 se propose, sur la base d'un protocole Before-After-Control-Impact (BACI) adapté pour inclure une Référence, d'estimer le gain (en terme de densité de juvéniles) résultant de la mise en place d'habitats artificiels, à l'échelle de l'habitat mais également du site dans sa globalité.

Le chapitre 6 constitue la synthèse générale de cette thèse. Les principaux résultats des chapitres 3, 4 et 5 y sont rappelés et discutés afin de proposer un cadre conceptuel et des outils d'évaluation pour l'intégration de la restauration écologique dans les stratégies de maintien et de rétablissement du bon état écologique du milieu marin en zone côtière.

Enfin, quelques annexes sont fournies à la fin du manuscrit pour approfondir certains aspects ainsi que pour présenter les résultats de travaux complémentaires à la thématique publiés durant la thèse.

Chapitre 2 :

Matériel et méthode général



1- Zone d'étude

La zone d'étude considérée dans cette thèse s'étend sur une centaine de kilomètres, couvrant ainsi le linéaire côtier du département des Pyrénées-Orientales (66). Cette zone, couramment appelée côte catalane française, est soumise aux conditions météorologiques, hydrologiques et hydrodynamiques générales du Golfe du Lion. Elle est ainsi sous l'influence d'un courant dominant orienté du nord-est vers le sud-ouest, le courant Liguro-Provençal (Taupier-Letage and Millot, 1986) qui charrie les alluvions provenant du Rhône. Ces apports importants de nutriments et matière organique induisent une forte productivité, faisant du Golfe du Lion une zone considérée comme mésotrophe dans une mer Méditerranée globalement oligotrophe (Bosc et al., 2004; Estournel et al., 1997). Le département des Pyrénées-Orientales est également soumis à des vents fréquents et violents, soufflant principalement du nord-ouest (Tramontane) ou du sud-est (Marin). Ces vents et la houle qu'ils engendrent génèrent des mouvements de masses d'eaux favorisant les échanges côte-large, (i) par Tramontane les eaux côtières sont poussées vers le large induisant des remontées d'eaux marines profondes (upwellings côtiers), (ii) par Marin les eaux de surface du large sont ramenées vers la côte et engendrent des phénomènes de downwelling vers les canyons (Millot, 1990; Ulses et al., 2008). Les sites d'études retenus sont tous inclus dans le périmètre du Parc naturel marin du Golfe du Lion (PNMGL). Cela permet de travailler sur une zone représentative du pourtour Méditerranéen français, incluant une côte sableuse (au nord), une côte rocheuse (au sud), plusieurs lagunes et cours d'eau, des infrastructures portuaires de différentes tailles et des ouvrages de protection des côtes (brise-lames, épis). L'acquisition de connaissances sur le milieu marin et ici particulièrement sur les écosystèmes urbanisés en mer, vient également en support à la mission d'évaluation et de suivi de l'état écologique des différents écosystèmes du parc. Cet outil de gestion, ayant été développé dans l'objectif d'intégrer les activités humaines et la conservation du milieu, représente également un bon moyen pour initier une démarche d'incorporation de la restauration écologique dans les stratégies de gestion du milieu marin. Les ports et zones naturelles échantillonnés durant cette thèse ont été choisis de façon à être le plus représentatif possible de la diversité de la zone d'étude dans la limite des contraintes logistiques et administratives. Ainsi, quatre ports d'études principaux (échantillonnés pour les chapitres 4 et 5) ont été sélectionnés, deux sur la

côte sableuse et deux autres sur la côte rocheuse. Ce travail s'intéresse aux petits fonds rocheux qui sont les zones naturelles principales (échantillonnées également pour les chapitres 4 et 5) se trouvant sur la côte rocheuse. Toutefois, dans un souci de représentativité il a été choisi de suivre une zone à la limite de la côte sableuse et une autre au sud de la côte rocheuse. Pour le chapitre 4, des sites secondaires, toujours compris dans l'emprise du PNMGL, ont été ajoutés, notamment des ports, des brise-lames et épis, ainsi que des sites naturels dans la Réserve naturelle marine de Cerbère-Banyuls (Figure 1).

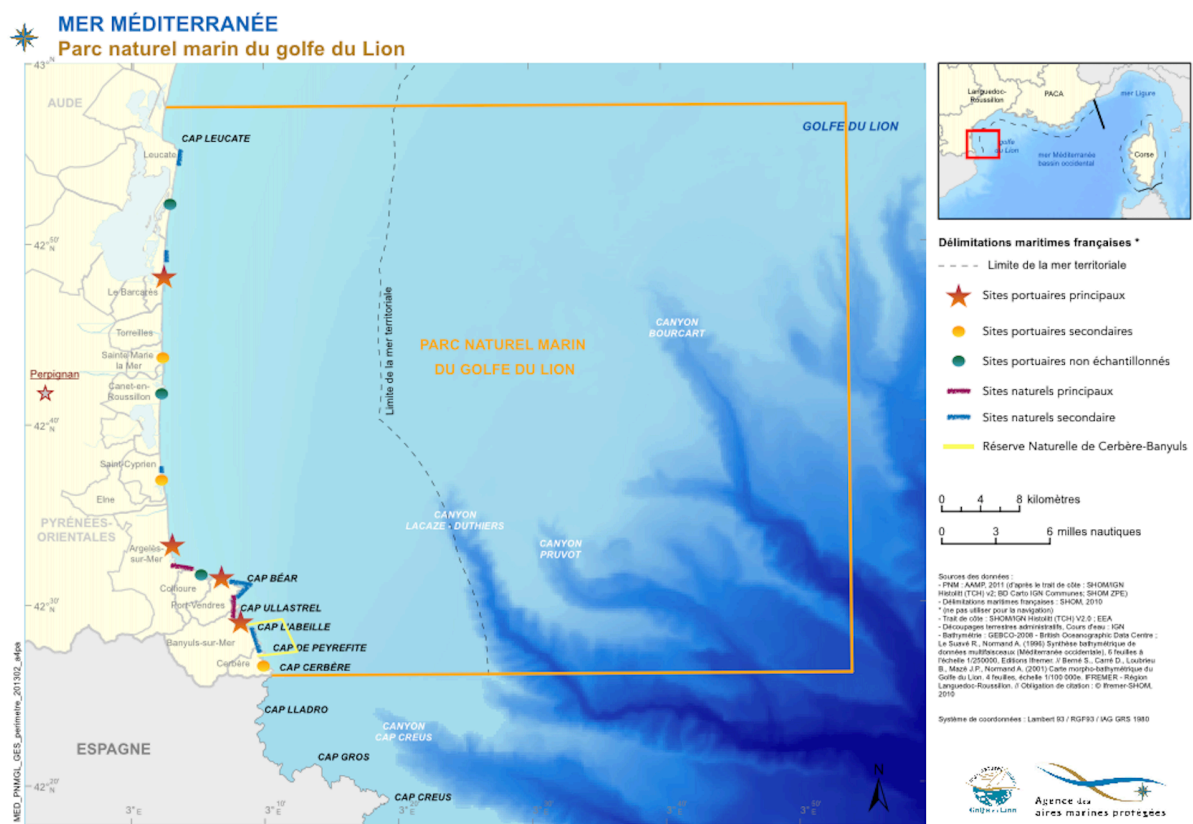


Figure 1 : Délimitation du Parc naturel marin du golfe du Lion, localisation des sites d'études et de la Réserve naturelle marine de Cerbère-Banyuls, modifié d'après <http://www.parc-marin-golfe-lion.fr>.

1.1 Parc naturel marin du golfe du Lion

Créé en octobre 2011, le PNMGL est le troisième parc naturel marin créé en France, après celui d'Iroise et de Mayotte. Le concept de parc naturel marin a été créé par la loi du 14 avril 2006, avec pour objectif une gestion cohérente des grands espaces maritimes où coexistent activités humaines multiples et patrimoine naturel

remarquable. Ils ont pour vocation de participer à l'acquisition de connaissances sur le milieu marin et de le protéger ainsi que de contribuer au maintien ou au développement d'activités maritimes durables. Le PNMGL s'étend de Leucate au nord à la frontière Espagnole au sud, il couvre ainsi environ 100 km de côte, mais se déploie également vers le large pour une superficie totale de 4010 km² (Figure 1). Il englobe ainsi trois canyons profonds (Lacaze-Duthiers, Pruvot et Bourcart) ainsi que l'ensemble des habitats naturels marins typiques de Méditerranée tels que les herbiers ou le coralligène permettant une gestion en cohérence avec l'interdépendance de tous ces écosystèmes. La préservation de l'identité socio-économique locale (pêche, transport maritime, plongée, sport de glisse...) est également au cœur des missions du parc.

1.2 Port du Barcarès

Construit dans les années 1960 lors de la mission Racine, le port du Barcarès est ouvert d'une part sur la mer et d'autre part sur la lagune de Salses-Leucate (Figure 2). Cette particularité, que l'on retrouve pour plusieurs ports sur le pourtour méditerranéen français (Leucate, Port-la-Nouvelle, Sète pour ne citer que les plus proches) en fait un bon représentant des conditions particulières que l'on peut trouver dans ce type d'environnement. En effet, les variations de salinés, de températures ainsi que les courants (essentiellement liés aux vents dominants, tramontane de direction nord-ouest et marin de direction sud-est) peuvent y être plus importantes que dans les ports ne présentant pas de connections avec une lagune. Les apports en matière sédimentaires et organiques peuvent également y être élevés, nécessitant des dragages fréquents (Arnaud and Raimbault, 1969; Charriere et al., 1991; Gadel et al., 1984; Herve, 1978). Deuxième port de plaisance des Pyrénées-Orientales, il abrite 950 postes à quai, 300 postes sur l'étang et 200 postes amodiés (conçédés par la mairie aux particuliers pour une durée déterminée) sur la marina et possède trois cales de halage. Sa surface totale est de 600 000 m², mais sa profondeur est faible (-2.5 m pour l'avant port et parfois moins d'un mètre pour les zones proches de l'étang) notamment due aux apports sédimentaires cités précédemment. Si la principale activité du port est la plaisance, il abrite aussi plusieurs bateaux de pêche artisanale, les pêcheurs ayant souvent les habilitations pour pêcher en mer comme sur la lagune. On y trouve également nombre de prestataires d'activités récréationnelles, notamment un club de

plongée, un bateau école, un bateau de promenade... En terme de gestion environnementale, le port possède une zone de carénage, des pompes à eau de cale, un point de récupération des déchets avec tri sélectif ainsi que des pompes pour eaux usées (gratuites). On y trouve également trois cales de halages et une pompe à carburant. Sur la durée de cette thèse le port bénéficiait du pavillon bleu.



Figure 2 : Vue aérienne du port du Barcarès, Google earth V 7.1.2.2041 (7/10/2013), 42°47'57.07 N, 3°02'08.21 E, <http://www.earth.google.com> [20 Février 2018].

1.3 Port d'Argelès-sur-mer

Le port d'Argelès-sur-mer est le plus récent de toute la zone d'étude. En 1975, la municipalité fit construire deux digues à l'embouchure de la Massane (un petit cours d'eau) afin de protéger la ville des inondations et une centaine de petits bateaux commença à s'installer dans ce qui allait devenir l'avant port. Mais ce ne fut qu'en 1986 que la construction d'un réel port fut autorisée (dernière autorisation de la mission Racine), les travaux s'achevèrent en 1989. Situé aux pieds des Albères, à la charnière entre la côte sableuse au nord et la côte rocheuse au sud, ce port de plaisance abrite 857

anneaux. Il possède une rampe de mise à l'eau, une station de carburant, une aire de carénage, ainsi qu'une éco-pompe de récupération des eaux noires et de fond de cale et une mini-déchetterie. De nombreux prestataires de loisirs nautiques sont implantés dans ce port (quatre clubs de plongée, deux loueurs de bateaux, des bateaux pour sports tractés, plusieurs bateaux de promenade...). Quelques pêcheurs petits métiers sont également installés à l'entrée du port. Ce port bénéficie du pavillon bleu depuis 1998.

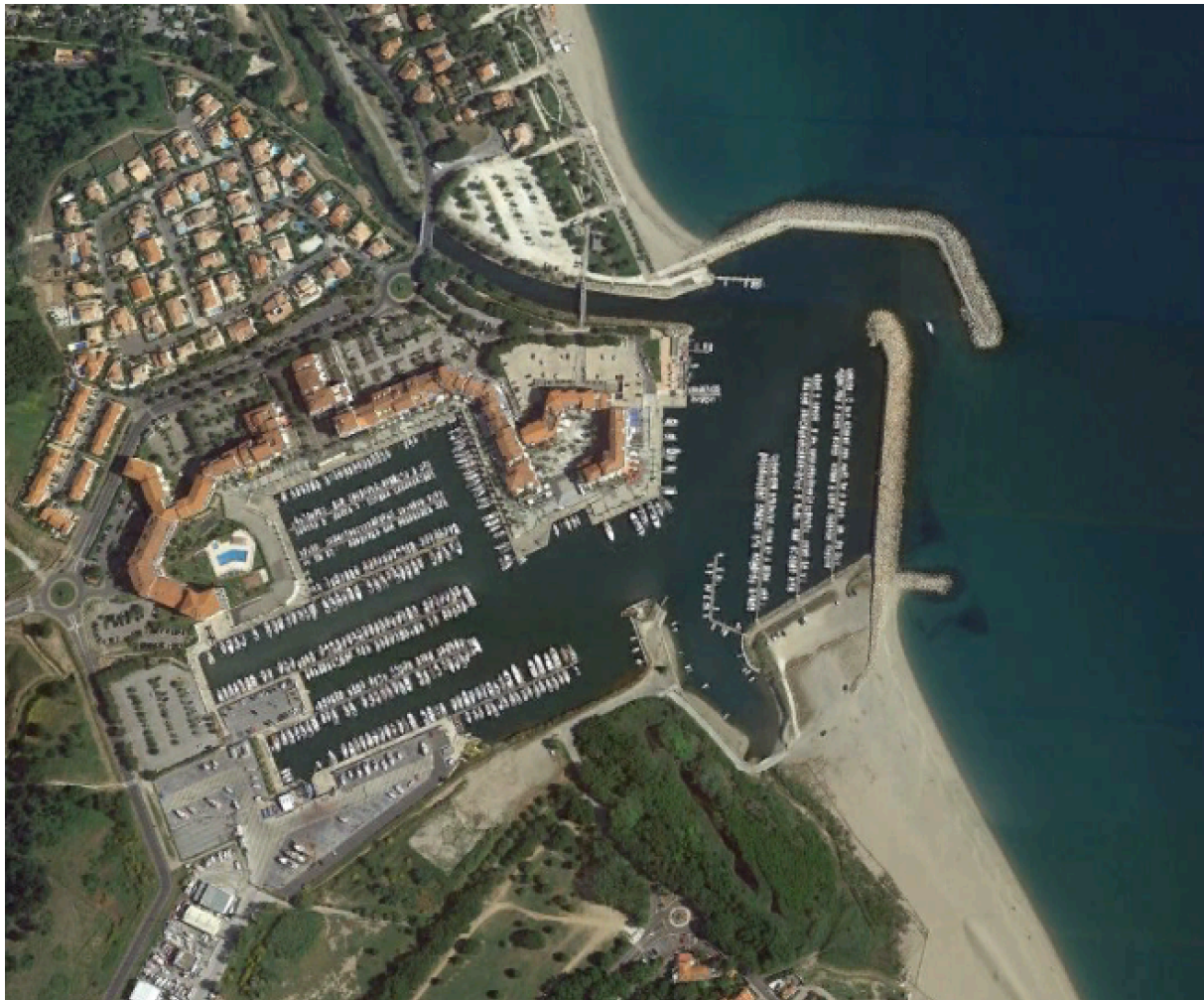


Figure 3 : Vue aérienne du port d'Argelès-sur-mer, Google earth V 7.1.2.2041 (7/10/2013), 42°32'29.80 N, 3°03'01.55 E, <http://www.earth.google.com> [20 Février 2018].

1.4 Port de Port-Vendres

Déjà au VI^{ème} siècle avant J.C., Port-Vendres servait de relais entre monde occidental et monde oriental, il était connu des navigateurs grecs sous le nom de « Portus Veneris ». Ce fut le premier port de commerce du Roussillon. Dans les années 1700, la nécessité d'abriter des navires de guerre engendra un agrandissement du port

qui fut creusé dans la roche. Dans les années 1840, de nouveaux travaux d'extension furent entrepris et permirent à Port-Vendres de devenir un port de commerce et de transport de passagers important. Durant la Seconde Guerre mondiale, le port fut largement détruit par des mines allemandes, les travaux de réfection ont duré plus de 10 ans et furent les derniers travaux majeurs ayant eu lieu dans ce port à l'heure actuelle. La profondeur à l'entrée du port est de 16 m, puis d'environ 8 m dans les bassins. D'une superficie de 13 600 m², ce port est essentiellement un port de commerce (second port fruitier de Méditerranée). La pêche y est également développée, le port étant le premier port de pêche des Pyrénées-Orientales, plusieurs pêcheurs petits métiers ainsi que les derniers chalutiers du département y sont installés. Le bassin le plus enclavé abrite un port de plaisance de 267 places. Quelques professionnels du tourisme sont aussi présents sur le port (club de plongée, bateau de promenade). Le port est équipé d'une station de carburant, de conteneurs à huile et batteries usagées, ainsi que de pompage des eaux usées et eaux noires et d'une aire de carénage. Le bassin de plaisance du port bénéficiait du pavillon bleu sur toute la durée d'échantillonnage de la thèse.



Figure 4 : Vue aérienne du port de Port-Vendres, Google earth V 7.1.2.2041 (7/10/2013), 42°31'08.66 N, 3°06'40.22 E, <http://www.earth.google.com> [20 Février 2018].

1.5 Port de Banyuls

Ce petit port de plaisance, fut lui aussi construit lors de la mission Racine au début des années 1960. Depuis, de nombreux travaux y ont été entrepris afin de l'agrandir et de l'entretenir, les derniers datent de 2010-2011 avec la réfection de deux quais mais de nouveaux travaux sont à prévoir afin de garantir la sécurité des navires lors de forts vents d'Est ainsi que pour augmenter la capacité d'accueil. Il abrite 370 anneaux avec une superficie de 3 300 m² et une profondeur de 4 m à l'entrée et 1.5 m dans le bassin. Malgré sa petite taille sa localisation à la lisière de la RNMCB le rend attractif et dynamique et plusieurs clubs de plongée y sont installés ainsi qu'un loueur de jet ski. Les pêcheurs professionnels ayant leur bateau amarré dans ce port de pêche possèdent l'autorisation de caler leur filet dans la zone de protection partielle de la RNMCB. Ce port possède une rampe de mise à l'eau.



Figure 5 : Vue aérienne du port de Banyuls, Google earth V 7.1.2.2041 (7/10/2013), 42°28'49.54 N, 3°09'09.74 E, <http://www.earth.google.com> [20 Février 2018].

1.6 Criques de Porteils et des Elmes

La zone naturelle la plus au nord correspond aux criques de Porteils, il s'agit du début de la côte rocheuse, juste après le port d'Argelès-sur-mer. Ce site se compose de petites plages de gravier peu fréquentées de par leur accès difficile (seule l'une d'elles est accessible facilement depuis un camping situé sur le haut des falaises) et de tombant rocheux (Figure 6-A). La profondeur sur les premiers mètres en s'éloignant du bord varie de moins d'un mètre à environ 4 m.

La deuxième zone naturelle, située plus au sud, commence à la plage des Elmes à l'entrée de Banyuls-sur-Mer et s'étend vers le sud en direction du village. Elle se compose d'une plage de gravier (pouvant être assez fréquentée en période estivale) à laquelle succède une zone rocheuse particulièrement sinueuse et peu profonde dont l'accès ne se fait que par l'eau (Figure 6-B). Sur cette zone la profondeur oscille de moins d'un mètre à environ 2 m.



Figure 6 : Vue aérienne (A) des criques de Porteils, $42^{\circ}32'05.43$ N, $3^{\circ}04'22.10$ E et (B) des Elmes, $42^{\circ}29'12.98$ N, $3^{\circ}09'31.79$ E, Google earth V 7.1.2.2041 (7/10/2013), <http://www.earth.google.com> [20 Février 2018].

2- Équipement d'ingénierie écologique utilisé

Ce travail de thèse a été mené sur des habitats artificiels conçus par la société Montpelliéraine Écocéan®. D'autres entreprises d'ingénierie écologique marine (Seaboost®, Safege®, Biotope®, Créocéan®...) proposent également des solutions de restauration écologique, notamment en milieu portuaire. Toutefois, à l'heure actuelle et en ce qui concerne la Méditerranée française, les d'habitats artificiels conçus par Écocéan® sont les plus utilisés dans les projets de restauration des infrastructures portuaires dans l'objectif de réhabiliter une fonction de nurserie, avec 16 ports équipés pour un total d'environ 1000 modules. Aussi, était-il pertinent de mener ces travaux de recherche en partenariat avec cette entreprise. Les habitats utilisés pour les cas concrets du chapitre 5 sont des Biohut® quai, ponton et kelp (Figure 7). Les deux premiers se composent d'une double cage en acier dont la partie interne, d'une maille de 2.5*2.5 cm, est remplie de coquilles d'huitres et la partie externe, d'une maille de 5*5 cm, restant vide. Les modules quai, fixés le long des quais par perforation ou attache magnétique, ont une dimension de 80*50*24 cm (Figure 7-A). Fixés sous les pontons à l'aide de bouts, les modules ponton possèdent une face supplémentaire et sont donc plus profonds (80*50*36 cm) (Figure 7-B). Les Biohut® kelps sont également fixés aux quais, généralement (mais pas obligatoirement) sous des Biohut® quai. Ils se composent de tiges en bois emboîtées dans un support métallique pour une dimension totale de 98*94*41 (Figure 7-C). Pour le chapitre 4, des modèles réduits de Biohut® quai ont été fabriqués à partir des mêmes matériaux que ceux utilisés pour les modèles originaux (plus de détails ont été donnés dans les chapitres). La conception de ces habitats est réalisée en privilégiant les circuits courts et la production locale, par exemple les tiges en bois sont réalisées par l'Établissement et Service d'Aide par le Travail (ESAT) « les Micocouliers » à Sorède (Pyrénées-Orientales), les coquilles d'huitres proviennent de partenariat avec les ostréiculteurs locaux, limitant ainsi l'empreinte écologique de la fabrication et favorisant l'économie locale.

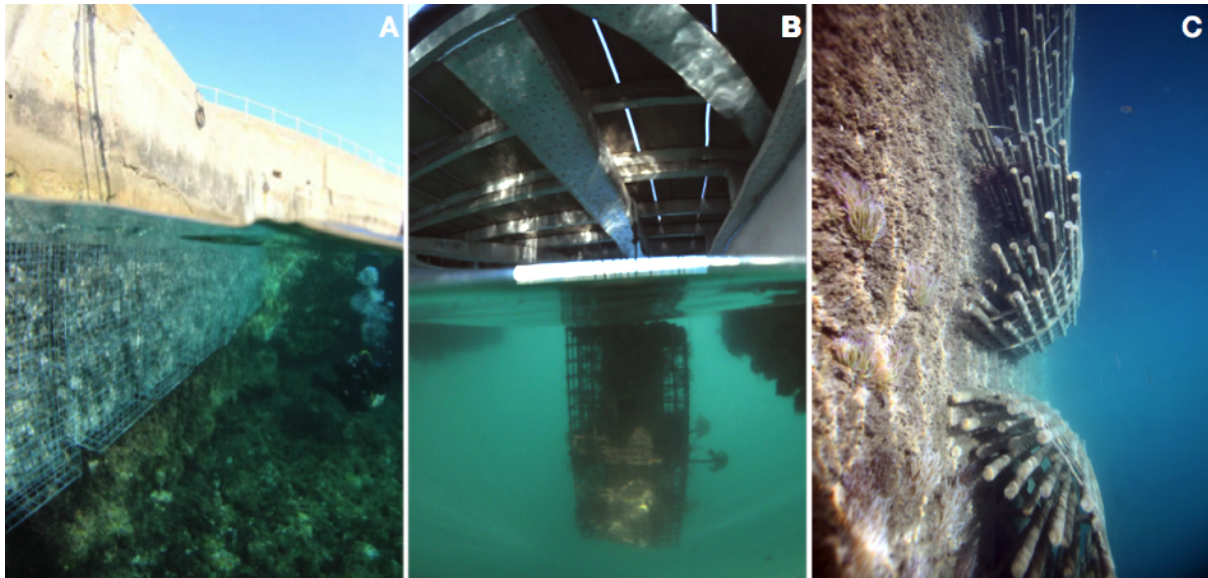


Figure 7 : Habitats artificiels utilisés dans cette thèse pour les cas concrets de réhabilitation de la fonction de nurserie en zones portuaires, Biohut quai (A), Biohut ponton (B), Biohut kelp (C). Crédits photo : Rémy Dubas, Alexandre Mercière, Didier Fioramenti. Plus de détail sur ces habitats sont disponibles dans les fiches produit fournies en annexe.

3- Approches employées

3.1 Expérimentation en mésocosmes

La première partie de cette thèse (chapitre 3) avait pour but d'évaluer le taux de survie de juvéniles de poissons côtiers sur les habitats artificiels utilisés en zones portuaires. Étant donné la difficulté d'évaluation de ce paramètre *in situ* du fait de la mobilité des juvéniles (Di Franco et al., 2013) ainsi que de la visibilité souvent médiocre en zone portuaire, il a été choisi de l'estimer par le biais d'expérimentation en mésocosmes.

Les premières études menées sur l'utilisation des habitats artificiels en zones portuaires ayant montré que ceux-ci sont essentiellement utilisés par les sars (*Diplodus* spp.) (Bouchouca et al., 2016; Lapinski et al., 2015; Mercader et al., 2017), ces derniers ont été retenus comme modèles. Il était initialement prévu de travailler sur trois espèces, le sar à tête noire *D. vulgaris* (Figure 8-A), le sar commun *D. sargus* (Figure 8-B) et le sparailon *D. annularis*. Les deux premiers s'installent dans des petits fonds rocheux hétérogènes, *D. vulgaris* en période hivernale (novembre à février) et *D. sargus* en période estivale (mai à juillet), le deuxième ayant des exigences plus strictes en terme d'habitat, notamment concernant la profondeur qui ne dépasse généralement pas 1 m

(Crec'hriou et al., 2015; Harmelin-Vivien et al., 1995; Vigliola et al., 1998). Le sparailon s'installe également en période estivale mais essentiellement dans les herbiers de posidonie dans des profondeurs plus importantes (6 m en moyenne)(Harmelin-Vivien et al., 1995). Aussi, le fait de le retrouver sur les habitats artificiels en zones portuaires était surprenant et suggérait une plasticité plus importante que celle envisagée jusqu'à présent (Bouchouca et al., 2016). Toutefois, faute d'une installation assez importante durant les 3 ans de cette thèse, cette espèce n'a finalement pas pu être étudiée. Pour les deux espèces retenues, les juvéniles ont été capturés à l'épuisette le long de digues (Figure 9-A et B) puis maintenus dans des aquariums de 500 L au Centre de Recherche sur les Ecosystèmes Marin (CREM) au Barcarès (Figure 9-E). Ces espèces bénéficiant d'une taille minimale de capture (23 cm pour *D. sargus*, 18 cm pour *D. vulgaris*), des autorisations de pêche ont été au préalable obtenues auprès de la Direction Inter-régionale de la Mer (DIRM, permis n°560).

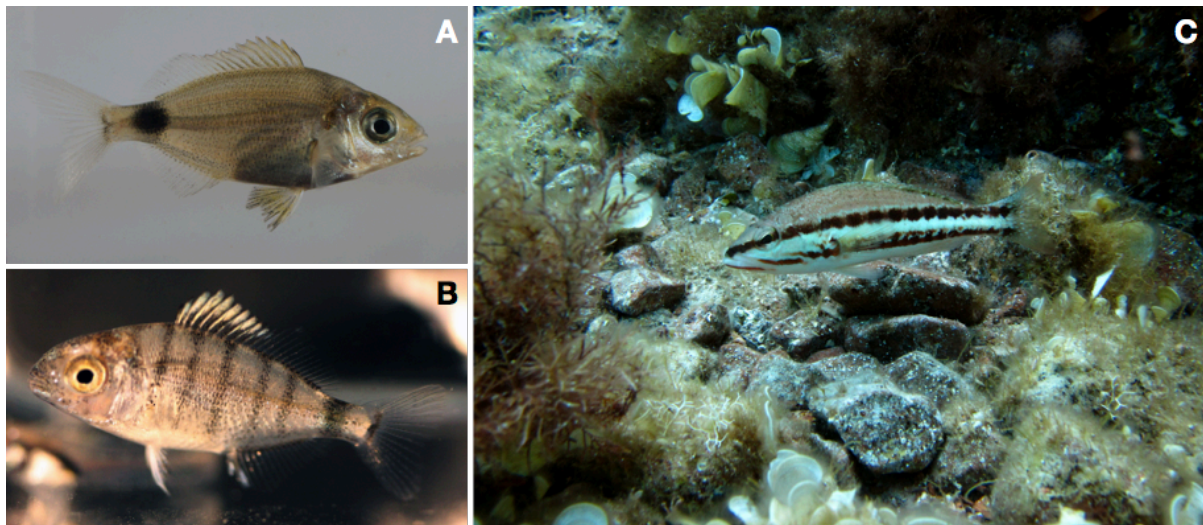


Figure 8 : Espèces modèles utilisées pour les expérimentations du chapitre 3, juvéniles de *D. vulgaris* (A), de *D. sargus* (B) et *S. cabrilla* adulte (C).

Le choix du prédateur s'est porté sur le serran chevrette *Serranus cabrilla* (Figure 8-C), petit carnivore très commun sur les côtes méditerranéennes. Sa petite taille et son agressivité en faisant un modèle bien adapté à l'expérimentation en mésocosme. Ils ont quant à eux été capturés en zones naturelles à l'aide d'une ligne appâtée (Figure 9-C et D) puis maintenus dans des bacs individuels de 80 L dans les mêmes installations que les juvéniles (Figure 9-F). Les expériences sur le taux de survie et la sélection d'habitat (dont le détail se trouve dans la section matériel et méthode du chapitre 3) ont été

menées dans des aquariums de 100 L toujours dans les installations du CREM. La thèse a bénéficié des installations acquises dans le cadre du projet européen Life+ SUBLIMO coordonné par le laboratoire CEFREM. Les autorités européennes gérant les projets ont encouragé une utilisation à des fins de restauration.

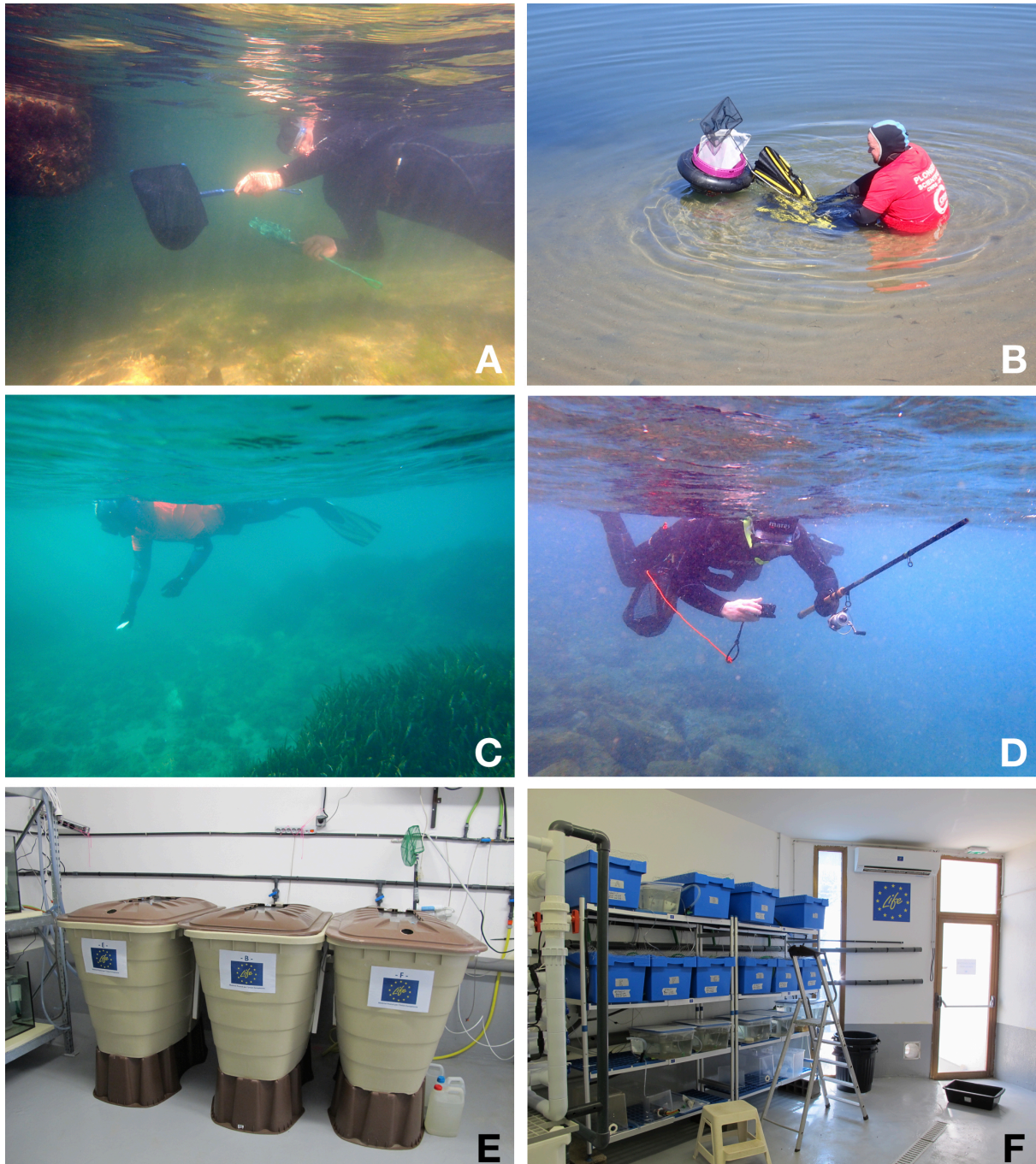


Figure 9 : Capture des juvéniles *D. vulgaris* et *D. sargus*, (A) utilisation des épuisettes, (B) matériel permettant le maintien des juvéniles le temps de la capture (seau rempli d'eau flottant grâce à une chambre à air). Capture des *S. cabrilla* avec fil et hameçon (C) ou canne à pêche (D). Bacs de stockage de 500 L pour les juvéniles (E) et de 80 L pour les prédateurs (F).

3.2 Approches de terrain

Les chapitres 4 et 5 reposent tous deux sur une évaluation des densités en juvéniles par comptage visuel (Underwater Visual Census, UVC) (Harmelin-Vivien et al., 1985). Étant donné les faibles profondeurs d'installation des juvéniles et la difficulté d'accessibilité de certaines zones, tous les comptages ont été réalisés en palme-masque-tuba (pas de plongée bouteille) (Figure 10A-C). L'échantillonnage s'est déroulé sur 2 ans (2015 et 2016) d'avril à octobre, ce qui correspond à la période de résidence dans les habitats nurseries pour de nombreuses espèces méditerranéennes (Biagi et al., 1998; Bussotti and Guidetti, 2011; Félix-Hackradt et al., 2013; Garcia-Rubies and Macpherson, 1995). Les comptages ont tous eu lieu de jour (entre 6h et 18h) et ont été réalisés par un nombre restreint de plongeurs entraînés à identifier les espèces ainsi qu'à estimer les tailles. Lors de chaque échantillonnage le plongeur notait sur une feuille plastifiée, le nombre d'individus observés, l'espèce et la taille (par classe de taille de 5 mm). Sur cette même feuille était également imprimées des silhouettes de poissons de différentes tailles (tous les 5 mm) afin d'aider à l'estimation (Figure 10-E et F). Pour le chapitre 4, la carte correspondant au site échantillonné était également imprimée et pour le chapitre 5 le plongeur y notait la référence du transect (le détail du protocole pour chaque méthode est donné dans le chapitre correspondant). L'échantillonnage en zone portuaire a nécessité la mise en place de certaines règles de sécurité, la première fut que le plongeur soit toujours accompagné d'un surveillant de surface et que le plongeur soit facilement visible dans l'eau (gilet jaune ou lycra rouge) (Figure 10-A-D), aux mois de juillet et août, quand l'intensité des activités maritimes est la plus forte, le surveillant de surface pouvait également être amené à porter un pavillon alpha (signalisation des plongeurs). La deuxième mesure mise en place fut le port d'une combinaison étanche (sauf lorsque la température était trop élevée) par le plongeur ainsi qu'un rinçage le plus rapidement possible après l'immersion. Malgré le temps passé dans l'eau, la présence de macro-déchets, de rejets de pêche et de quelques nappes d'huile ou de carburant, aucun des plongeurs n'a déclaré de problème de santé sur la durée de l'échantillonnage.

L'objectif du chapitre 4 était d'estimer le rôle des infrastructures anthropiques en tant qu'habitat juvénile (par comparaison avec des zones naturelles) sur la base d'un seul échantillonnage annuel (fin Juillet) mais à grande échelle spatiale. Les sites échantillonnés étaient répartis sur la totalité de la zone d'étude et incluaient les sites

principaux et secondaires (Figure 1). Cela représente pour chaque année une cinquantaine de kilomètres de côte échantillonnés sur environ deux semaines pour une équipe de six à dix plongeurs et une à deux personnes assurant la sécurité.

Dans le chapitre 5, l'évaluation du gain (en terme de densité de juvénile) pouvant résulter de l'utilisation d'habitats artificiels en zones portuaires a été faite par le biais d'un protocole Before-After-Control-Impact (BACI). Ce type d'approche fut traditionnellement développé pour les études d'impacts, puis pour l'évaluation de l'efficacité de mesures de protection ou encore de projets de restauration écologique. Il est basé sur la comparaison d'un site avant et après l'implémentation des actions dont on cherche à mesurer l'effet (Before vs After) ainsi que du dit site avec un (ou des) site(s) témoin(s) (Control vs Impact) ; l'interaction des deux (BACI) permettant la prise en compte de l'effet testé en s'affranchissant de la variabilité temporelle naturelle. Étant donné les fortes variations inter-annuelles du recrutement chez les poissons (Myers et al., 1997; Ospina-Alvarez et al., 2015; Pepin, 2016), cet aspect est particulièrement important pour l'évaluation de l'effet des habitats artificiels sur le potentiel des ports à servir d'habitats pour les juvéniles. Dans ce chapitre deux ports ont été choisis pour bénéficier de l'installation d'habitats artificiels (dont on a cherché à évaluer l'effet), le port du Barcarès sur la côte sableuse et celui de Port-Vendres sur la côte rocheuse. Ces ports ont ainsi été échantillonnés en 2015 sans qu'aucun aménagement n'eut été entrepris, puis en 2016 suite à la mise en place des habitats artificiels. Les ports d'Argelès-sur-mer sur la côte sableuse et de Banyuls sur la côte rocheuse ont quant à eux servi de témoins, auxquels ont également été ajoutées deux zones naturelles servant de référence (les criques de Portails et des Elmes). Ces six sites principaux ont été suivis de façon mensuelle d'avril à octobre 2015 et 2016. En moyenne, 9 transects de 60 m étaient réalisés pour chaque site (voir détail du protocole dans le chapitre 5) ce qui nécessitait environ une demi-journée d'échantillonnage durant les deux ans de suivi ce qui a représenté presque 60 jours complets de terrain, soit environ 250 h de comptage et 100 km parcourus à la nage.

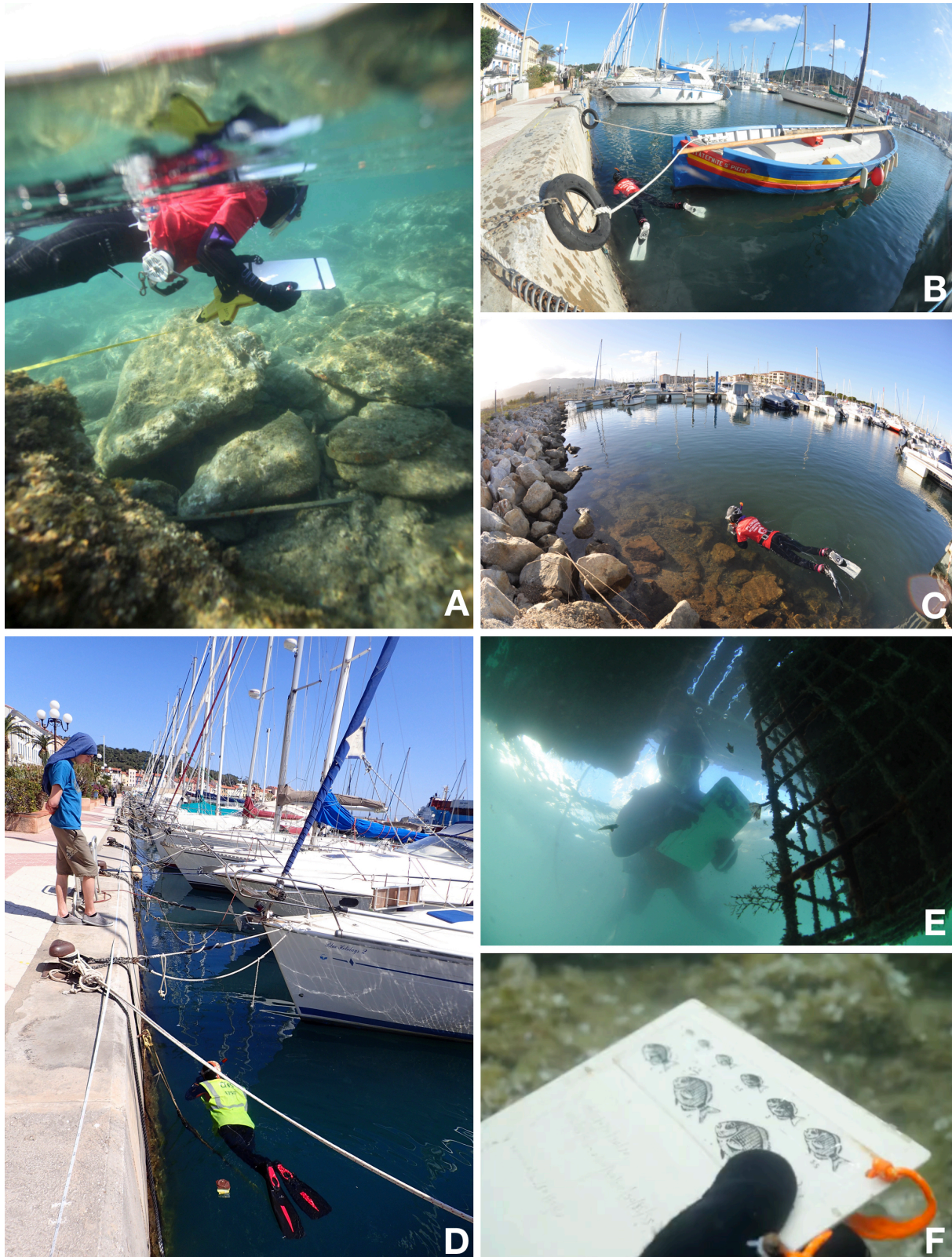


Figure 10 : Évaluation des densités en juvéniles par UVC, en zone naturelle peu profonde avec utilisation d'un mètre enrouleur directement par le plongeur (A), en zone portuaire le long d'un quai (B) et d'engrochements artificiels (C), mesure du transect en surface par le surveillant de surface (D), plaquette et feuille plastifiée avec silhouettes pour l'estimation des tailles (E et F).

4.3 Traitement des données

Dans les chapitres 4 et 5, seuls les juvéniles de l'année ont été pris en compte. Suivant l'espèce et la période de l'année, il s'agissait d'individus venant de s'installer ou s'étant installé depuis moins d'un an et n'ayant pas encore quitté l'habitat juvénile. Par exemple, pour le sar commun, *Diplodus sargus*, qui s'installe généralement aux alentours du mois de juin, les individus d'une taille supérieure à 50 mm n'étaient pas pris en compte en juin ou juillet (mois présumés d'installation) car il s'agissait certainement d'individus s'étant installés l'année précédente. Par contre, au mois d'avril, des sars de 90 mm étaient comptabilisés car il s'agissait certainement d'individus de l'année s'étant installés en juin. Toutes les données de comptage ont été standardisées par unité de surface: individus par 10 m² pour le chapitre 4, et individus par 60 m² (longueur des transects) pour le chapitre 5.

Différentes approches statistiques ont été utilisées pour chaque chapitre, chacune d'elles étant décrite plus en détail dans le chapitre correspondant.

Pour le chapitre 3 les taux de survie ont été estimés par la méthode Kaplan-Meier (Kaplan and Meier, 1958). Cette méthode historiquement utilisée en sciences médicales est aujourd'hui plus largement utilisée pour l'étude des cinétiques de mortalité dans divers domaines. En écologie, elle peut par exemple être utilisée en étant couplée à de la télémétrie ou du marquage GPS afin d'estimer le taux de survie de différents animaux (Garrison et al., 2007; Heupel and Simpfendorfer, 2002). Dans le chapitre 3, cette méthode non-paramétrique d'estimation des probabilités de survie a permis de comparer l'effet de l'habitat sur la survie des juvéniles. Ces estimations ont été complétées par des analyses multivariées (PERMANOVA) des différents comportements des juvéniles et des prédateurs. La sélection d'habitat a quant à elle été analysée via l'utilisation de l'indice de Jacob (Jacobs, 1974) couplé à un test non paramétrique de comparaison de moyenne (test de Wilcoxon).

Dans le chapitre 4, où il était question de comparer les différents types de sites (naturels, infrastructures de défense des côtes et ports) et d'habitats (à l'intérieur des ports), les données univariées de densité en juvéniles et multivariées de composition en espèces ont été comparées par permutation. Étant donnée la non-normalité des données et la complexité du design (i.e. multifactoriel avec interactions de facteurs) l'utilisation d'analyse de variance (ANOVA) et d'analyse de variance multivariée (MANOVA) par permutation représentait une approche adaptée (Anderson, 2001) qui, pour les données

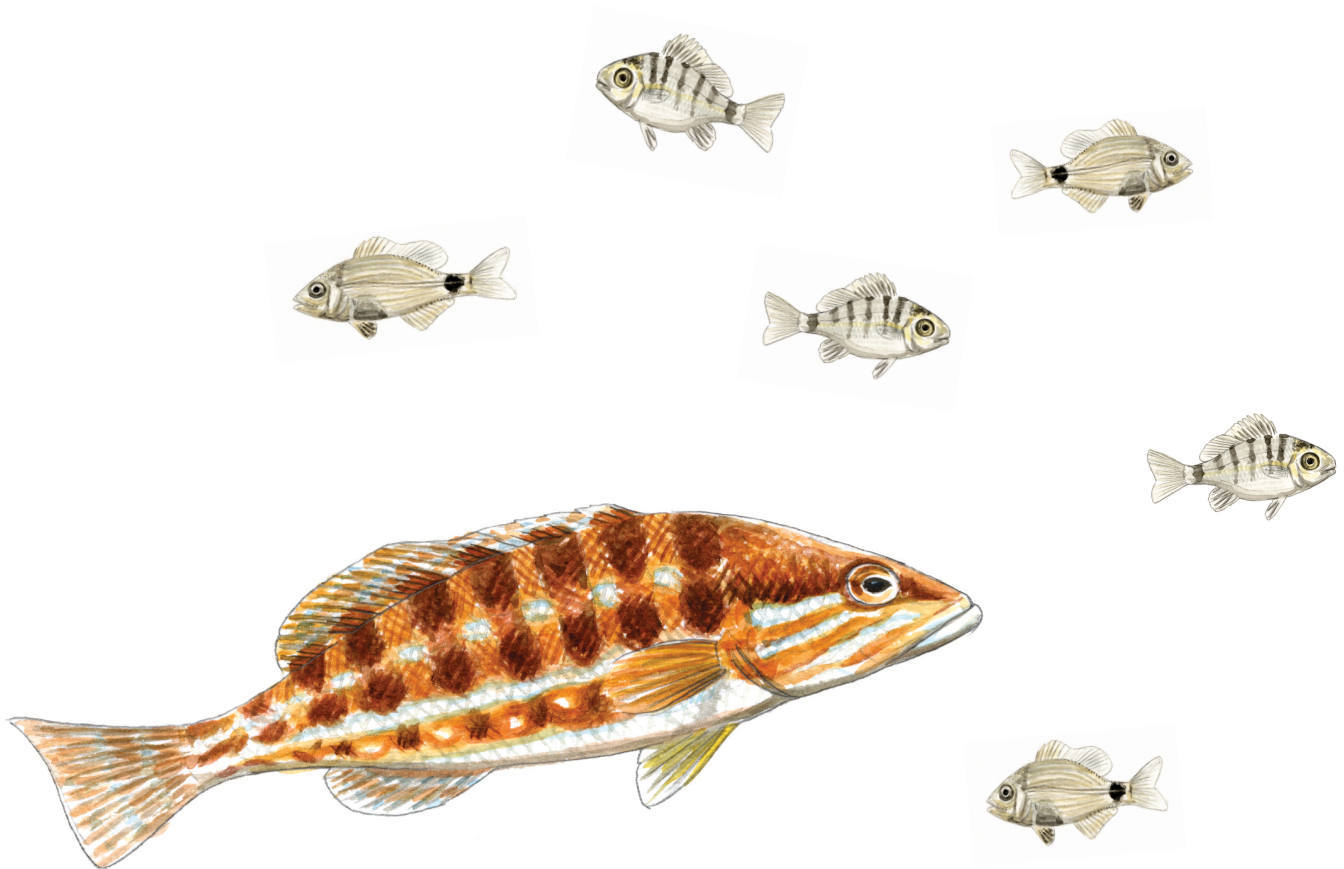
multivariées a été complétées par une analyse des pourcentages de similarité (SIMPER) afin de déterminer la contribution des différentes espèces à la dissimilarité entre habitats.

Les nombreuses contraintes liées au design expérimental du chapitre 5 (i.e. mesures répétées temporellement, plan d'échantillonnage déséquilibré) ont nécessité l'utilisation de méthodes statistiques encore peu utilisées en écologie. Il a en effet été choisi de traiter ces données selon un design BACI avec multiples témoins (Underwood, 1992) analysé par une méthode semi-paramétrique couplant modèles mixtes et penalized splines (Bolker et al., 2009; Ruppert et al., 2003). L'utilisation de modèles mixtes (Linear Mixed Model (LMM) et Generalised Linear Mixed Model (GLMM)) permet la prise en compte de la nature répétée (au cours du temps) des données ainsi que des effets aléatoires liés à la considération de plusieurs sujets (transects) et échelles spatiales (sites, habitats). Les penalized splines permettent quant à elles de tenir compte des déviations à la normalité dans un compromis entre courbes de régressions (très dépendantes du nombre et de la position des nœuds) et courbes de lissage (temps de calcul très long, difficultés d'interprétation), elles représentent ainsi une méthode de lissage optimisée suivant la complexité et la précision du modèle (Durban et al., 2004). Cette méthode a été complétée par l'utilisation de courbes de contrastes comme test post-hoc. Les courbes de contrastes calculent la différence entre deux courbes permettant d'identifier quelles portions de celles-ci diffèrent (suivant la co-variable d'intérêt, ici le temps) (Durban et al., 2004).

Les analyses par permutation ainsi que les analyses multivariées (chapitre 3 et 4) ont été menées sous PRIMER 6 avec l'extension PERMANOVA (Clarke and Gorley, 2006; Clarke et al., 2014). Toutes les autres analyses ainsi que les graphes ont été réalisées sous R (R Core Team, 2017).

Chapitre 3 :

Rôle d'un habitat artificiel sur le taux de survie de juvéniles de poissons côtiers



1- Is habitat diversity a key to restore the nursery function for juvenile coastal fish? An ex-situ experimental test of the effect of habitat type on predation-induced mortality of juveniles *Diplodus* spp. (pour soumission dans Restoration Ecology)

Is habitat diversity a key to restore the nursery function for juvenile coastal fish? An ex-situ experimental test of the effect of habitat type on predation-induced mortality of juveniles *Diplodus* spp.

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Abstract

Shallow coastal waters are particularly threatened by seascape modifications generated by increasing human activities (commerce, industry, tourism...) and demand for coast protection. Indeed, man-made coastal infrastructures have become ubiquitous components of coastal landscape, leading to habitat degradation, fragmentation and loss, which in turn affect the abundance and diversity of marine organisms as well as community structure, and the whole functioning of the ecosystem. Marine coastal fish have a complex life cycle requiring different essential habitats to be fulfilled. One of them is known as nursery habitat, a place where juveniles can settle in large number, survive and grow to finally contribute to adult population. Nursery habitats are mainly found in shallow, sheltered zones, thus particularly impacted by coastal urbanization, notably by the presence of ports and marinas. Indeed, the vertical featureless structure of docks is very unlikely to be used by juveniles, which need complex habitat to find food and shelter from predators. Also, recent attempts to rehabilitate the nursery function in those environments by the use of small artificial habitats have proved efficient in increasing juvenile densities compared to bare docks. However nothing is known about the survival of juveniles on those habitats. Here we set up tank experiment to test the effect of different habitats (including artificial habitat) on the survival of juvenile of two species of seabreams when facing stalk-attacking comber. We also explore juvenile habitat selection to determine if juvenile chose the habitat procuring the best survival rate. Habitat choice was coherent with natural preferences for those species and with survival results. However, the effect of the artificial habitat on survival was very variable between species. Our results suggest that habitat diversity might be of prime importance to sustain juveniles of different species even from the same genera and stress the need for the development of diverse artificial habitats to counterpart the adverse effect of seascape homogenization, which should be coupled with the conservation of remaining natural habitat mosaic.

Keywords: juvenile fish, survival rate, artificial habitat, seascape homogenization, predation, Mediterranean

1. Introduction

Landscape modification, resulting of habitat degradation, fragmentation or loss is known to be a key driver to species extinction leading to biodiversity loss in all ecosystems (Foley, 2005; Hewitt et al., 2010). Homogenized landscape not only impacts the abundance of organisms but also their distribution, the structure of communities and the functioning of the ecosystem (Brokovich et al., 2006; Fisher et al., 2007) reducing valuable functions and services (Cardinale et al., 2012). Marine ecosystems are not spared this threat (Coll et al., 2010; Halpern et al., 2008; Lotze et al., 2006), which is of particular intensity in coastal area as they concentrate most of the human population (Airoidi and Beck, 2007; Creel, 2003). Coastal shallow waters are crucial for early life stages of many species, the heterogeneity of the costal seascape resulting in a large variety of habitats providing food and shelter essential for juveniles (Beck et al., 2001). Habitat structure has an important influence on benthic and demersal organisms, including necto-benthic juvenile fish (Cheminée et al., 2017; Cuadros et al., 2017; Thiriet et al., 2016). It is composed of habitat complexity (abundance of structural components) and habitat heterogeneity (variety of structural components) of which results a given amount, composition and three-dimensional arrangement of physical matters (abiotic and biotic) under a determined spatio-temporal scale (Beck et al., 2001; Byrne, 2007). Habitat transformations and subsequent altered habitat quality (census Dahlgren and Eggleston, 2000) might have a particular impact on juvenile fish as this factor is determining for settlement and recruitment success (Cheminée et al., 2014; Nagelkerken et al., 2015; Parsons et al., 2015). Indeed, mortality during fish early life is great, possibly reaching more than 90% by the end of the larval stage (Houde and Hoyt, 1987). Post-settlement process, such as juvenile growth and survival, which are directly linked to habitat availability and quality, are also known to be of prime importance in the sustainability of populations (Nagelkerken et al., 2015; Parsons et al., 2014). Habitat homogenization and simplification might then threatened the nursery functions played by coastal areas (Cheminée et al., 2016; Connell and Jones, 1991; Piko and Szedlmayer, 2007).

Restoring habitats and landscape attributes (heterogeneity, connectivity) is one of the most widespread approach in ecological restoration. For terrestrial and freshwater ecosystems this might be achieved by a large variety of approaches such as replanting native plants, introducing grazing species, transplanting or removing soil, increasing the sinuosity of riverbanks or the connectivity of streams (Jaunatre et al., 2014; Mahlum et al., 2017;

Pedersen et al., 2007). Probably due to the inherent properties of marine systems, which are hardly accessible and highly dispersive, the range of tools available to restore marine habitats remains restrictive. Thereby, most marine restoration projects are based on the use of artificial habitats to increase the diversity and abundance of marine organisms or promote certain functions in degraded ecosystems (Seaman, 2007), while projects using living organisms are limited to a few coral, sponges, shellfish or seagrass and phanerogams transplants (Jaap, 2000; Ng et al., 2015; Perkol-Finkel et al., 2012).

Marine restoration is more recent than its terrestrial or freshwater counterpart, and projects are still scarce. However, the need to reduce the impact of coastal development, prompted marine ecological restoration with actions mainly directed on habitat structure and complexity (Brown and Chapman, 2014; Hellyer et al., 2011; Paalvast et al., 2012; Sella and Perkol-Finkel, 2015). Focusing on the nursery function for coastal fish within harbors, (Bouchoucha et al., 2016; Mercader et al., 2017; Patranello et al., 2017) showed that increasing habitat complexity by the use of small artificial habitats leads to increased juvenile densities. However, the observation of higher densities is not enough to conclude on the nursery role of the artificial habitats. Indeed, the nursery value of a habitat is given by its relative contribution to the adult population by comparison to other nearby habitats. This contribution results from four different factors: (i) higher densities, (ii) better survival rate, (iii) better growth rate and (iiii) facilitated migration toward adult habitats (connectivity) (Beck et al., 2001). In the case of artificial habitats, the question of survival is of particular interest as higher densities could also result of a concentration effect (Bortone, 1998; Brickhill et al., 2005). Indeed, if juveniles are concentrated on the artificial habitat but do not benefit from a better survival rate, this habitat won't play its nursery role and might even induce adverse effects by making juveniles more accessible to predators. Mortality by predation combined with competition for shelter holds as the main causes for density dependent mortality of juveniles (Anderson, 2001b; Hixon and Jones, 2005). Also, even if other causes of mortality exist (starvation, pollution, diseases...), we focused our study on predation-induced mortality.

The main objective of this work was to determine if mortality rate on artificial habitat used as experimental nursery is equivalent to the one of other habitats. Although, juvenile depletion from a given habitat results from two distinct processes, mortality and emigration, which are difficult to differentiate in open environments. Previous study revealed that, in the Mediterranean sea, the artificial habitat used for harbor restoration

are mainly used by *Diplodus* spp. (seabreams) (Bouchoucha et al., 2016; Mercader et al., 2017). At juvenile stage those species don't undertake large displacement, but they can still move at the scale of a whole cove (Macpherson, 1998), which prevents accurate study of their mortality on the smaller scale represented by the artificial habitats. Furthermore, visibility inside harbors is often poor making it difficult to precisely follow cohorts. Also, given those ecological constraints, tank experiments represented a good alternative to study the mortality of juvenile seabreams. Experiments permitted to estimate predation-induced mortality rates of juveniles on different habitat types and to explore the influence of those habitats on prey and predator behavior. As the distribution of juveniles depends on habitat availability, complexity and species preferences (Bell and Westoby, 1986; Horinouchi et al., 2013), we also evaluated whether juveniles were preferentially choosing a certain habitat type and if this choice was consistent with the habitat providing the best survival rate.

2. Material and Methods

2.1. Studied fishes

We focused on juvenile sparids of two species: the two-banded sea bream (*Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817)) and the white sea bream (*Diplodus sargus* (Linnaeus, 1758)), which were used as model prey species. These species are common in Mediterranean coastal waters and are known to settle in shallow coastal habitats. Juveniles of *D. vulgaris* and *D. sargus* settle in heterogeneous rocky habitat made of small blocs, pebbles, gravels or coarse sand (Harmelin-Vivien et al., 1995; Macpherson, 1998). Both species can also be found in high densities on artificial structures such as breakwaters or jetties (Clynick, 2008; Pastor et al., 2013; Tortonese, 1965) and have been observed inside ports and marinas, especially on artificial habitats (Bouchoucha et al., 2016b; Mercader et al., 2017c). If they use the same habitat as nursery, they do not settle at the same time period, *D. vulgaris* post-larvae reach the shore from December to March, while those of *D. sargus* arrive between May and June, which avoids competition between those two species (Macpherson, 1998; Vigliola and Harmelin-Vivien, 2001a).

We used the comber (*Serranus cabrilla* (Linnaeus, 1758)) as a Mediterranean predator model. This specie mainly lives around rocky substrates and meadow, which are used as habitats for its stalk-attacking strategy to predate (Louisy, 2015). The comber is an opportunistic macro-carnivore of small size (10 to 25 cm when adult) and its diet is mainly

composed of mollusks and crustaceans but contains bonny fishes as well (Cresson et al., 2014; Relini et al., 2002; Tuset et al., 1996)

2.2. Fish collection and housing

Model fish species were not available from aquaculture; also individuals were collected in the natural environment. None of these species are endangered or protected and sampling did not include any sites within marine protected areas. Fishing protocols and sites were approved by the Direction Inter-Régionale de la Mer (DIRM, the French administration of maritime affairs) by the permit n° 560. All fishes were captured by snorkeling, which permitted to select the right species and to have fish of the most homogenous size as possible. Prey models were collected using hand nets, while combers were fished using line and hook. Two collection campaigns, corresponding to the two prey models, were realized. For both campaigns combers were fished in the Bay of Paullille in Port-Vendres (42° 50' 21'' N 3° 12' 46'' E) on February 24th and 25th 2016 for the first and on June 10th 2016 for the second. *D. vulgaris* were collected between February 10th and 16th 2016 on the jetties of Leucate and Port-la-Nouvelle (42° 87' 29' 'N 3° 04' 94'' E and 43° 01' 64'' N 3° 06' 60'' E, respectively). *D. sargus* were caught on the same sites on June 8th and 10th 2016.

After collection, the greatest care has been taken to minimize damage and stress caused to the fishes. Juveniles were held in 500 L tanks (maximum 200 individuals/tank), while combers were placed in individual tanks of 45 L to avoid any aggressive behavior among them. All tanks (housing and experimental, see next section) were connected to the same filtration system filled with natural seawater coming from Canet-en-Roussillon municipal aquarium. Water temperature was different between the campaigns in order to be as close as possible to the natural conditions, 17 °C in February, 22 °C in June and July; salinity (37) and pH (8), as well as the photoperiod (12 h/ day of artificial neon light) were constant through all experimental campaigns. Physico-chemical parameters (pH, NH₃, NO₂, NO₃, salinity and temperature) were checked and adjusted twice a week. Fish were acclimated for two weeks before starting the experiments in order to allow them to recover from catching and to get used to captivity conditions. Juveniles were fed twice a day with defrosted *Artemia* sp. and combers once a day with a defrosted *Atherina* sp. Combers were not fed for 48 h before each experiment to make sure that they were all in the same starvation state at the beginning of all trials. At the time of experiments fishes were at a mean size of 2.4 ± 0.1 cm for *D. vulgaris*, 2.3 ± 0.2 cm for *D. sargus*, *S. cabrilla* were 15.1 ±

1.8 cm and 15.5 ± 1.4 cm for experiment with *D. vulgaris* and *D. sargus* respectively. Once the experiments were done, all predators and juveniles that had not been eaten during experiments were released alive on their capture site.

2.3. Experimental design

All experiments were led in identical 100x50x40 cm tanks placed in the same room as holding tanks and connected to the same filtration system (same water treatment). For mortality experiments an activated carbon-filter was added to each experimental tank between each trial in order to clear away dissolved fish chemicals from trial to trial (Martin et al., 2010). To avoid any disturbance filtration and air pumps were turned off and the access to the aquarium room was forbidden during the whole duration of experiments.

The bottom of all tanks was covered with a green velour carpet; the back and the sides of them were masked with auto-adhesive blue film to prevent exterior perturbations during experimental trials. We conceived four different types of habitats, two mimicking typical natural nursery habitats for sparids: rocky chaotic clusters (R) and posidonia meadow (M), one artificial habitat (AH) and a control (C) (Figure 1). Each habitat was conceived to occupy a volume of approximately 60 dm³, dividable into two equivalent parts (of 30 dm³) so it can be used in both experiments (mortality and habitat selection). The rocky chaotic clusters consisted of quarry stones (the same as used to build jetties and ripraps in the area) randomly placed in the aquarium to provide heterogeneous shape and size of cavities. The stones were piled up to form an approximately 25x25x100 cm habitat. In order to keep the same disposition among each trial, a picture was taken on the first replicate and used to identically reproduce this habitat for the other replicates. Meadows were made of plastic algae fixed to two 50x25 cm Plexiglas planks. Each plank was composed of 12 feet with 20 leaves of 20 cm height and 10 feet with 12 leaves of 25 cm disposed randomly (for a total dimension of the habitat of 25x25x100 cm). The total leave density resulting of the disposition was of 2880 leaves/m² for 95 % to 100 % recovery, which corresponds to a medium dense meadow (type II (Buia et al., 2004; Pergent et al., 1995)) and is representative of what can be found in the area between 0 and 3 m depth (Pergent et al., 2015; Rotini et al., 2013). The artificial habitat used for this experiment was a reduced version of the Biohut®, a small artificial habitat commercialized by the Ecocean® company. It is composed of a pair of stainless steel alloy cages (as used in (Bouchoucha et al., 2016b; Mercader et al., 2017c)). The inner cage has a 2.5 cm mesh and

is filled with a biogenic component (oyster shells), the outer cage has a 5 cm mesh and is left empty. The use of a larger mesh enables juvenile fish to go in and out without any inconvenience and is supposed to offer a predator free zone. The original version of this habitat is a 80x25x50 cm rectangle. Here we used two reduced version of 30x25x35 cm, which were hung on top of the tank, leaving a 5 cm space between the tank bottom and the habitat. For the control habitat, only two weighted plastic tubes (L=20 cm, $\varnothing=8$ cm) were added to the green velour carpet (one in the middle of each side of the tank). Control could have been left completely bared but test experiments showed that combers were too stressed by the total absence of habitat, for this reason we added the plastic tubes so they could use them to hide.

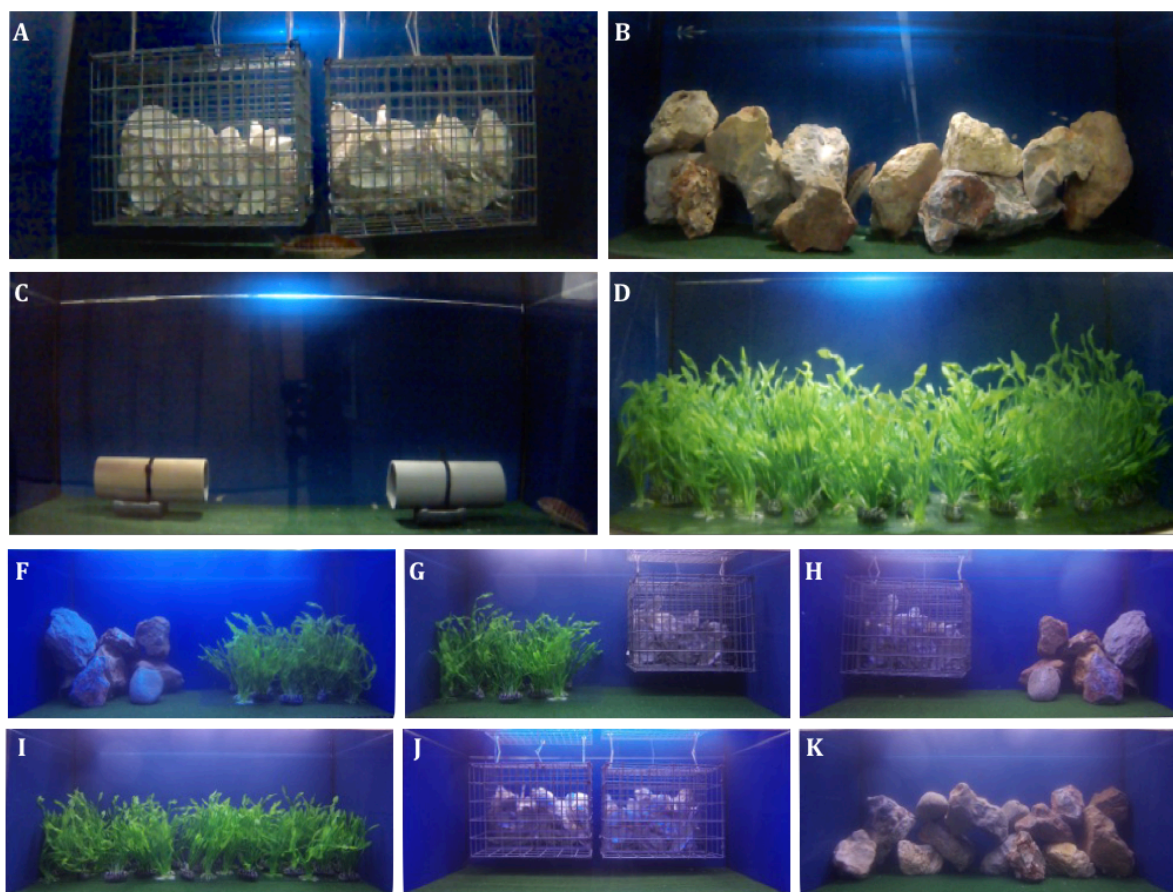


Figure 1: Habitat types used for survival experiments (A to D) and habitat selection experiments (F to K). Artificial Habitat (A), Rock (B), Control (C), Meadow (D), Combination Rock-Meadow (F), Meadow-Artificial Habitat (G), Artificial Habitat-Rock (H) and controls (I to J).

2.3.1. Survival

For this experiment, four tanks were used, each of them presenting a habitat (AH, M, R or C) occupying the approximate volume of 60 dm³ (Figure 1). A see-through plastic plank was placed in the middle of the tank to divide it into two half, preventing encounter between prey and predator, but letting them see each other. Five juveniles were placed on one side and the predator on the other one for 30 min, letting them time to recover from manipulation, acclimate to the new tank and explore the habitat. The position (right or left) of the juveniles and the predator during this acclimation time was switched at each replicate. Ensuing the 30 min of acclimation, the plastic plank was removed and experimentation begun. For 2 h tanks were recorded using a camera (GoPro hero3) placed in front of it, allowing having the exact time of every predation event. In addition, behavioral data (number of Approach, Attack and Escape, cf. Supplementary material 1 for the description each behavior) were recorded every 30 s by direct observations during the first 30 min of experimentation. At the end of the experiment surviving juveniles and predator were removed from experimental tanks, predators were replaced in their individual tanks and juveniles were put back in a new housing tank to avoid to use them a second time. For each prey species eight trials were run and to ensure complete randomization (and so eliminate any potential bias due to position on the shell) each habitat was placed in a tank for two runs then moved to the next tank and so on until it has been placed twice in each tank. To prevent predator from encountering twice a same habitat (and so an eventual risk of learning processes) and to limit potential bias due to inter-individual behavioral variability, two combers were randomly assigned to a tank in the way that each of them would run the experiment once for each habitat.

2.3.2. Habitat selection

Habitat selection was investigated for juveniles *D. vulgaris* and *D. sargus* alone so no prey-predator interaction was taken into consideration. Experiments were all led in the same tank. Habitats were disposed in the tank by combination of two (M/AH, R/AH, M/R), each one occupying half of the tank and representing approximately a volume of 30 dm³ (Figure 1). In complement of the tree combinations, tree control experiments were led in which the same habitat was present in the whole tank (AH1/AH2, M1/M2, R1/R2). Those control experiments were conducted in order to detect any potential preference for a side of the tank. Five juveniles were laughed in the middle of the tank, and observations begun 1 min

after their introduction. Test experiments had shown the fish seemed to need this acclimation time to swim “normally” in the tank after their introduction. The same camera as the one used for the mortality experiments was placed in front of the tank and settled to take a picture every 2 s during 5 min, which would later allow determining the position of the juveniles (cf. next section). As for the previous experiments, all fishes were removed from the tank and placed in a separated housing tank to avoid using twice the same fish. Eight replicates were run for each species and after four replicates, habitats were switched from one side of the tank to another in order to limit potential experimental artifacts.

2.4. Data acquisition

For survival experiments, the 2 h videos were viewed; each lethal interaction and the time at which it occurred were reported to allow the calculation of the mortality kinetic. As mentioned previously, qualitative behavioral data were recorded only for the first 30min. For habitat selection experiments, pictures were first corrected for the distortion due to the fish eye of the camera using Photoshop® (version CC 2015). The position of the fish in a X Y plan was then incremented using IMAGEJ (version 1.51j8). Due to battery issues, only 4 min 30 s (out of the indented 5 min) could be analyzed for all trials, which still represents 130 pictures, 650 coordinates by replicate and 5200 coordinates for each treatment (M/AH, R/AH, M/R, AH1/AH2, M1/M2, R1/R2). The intermediate area separating the two habitats in a tank was used as a limit to evenly divide each tank into two parts corresponding to the different habitats. Each pair of coordinates (statistical fish) was then assigned to a habitat.

2.5. Statistical analysis

For all statistical analyses the significance threshold was fixed at $\alpha = 0.05$. Survival and habitat selection analysis were run on the R environment (R Core Team, 2017) and behavioral analysis were led using PRIMER 6 software with the PERMANOVA add-on (Clarke and Gorley, 2006; Clarke et al., 2014).

2.5.1. Effect of habitat on juvenile survival

To compare the survival of the juveniles between the four habitats (AH, R, M and C), we determined juvenile survival probabilities in each habitat using the Kaplan-Meier (KM) method. This method allows to non-parametrically estimate the survival probability for

censored and uncensored survival times (survival curves) (Kaplan and Meier, 1958). Equality of the survival function between habitats was tested using the Peto and Peto modification of the Gehan-Wilcoxon test as hazard ratio was not constant over time and not proportional between habitats (crossing curves) (Bewick et al., 2004; Diez, 2013). If the hypothesis of equality was rejected, pairwise comparisons were performed using the Peto and Peto test with BH-adjusted p-values ((Benjamini and Hochberg, 1995). All survival analysis were done using the “survival” package (Therneau, 2015) for the R environment.

2.5.2. Fishes Behavior

To compare behavioral patterns of the fishes between habitats we used the total number of observed behavior for each behavioral variable (Approach, Attack and Escape) in each trial. Multivariate Analysis of Variance were led on Bray-Curtis dissimilarity matrixes with the addition of a dummy variable. P-values were calculated by 999 random permutations of unrestricted raw data as our design contained only one factor (habitat) and Type III sum of square (Anderson, 2001a). The Monte-Carlo test was used when less than 200 permutations were generated. Post-hoc pairwise tests were performed when relevant. SIMPER analyses were conducted when PERMANOVAs on behavioral patterns were significant in order to determine the relative contribution of each behavioral variable to differences between groups of habitats.

2.5.3. Habitat selection

The Jacob's Selection Index (SI) (Jacobs, 1974) was used to determine which habitat (AH, M or R) juvenile fishes preferentially chose. For each of the 8 replicates SI were calculated with 650 points (X-Y coordinate) corresponding to the position of each of the five juveniles every two second. This index is based on the following formula:

SI = (nH1 – nH2)/(nH1 + nH2), where n refers to the number of points observed in the habitat 1 (H1) and in the habitat 2 (H2). This index ranges between -1 and 1. SI = - 1 meaning a preferential choice for the habitat on the left (habitat 1), SI = 1 for the on the right (habitat 2), SI = 0 means no particular choice. Mean SI for controls and combinations of the 3 habitats were compared to zero using a one-sample Wilcoxon test. If controls differ from zero, this would mean that observed choices are not linked to habitat type but to other unknown factors. While if controls don't differ from zero but a combination does that would mean significant choice toward a habitat.

3. Results

3.1. Survival

Habitat type influenced juvenile survival for both species. For *D. vulgaris* the effect of habitat type on survival probabilities was significant (p-value 0.002) with the AH furnishing the best survival time (means survival time 108.16 ± 5.18 min) followed by the control (98.43 ± 6.70 min) and the rock (93.38 ± 6.92 min), survival was the lowest on meadow (88.88 ± 6.06 min) (Figure 2-A). Habitat type also significantly influenced the survival of *D. sargus* (p-value = 0.0053) but this effect was very different than the one observed for *D. vulgaris*. Indeed, survival was equivalent on control (mean survival time 115.40 ± 2.60 min), meadow (115.23 ± 2.84 min) and rock (115.22 ± 2.41 min) but lower on AH (98.23 ± 6.24 min) (Figure 2-B). Mortality was globally lower for *D. sargus* (only 23 juveniles were eaten which represent 14% of total individuals) than for *D. vulgaris* (29% of total juveniles were eaten). It is also to note that the lowest survival probability (at the end of the experiment, 120min) for *D. sargus* (on artificial habitat) is equivalent to the survival probability of *D. vulgaris* on rock (upper 0.86, mean 0.70, lower 0.57).

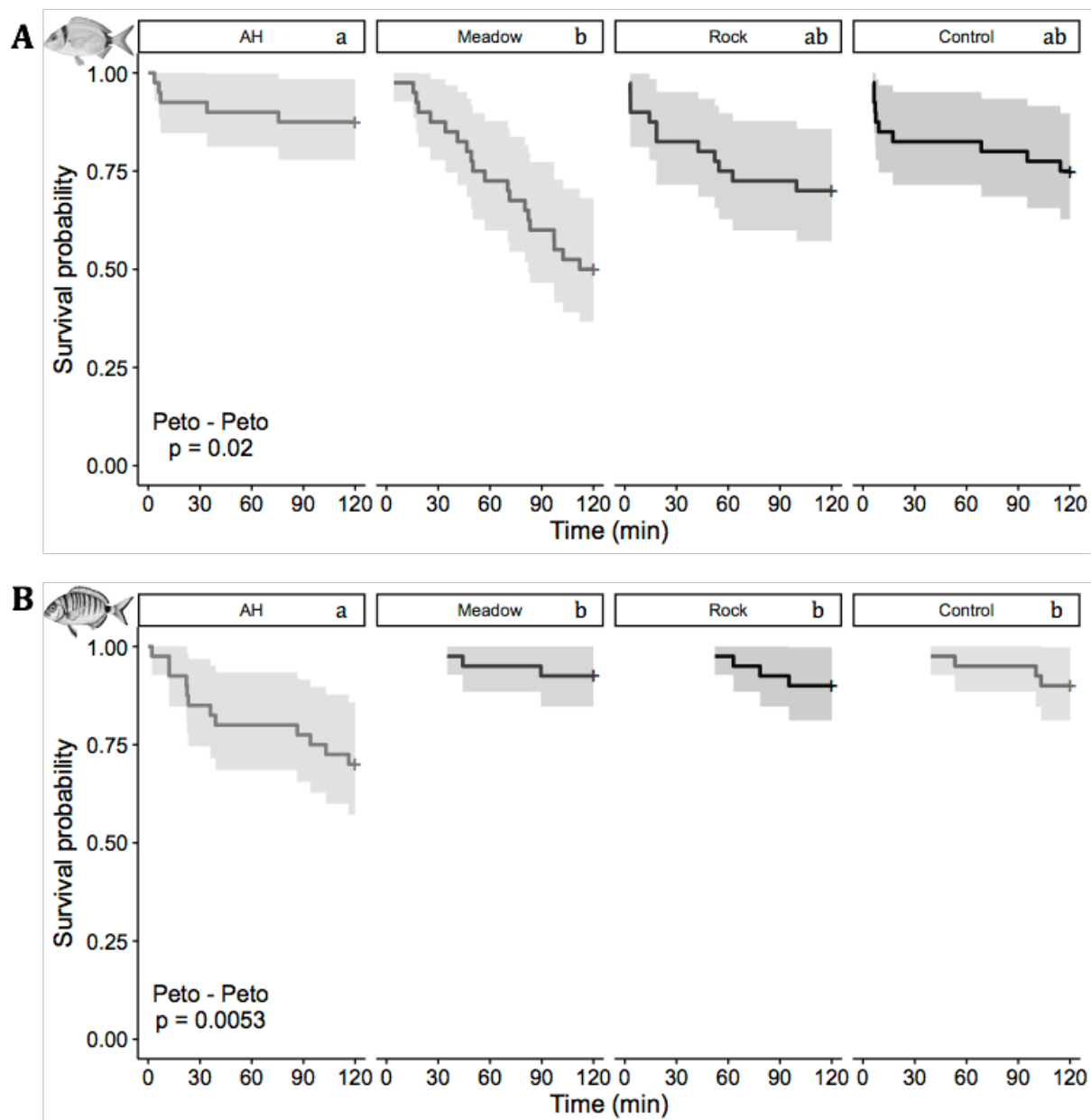


Figure 2: Kaplan-Meier survival curves for each habitat with 95% confidence interval, lowercase indicate the results of pair-wise tests: habitats sharing at least one character do not differ. (A) *D. vulgaris* and (B) *D. sargus*.

3.2. Fishes behavior

Behavioral patterns slightly varied according to habitat type. For *D. vulgaris* differences between habitat types were significant (p -value = 0.004) but only the control experiment significantly differed from all other habitat types (AH, meadow, rock), which did not differ one from the other. Fishes on the control were globally less active but the difference resulted mainly from the lower number of approaches, which was responsible for most of

the dissimilarity between control and other habitat types (SIMPER results: 59.11% with meadow, 44.18% for rock, 47.39% for AH) (Figure 3-A).

For *D. sargus* habitat types did not significantly influenced behavioral patterns. However, fishes seemed to be more active on the AH, while almost no activity was recorded on control (Figure 3-B).

3.3. Habitat selection

For both species no habitat selection was observed for all controls with mean SI being close to zero, indicating that when confronted to the same habitat in the whole tank the fishes made no choice (Figure 4). Surprisingly no significant deviation from zero was observed for any of the combinations of habitat and for both species, so no choice seemed to be made by the juveniles. However, a trend close to the significance threshold was detected for both species that used slightly more rocks than meadow (p-value = 0.148 and 0.109 for *D. vulgaris* and *D. sargus* respectively) and, for *D. vulgaris* only, more AH than meadow (p-value = 0.058).

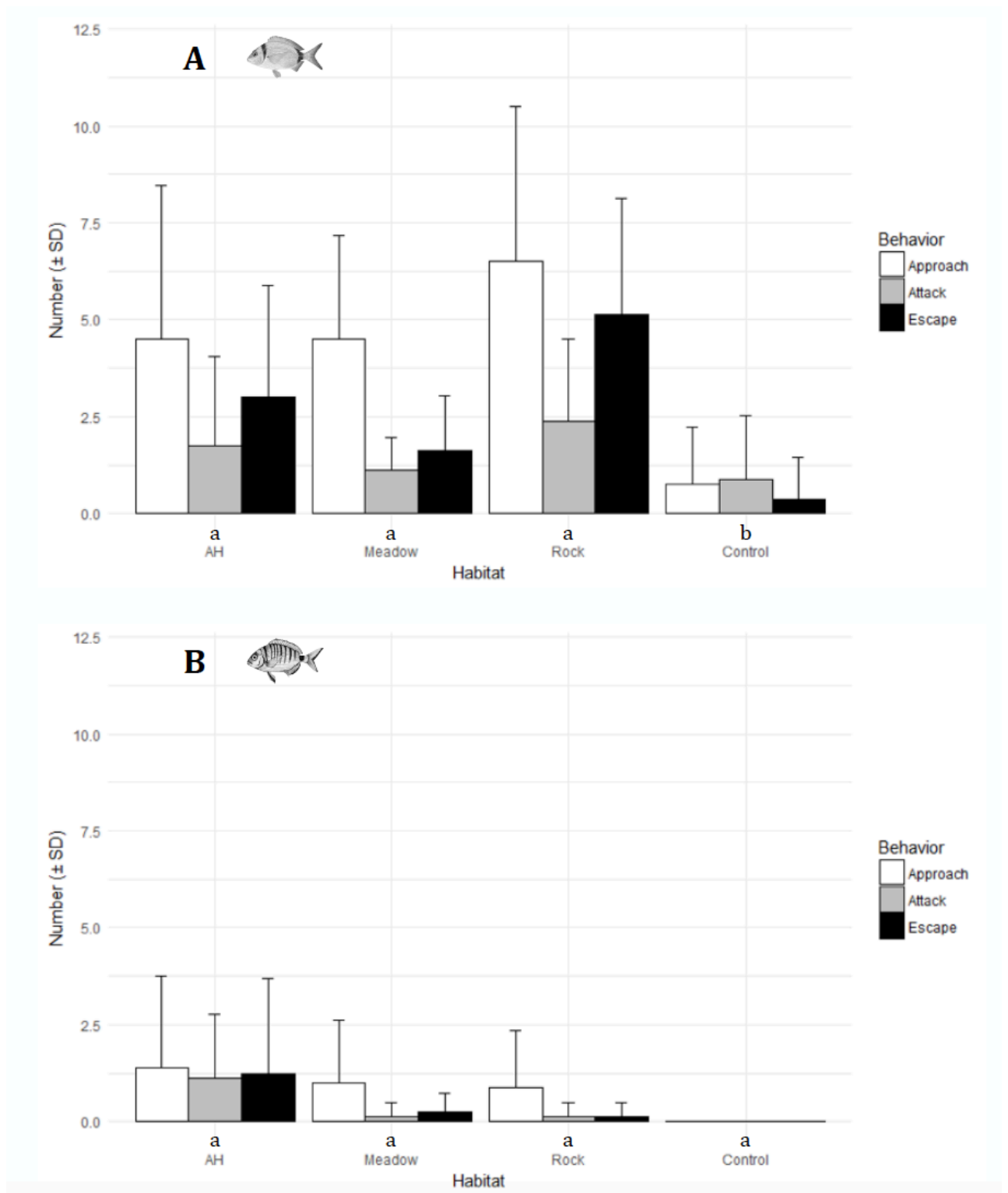


Figure 3: Mean number of behavioral observations for the first 30min of the predation experiments on (A) *D. vulgaris*, (B) *D. sargus*, lowercase indicate the results of pair-wise tests: habitats sharing at least one character do not differ.

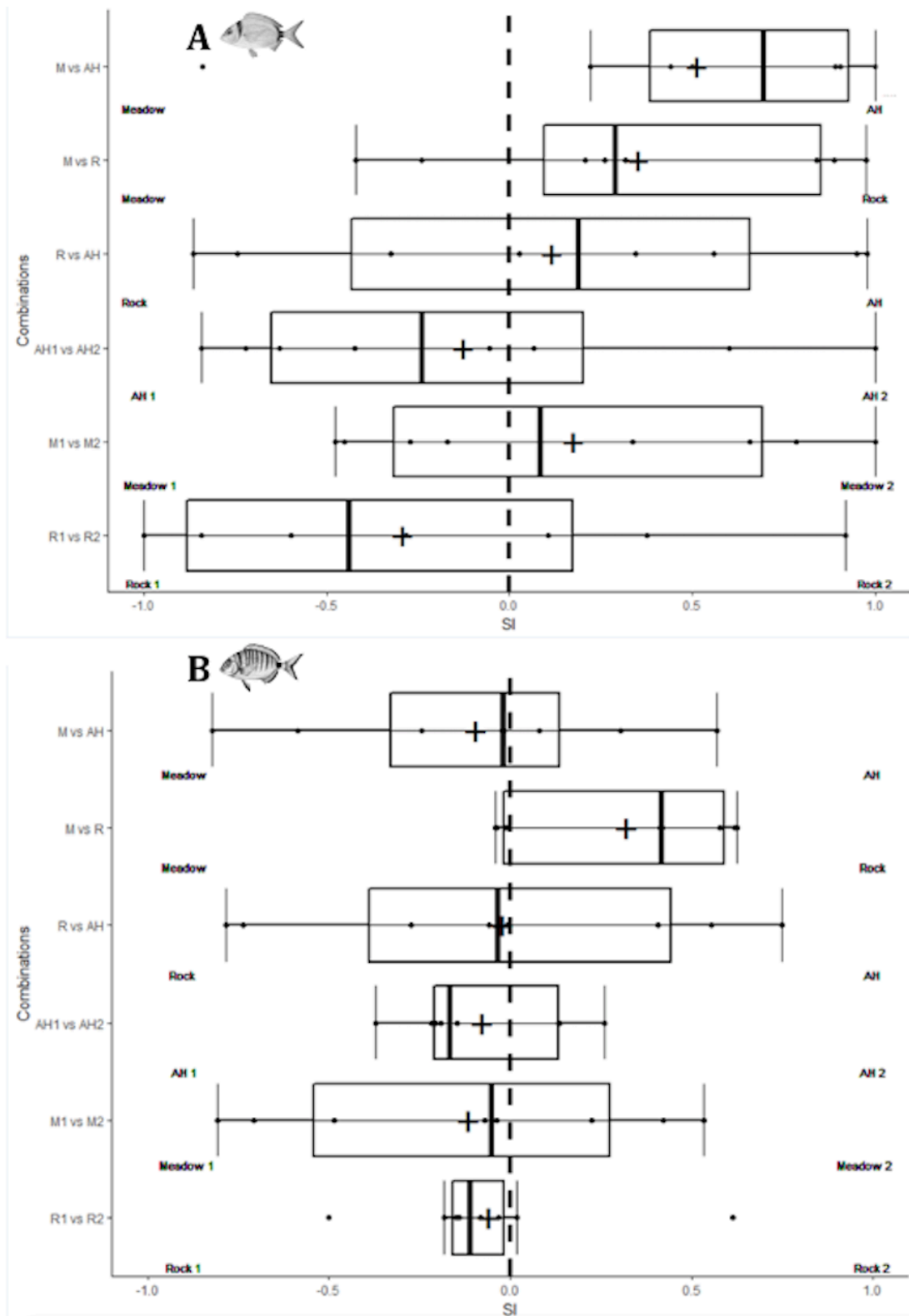


Figure 4: Boxplot of the repartition of Jacob's selection index for (A) *D. vulgaris*, (B) *D. sargus*. Vertical black lines indicate the median, the ends of the boxes the first and third quartiles, the whiskers the values whose distance from the box is at most 1.5 times the inter-quartile range, the point are extremes value and black crosses represent the mean values.

4. Discussion

Previous studies on the use of small artificial habitats to enhance ports and marinas ecological values (i.e. trying to compensate ecological functions of lost natural habitats), notably as juvenile habitat, had recorded greater densities of juvenile fishes on artificial habitat than on bare adjacent docks (Bouchoucha et al., 2016b; Mercader et al., 2017c; Patranella et al., 2017). However, it was unknown if this pattern was due to increased survival rate in AH compared to bare docks (increased production), or if this pattern was rather due to net immigration into AH of juveniles coming from adjacent habitats (active habitat selection resulting in concentration). On the AH used in this experiment juvenile *D. vulgaris* benefited from a survival rate comparable to the one observed on rocks (their known natural nursery habitat). Nevertheless, *D. sargus* juveniles experienced the highest mortality rates in this habitat compared to the other tested habitats. Beyond the use of the AH, our study revealed inter-specific variations among species of the same genera, and a greater than expected plasticity in the behavior of the juveniles highlighting the importance of habitat diversity for species maintenance.

4.1. Role of the artificial habitat as juvenile habitat

We found that the effects of AH on juveniles mortality rates, habitat preferences and behaviors were markedly different between the two *Diplodus* spp. AH seemed particularly suitable for *D. vulgaris* juveniles, which survive longer in AH, and did not discard AH compared to their natural habitat (rock, (Harmelin-Vivien et al., 1995)) during habitat choice experiment. The structure of this habitat might them provide comparable functionality to those of heterogeneous and complex natural rocky bottom (Bouchoucha et al., 2016b) which is also corroborated by the absence of difference in behavioral patterns between the two habitats. Surprisingly, results were much contrasted for *D. sargus*, the lowest survival being found on the AH when compared to other tested habitats. When submitted to different habitats juveniles *D. sargus* did not choose the AH. If the effect of the AH diverged depending on the species, coherence between the chosen habitat and the habitat providing the best survival rate seemed to occur for both species, suggesting that species experiencing low survival rate on the AH might not settle on it. This could in a way prevent detrimental effect on species for which this kind of AH is probably not suitable. This result is concordant with an *in situ* study which found that, within Mediterranean marinas, juveniles of *D. vulgaris* used more the AH than juveniles of *D. sargus* (Bouchoucha

et al., 2016b). The same study also pointed up a different use of the AH depending on the developmental stage of the juveniles, settlers (<2.3 cm) showing high dependence to the AH, while intermediate and post-dispersal stages (>2.3 cm and >4cm) enlarge their habitat by also using the adjacent bare docks. The fish used for this experiment were at the limit between settlement and intermediate stages (Ventura et al., 2014) and so might started to show less preference for a given habitat. Carrying out the experiment on smaller fishes might have given different survival and habitat choice results. It is also to note that during all experimental trials combers never entered the AH. Likewise, in the field, predators have never been observed inside the AH placed in harbors and marinas, with the exception of small gobids (authors personal observations), suggesting an efficient refuge role from at least predators bigger than 15 cm and showing high affiliation to substrate. This is not the case of all AH designs as mentioned by (Patranella et al., 2017) and sustains the hypothesis of an adapted structure to provide protection to juveniles. However, refuge role against transient predators deserve further investigation.

4.2. Effect of habitat type on predation-induced mortality and habitat selection

With regards all tested habitats and not only the AH, habitat selection results were consistent between species and with the literature on habitat preferences in natural environments. Indeed, even known this result was not statistically significant, juveniles had a tendency to choose rock and neglect meadow. Those species are known to use shallow sheltered rocky area with pebbles and rocks as nursery ground while they do not settle on meadow (Harmelin-Vivien et al., 1995; Macpherson, 1998; Pastor et al., 2013; Vigliola et al., 1998) and rather use it as a foraging habitat when adults (Divanach, 1985; Tortonese, 1965). However, as mentioned above, our study revealed important inter-specific variations concerning the effect of habitat type on survival rate, particularly for meadow. For *D. vulgaris* this habitat procured the lowest survival rate while the highest survival was observed for *D. sargus*. Mortality was also much lower in experiments with *D. sargus* for all habitats, and both, juveniles and predators, exhibited a low level of activity resulting in few prey-predator interactions. Two hypotheses may be considered. First *D. sargus* are known to be territorial and mobile fish (D'Anna et al., 2011) which might make them harder to catch. The second hypothesis is linked to the biological cycle of the comber whose reproduction occurs between April and July (García-Díaz et al., 1997) which might lead to increased food intakes before reproduction (resulting in a more active hunting

during the previous months), and reduced feeding activity during the reproduction period. This could explain the contrasted number of attacks between the two sets of experiments (around 3 times lower for summer experiments with *D. sargus* than for winter experiments with *D. vulgaris*). Nevertheless, the above results as well as those from other studies on artificial structures revealed a greater than expected plasticity in fish. This effect is notable in the behavior of juveniles which are able to settle on artificial structure which can sometime be very different of their natural habitat (Bouchoucha et al., 2016b; Clynick, 2006; Guidetti, 2004; Martin et al., 2005; Pastor et al., 2013).

Another surprising result of this study was the particularly low mortality rate observed on control experiments, while it was expected that the lack of habitat would be detrimental for juveniles with high mortality rates. Indeed, previous studies showed that lack of habitat structure results in high predation success (Heck et al., 2003; Orth et al., 1984; Schultz et al., 2009; Thiriet, 2014). However, predators have predation strategies adapted to the habitat they hunt in (Savino & Stein 1989). For *S. cabrilla*, a stalk attacking predator, it consist of furtively approaching the prey using habitat as camouflage before attacking (Schultz et al., 2009; Thiriet, 2014), also the total lack of habitat might be detrimental for this predator. Other predators with different predation strategies, notably transient chase and attack predators, might have reacted differently to this absence of habitat structure (Horinouchi et al., 2009). Prey identity might also have an influence, for instance juvenile *D. sargus*, which can settle in open environment such as pebble beaches, can be well adapted to avoid predators in such environments. Habitat structural complexity influences fish abundance and diversity (Graham, 2004; Gratwicke and Speight, 2005; Willis and Anderson, 2003) as well as size spectra by reducing predation induced mortality of certain size classes (Rogers et al., 2014). Habitat heterogeneity and diversity might also play an important role in species maintenance and even ecosystem functioning via habitat complementary (Alsterberg et al., 2017). In all ecosystems prey might adapt their habitat use (and other behavioral traits such as foraging activity) depending on the presence of predators which is an indirect effect of predation on prey population known as risk effect (Cowlshaw, 1997; Hamilton and Heithaus, 2001; Wirsing et al., 2007). For example, (Horinouchi et al., 2009), found that juvenile gobies were using seagrass or bare sand habitat depending on which predators were presents. In our study juveniles faced variating mortality rate depending on the habitat but did not have the possibility to change habitat

when facing predation. Also, if evolving in an heterogeneous seascape they might use different habitat depending on the presence and the nature of the predators.

4.3. Habitat diversity as a key for restoration and management efforts of coastal waters

Our results showed highly variable responses of the effect of the tested AH between species of the same genera. Moreover juvenile *Diplodus* spp. are known to undergo ontogenic shifts in habitat used, enlarging their niche by vertical (for *D. vulgaris*) or horizontal (for *D. sargus*) migration (Macpherson, 1998; Ventura et al., 2015; Vigliola and Harmelin-Vivien, 2001a). Those shifts have also been observed on AH within harbors (Bouchoucha et al., 2016b; Lapinski et al., 2015b). During experiments most juveniles were observed under the AH, which seems to be the same in situ (authors unpublished data), suggesting that placing AH at different depths could enhance their role as refuge for juvenile fishes. Our results also highlighted the need for various AH designs to mimic the heterogeneity of the seascape mosaic and so furnish complementary habitats to juveniles of different species or even for different developmental stages of a same species. The size of the cavities seem to be of prime importance to prevent the installation of stalk-attack and ambush predators (Patranella et al., 2017), but their number and diversity might also be a determining factor to favor multiple species and size classes (Rogers et al., 2014). Other factors such as the material employed, which might allow the development of fooling (potential food), the arrangement of the different structural components or the size and density of habitats might enhance the potential of man-made structure as juvenile fish habitat. Low specialization, high tolerance to disturbance and ability to live in modified habitats increase resistance to habitat loss, while ability to move in and out of modified environment combined with high dispersal ability increase resistance to habitat fragmentation (Fischer and Lindenmayer, 2007). Also the set of species able to live in highly urbanized area such as harbors might be restricted to generalist species. To prevent the biotic homogenization often resulting of anthropogenic disturbances (Devictor et al., 2008; Olden, 2006) management effort should also focus on the preservation of diverse natural habitat. However, urban ecology and restoration ecology might raise new questions on the ecology and particularly the level of plasticity of many species, for example species only rarely observed at juvenile stage in natural areas, such as the common dentex (*Dentex dentex*), the black seabream (*Spondyliosoma cantharus*), pipefishes (*Syngnathus* spp.) (authors unpublished data) or even the protected Dusky grouper (*Epinephelus marginatus*)

(Mercader et al., 2016) have been seen within harbors, suggesting that even more specialized species could be able to live in those areas if suitable complex habitats are present. Also, marine anthropogenic structures should not be neglected in management and conservation plans, as they might be able to provide some ecological functions.

5. Conclusion

Our study highlighted variations of mortality rate according to habitat type and notably of the refuge effect of the tested AH. It also showed that the studied species did not make any clear habitat choice and that plasticity in habitat use might be higher than previously thought. However, those results don't necessarily involve that the same thing is happening in natural environment. In our tank experiment fishes were submitted only to differences in habitat structure but other factors like the presence of conspecifics, olfactory and chemical signals, food availability or predators densities may affect habitat choice (Barth et al., 2015; Lecchini et al., 2007; Thiriet et al., 2014). Likewise, in the field, mortality rate might be influenced by many natural and anthropic factors. Indeed, in highly urbanized areas pollution and acoustic disturbances might influence the survival of juveniles. Also, complex field experiments taking into account all factors and their interactions would be necessary to assess the global mortality rate on artificial and natural habitats.

Our study proved that AH might not have any detrimental effect on juvenile survival and might even have a beneficial effect for at least *D. vulgaris*, complementing previous study on the use of AH as a mean to rehabilitate the nursery function in degraded environments. The variations observed also highlighted the need for diversity in AH design and location in order to benefit multiple species and developmental stages and so help to the maintenance of marine fish abundances and diversity.

Acknowledgements

This work was financially supported by the Agence de l'eau Rhône Méditerranée Corse. The authors would like to thank Nicolas Tapia, Laurie Lebre, Gilles Saragoni, Alan Brazo, Quentin Thernon and Gaël Simon, for they help in fish capture and housing. They also thank the Ecocean company for providing the material needed to build the AH used in this study as well as the personnel of the municipal aquarium of Canet-en-Roussillon for providing seawater.

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Supplementary material 1

Behavioral repertoire describing prey and predator behavior during survival experiments

Model	Behavior	Habitat	Description
<i>S. cabrilla</i> (predator)	Approach	All	Individual in stealth approach. Gaze towards prey. Dorsal fin raised.
	Attack	All	Swim fast towards the prey with an open mouth. Fins joined to the body.
<i>D. vulgaris & D. sargus</i> (prey)	Escape	All	Following an approach behavior or an attack of the predator. Swim fast towards the habitat to avoid the predator. If several juveniles flee at the same time for a unique predatory behavior, only one escape is counted. If an attack results in at least one death, no escape is counted.

2- Résumé du chapitre

L'objectif de ce chapitre était d'estimer le taux de survie des juvéniles face à la prédation sur les habitats artificiels à vocation de nurserie et de le comparer à celui observé sur des habitats assimilés à des habitats naturels. Ces taux de survie ont été estimés par le biais d'expériences en aquarium sur quatre types d'habitats différents (i) habitat artificiel, (ii) roche, (iii) herbier et (iv) témoin (aquarium vide pouvant représenter un quai témoin). Des juvéniles de deux espèces de sar, *D. vulgaris* et *D. sargus*, ont été soumis à un prédateur le serran chevrette *S. cabrilla*. Les résultats étaient contrastés entre les deux espèces. *D. vulgaris* présentait les meilleures probabilités de survie (estimées par la méthode de Kaplan-Meier) sur l'habitat artificiel suivi par la roche et le témoin (probabilités équivalentes), et les plus faibles sur l'herbier. Au contraire, pour *D. sargus*, c'est sur l'habitat artificiel qu'elles étaient les plus faibles, les autres habitats procurant des taux de survie équivalents, et tous étaient supérieurs à celui de l'habitat artificiel. Les résultats des expériences de sélection d'habitat réalisées en complément ont montré que les juvéniles des deux espèces ne choisissent pas nettement un habitat plus qu'un autre. Ils paraissent toutefois avoir une préférence pour la roche en comparaison à l'herbier. Les juvéniles de *D. vulgaris* semblent également délaisser ce dernier au profit de l'habitat artificiel lorsqu'ils font face à une combinaison de ces deux habitats. Bien que difficilement généralisables, et ne permettant pas de déterminer quelle part est jouée par les phénomènes de concentration et de production (meilleure survie) dans la présence de plus fortes densités en juvéniles sur les habitats artificiels tels que les quais et pontons témoins, cette étude a permis de mettre en évidence trois points essentiels pour la réhabilitation de la fonction de nurserie via l'utilisation d'habitats artificiels : (i) pour certaines espèces, il est possible que ces habitats procurent un taux de survie équivalent voire supérieur à ceux observés sur des habitats naturels, (ii) certaines espèces peuvent avoir un taux de survie plus faibles sur les habitats artificiels, mais comme cet habitat n'est pas préférentiellement choisi, les risques d'effets délétères (concentration sur un habitat ne jouant pas un rôle de refuge efficace) sont donc peu probables, (iii) même pour des espèces du même genre et présentant des exigences similaires en terme d'habitat juvénile, l'effet de l'habitat artificiel est contrasté. Ces résultats suggèrent qu'une réhabilitation efficace devrait passer par l'utilisation d'une multitude d'habitats différents.

Chapitre 4 :

Rôle des infrastructures portuaires en tant qu'habitat juvénile



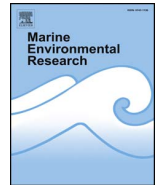
1- Spatial distribution of juvenile fish along an artificialized seascape, insights from common coastal species in the Northwestern Mediterranean Sea (article accepté dans Marine Environmental Research)



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Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev



Spatial distribution of juvenile fish along an artificialized seascape, insights from common coastal species in the Northwestern Mediterranean Sea

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ARTICLE INFO

Keywords:

Juvenile fish habitat
Coastal urbanization
Harbor
Coastal management
Mediterranean

ABSTRACT

Along the littoral, a growing number of anthropogenic structures have caused substantial habitat destruction. Despite their detrimental impact, these constructions could play a role in the functioning of coastal ecosystems. The objective of this work was to assess the distribution of juvenile coastal fish along a seascape composed of various natural and artificial habitats in order to determine the potential role of coastal infrastructures as juvenile habitat. We surveyed juvenile populations on various infrastructures and natural sites along a 100 km shoreline of the French Mediterranean coast. Juvenile densities varied according to the level of artificialization of the sites. Densities were the highest on coastal defense structures, intermediate in natural sites and lowest in harbors. Focusing inside harbors revealed highly variable densities depending on the type of habitat, with densities on ripraps or jetties that were equivalent to those of natural sites. Our results underline the importance of anthropogenic structures as potential juvenile habitats, which is too often not considered in management plans.

1. Introduction

Due to an ever growing global population and a general migration to the coast, coastal areas already concentrate more than 60% of the human population while they represent less than 15% of the planet's land surface (EEA, 1999) and this proportion is expected to reach 75% by 2025 (Airoldi and Beck, 2007; Creel, 2003). As a result, the land-sea interface is subject to an unprecedented variety and magnitude of anthropogenic pressures making them particularly vulnerable. This translates into a multitude of consequences such as resource over-exploitation, pollution, invasive species and habitat modifications (Crain et al., 2009; Dugan et al., 2011). The latter is known to be one of the greatest threats to marine biodiversity and ecosystems (Coll et al., 2010; Dafforn et al., 2015; Halpern et al., 2008) and is exacerbated by the flourishing number of coastal anthropogenic structures (e.g. harbors, marinas, coastal defense structures such as seawalls, breakwaters, groins, etc.) triggered by urbanization, commerce, industry, tourism and the need to protect the coast from erosion and flooding (Bulleri and Chapman, 2010; Gerland et al., 2014; Scyphers et al., 2015). The main consequence of coastal hardening is that it destroys, transforms or

homogenizes the natural seascape mosaic, replacing the original patchiness of heterogeneous subtidal environments by homogenous and often less complex artificial habitats. It has been shown that the reduction of complexity and heterogeneity of seascapes leads to lower abundances and the increased mortality of organisms (August 1983; Brokovich et al., 2006; Fisher et al., 2007). One of the essential functions offered by coastal habitats is their nursery role for marine organisms. The coastal seascape mosaic offers a wide variety of habitats, which provides suitable food and shelter essential for the juvenile stages of many different species (Beck et al., 2001).

Most coastal fish have a complex life cycle composed of two phases, a pelagic and a benthic (Armsworth, 2002; Jones, 1988; Mora and Sale, 2002; Öhman et al., 1998). The former is also known as the dispersive phase in which eggs are released into the water column and then hatch to produce larvae that disperse in open waters. After a period of about one month, during a transition called settlement, the larvae may reach the shore (Di Franco et al., 2013) and become a post-larva that will establish in its new benthic juvenile habitat. Newly settled juveniles will then grow in their juvenile habitat for approximately six months (variable upon taxa) until they reach a size permitting them to avoid

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<https://doi.org/10.1016/j.marenvres.2018.02.030>

Received 15 November 2017; Received in revised form 24 February 2018; Accepted 26 February 2018
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most predation (around 8 cm), at which point they actively leave this habitat to recruit into the adult population (Vigliola and Harmelin-Vivien, 2001). The juvenile stage is critical as mortality is great (Houde and Hoyt, 1987; Macpherson et al., 1997; Planes et al., 1999; Vigliola et al., 1998) and the number of individuals that will eventually contribute to the renewal of adult populations is highly dependent of the quality of juvenile habitat. According to Beck et al. (2001), nurseries are habitats that contribute a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other juvenile habitats. The “nursery value” of a given habitat, which is a relative value, results from a combination of four parameters: (1) the initial density of juveniles, (2) their survival rate, (3) their growth rate and (4) their ability to migrate from the juvenile habitat and recruit into adult habitats. As it is logistically difficult to assess parameters (2), (3) and (4), the number of juveniles present in a given habitat at a given time between settlement and recruitment has often been used as a proxy of its nursery value (Cheminée et al., 2017a; Cuadros et al., 2017a; Macpherson and Zika, 1999; Pastor et al., 2013) and permits comparison between sites. Besides, the concept of “effective juvenile habitats” (Dahlgren et al., 2006) brings complementary information. Those habitats are habitats whose densities of juveniles are small, but have a high overall contribution to adult population due to the large surface they might represent in the seascape, which might be the case of coastal anthropogenic structures.

Because the alteration of nursery habitats can have direct adverse effects on juvenile survival and the subsequent maintenance of adult populations, it is of prime importance to identify and localize them in order to focus conservation efforts. Some recent studies have focused on these goals (Cheminée et al., 2013, 2014; Cuadros et al., 2017b) but anthropogenic structures were only slightly taken into consideration. However, structures such as breakwaters have been shown to host high juvenile densities of certain coastal fish (Dufour et al., 2009; Pastor et al., 2013; Pizzolon et al., 2008; Ruitton et al., 2000). Therefore, their potential role as juvenile habitat should not be neglected especially in the context of their growing ubiquity in the coastal seascape.

The main objective of this study was to assess the spatial distribution of juvenile coastal fish in a seascape composed of natural habitats and various anthropogenic structures. This was undergone by working on a relatively large spatial scale (around 100 km of coastline) permitting the inclusion of different artificialized and natural sites. We focused on Mediterranean coastal species settling in shallow heterogeneous rocky habitats. We first compared different levels of artificialization using a snap-shot of juvenile densities found in natural habitats versus those present on Coastal Defense Structures (CDS) and inside harbors (i.e. the two most widespread coastal anthropogenic structures in the area). Furthermore, as very little is known about these urban ecosystems despite their universality, we then concentrated inside harbors where we assessed the effect of habitat type on juvenile densities.

2. Material and methods

2.1. Study area and sampling strategy

The study was conducted on the southernmost French Mediterranean coast in the Gulf of Lion (NW Mediterranean). The sampled area stretches from Leucate to Cerbère (at the border between France and Spain) for approximately 100 km. This coast can be divided in two different types of regions, a sandy coast (SC) to the north, and a rocky coast (RC) to the south (Fig. 1-a). The entire study area is included in the Gulf of Lion Natural Marine Park (GLNMP) and encompasses the Cerbère-Banyuls Natural Marine Reserve (CBNMR). Within this area harbors are scattered along the entire studied shoreline and represent around 20 km of shoreline, which is approximately the same amount of linear coast as the RC. Juvenile habitats were identified and measured by the use of aerial images as in Cheminée et al. (2017a, 2017b): identification criteria of juvenile habitats consisted of

shallow, protected from strong swell, gently sloping habitats with a heterogeneous substrate consisting of small blocks and rocks. Among the 83 sites identified as potential nurseries, 29 natural sites (Fig. 1-b) and 10 CDS (Fig. 1-c) were randomly chosen for sampling. Additionally, seven harbors (Fig. 1-d) were added to this sampling array, out of the nine present in the study area, for a total of 46 sampled sites. Within each harbor, random samples were performed among the different types of habitat: outer jetty, inner jetty, natural (which can consist of a hard or soft bottom depending on the region), dock (concrete walls) and riprap (see Fig. 1-e to h for description). Each harbor contained between four and five habitat types. Minimums of three replicates were performed for each habitat type in each harbor.

2.2. Studied species

This study focused on species that use the above described heterogeneous rocky and sandy habitats as a nursery ground (Harmelin-Vivien et al., 1995). For the first part of our study, comparing natural, CDS and harbor sites, we considered the following eight species for our surveys as a previous study showed they were present in the study area (Cheminée et al., 2017a) and are strongly affiliated to the studied habitat (Cheminée et al., 2011; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola, 1998): white seabream (*Diplodus sargus sargus* (Linnaeus, 1758)), sharpnose seabream (*Diplodus puntazzo* (Walbaum, 1792)), yellowmouth barracuda (*Sphyraena viridensis* (Cuvier, 1829)), ornate wrasse (*Thalassoma pavo* (Linnaeus, 1758)), dusky grouper (*Epinephelus marginatus* (Lowe, 1834)), zebra seabream (*Diplodus cervinus* (Lowe, 1838)), red porgy (*Pagrus pagrus* (Linnaeus, 1758)) and common dentex (*Dentex dentex* (Linnaeus, 1758)). In the second part of our study, we focused within harbors and as very little is known about juvenile assemblages in those infrastructures, we decided to extend our selection for those sites. We considered all observed species with the exception of those forming large mobile schools (eg. *Sarpa salpa*, *Pagellus* spp.) and those of the labrid family (only *T. pavo* is included as it is part of the original sampling list of species) as the youngest individuals are hard to observe and might require a different sampling procedure. The sampled species for each part of the study are recorded in Table 1.

2.3. Sampling procedure

Sampling was performed according to the widely used Underwater Visual Census (UVC) protocols (Harmelin-Vivien et al., 1985). Trained and inter-calibrated divers snorkeled along the coast at a slow and steady pace and identified, counted, and estimated the size of juvenile individuals from any of the target species along a 1 m wide belt transect parallel to the coast. Transects were defined on a waterproof map depicting the coastline so divers knew where to begin and stop their transects. Observations were recorded on the same map, which also provided examples of different juvenile sizes (in increments of 5 mm) to aid in size estimations. We used 5 mm size classes to estimate Total Length (TL). Which is consistent with a previous study that estimated the precision of such underwater size estimation to be of ± 3.5 mm (Macpherson, 1998). For most rocky reef fishes in the Mediterranean, size at settlement is around 10 mm TL (Cheminée et al., 2013; Crechriou et al., 2015; Garcia-Rubies and Macpherson, 1995). The smallest specimens of the taxa studied were considered newly settled individuals. Our visual censuses took into account only the young of the year (YoY or y0 individuals), which might be newly settled individuals (for species settling during spring and summer) or individuals having settled a few months prior (for species settling during fall and winter) (maximum sizes retained for each species are available in supplementary material 1).

Sampling was performed during the last two weeks of July 2015 and 2016 which corresponds to one or two months after the known settlement or post-settlement periods of many Mediterranean species

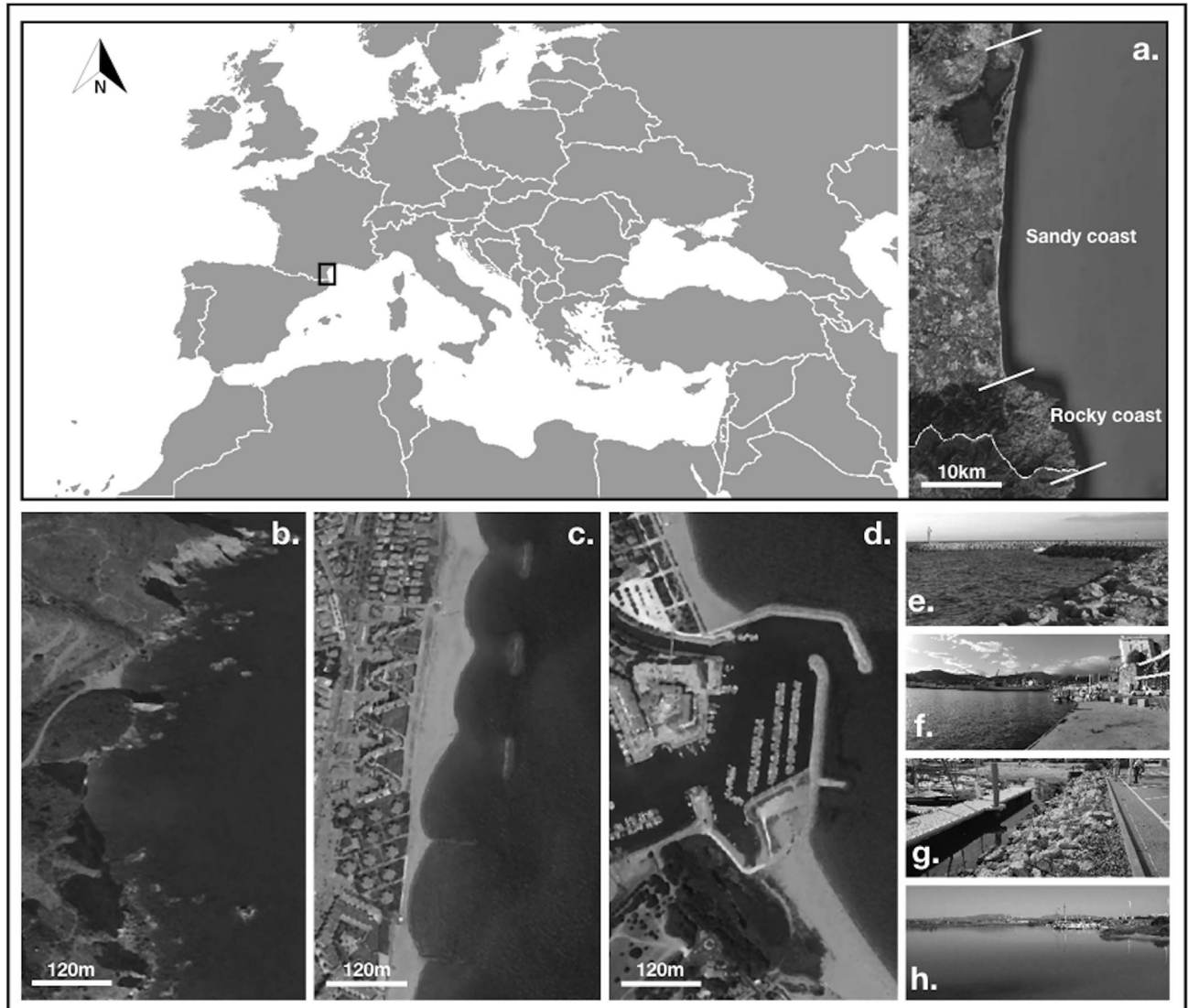


Fig. 1. (a.) Location of the study area in the Northwestern Mediterranean and delimitation of the two regions (rocky and sandy coasts noted respectively RC and SC). Examples of (b.) natural site, (c.) coastal defense structures (CDS), (d.) harbor. Examples of the different habitat types, (e.) jetties, (f.) dock, (g.) riprap and (h.) natural.

Table 1
Species considered for sampling in all sites (natural, CDS and harbors) and for the focus within harbors.

	all sites	within harbors
<i>Chromis chromis</i>		+
<i>Dentex dentex</i>	+	+
<i>Dicentrarchus labrax</i>		+
<i>Diplodus annularis</i>		+
<i>Diplodus cervinus</i>	+	+
<i>Diplodus puntazzo</i>	+	+
<i>Diplodus sargus</i>	+	+
<i>Diplodus vulgaris</i>		+
<i>Epinephelus marginatus</i>		+
<i>Mullus sp.</i>		+
<i>Oblada melanura</i>		+
<i>Pagrus pagrus</i>	+	+
<i>Sparus aurata</i>		+
<i>Sphyræna viridensis</i>	+	+
<i>Spondyliosoma cantharus</i>	+	+
<i>Thalassoma pavo</i>	+	+

(Crec'hriou et al., 2015; García-Rubies and Macpherson, 1995; Raventos and Macpherson, 2001). In this context, we can consider that the main part of the total observed individuals will integrate into the local population and provides a snapshot of the future recruitment as most of the mortality as already occurred (Macpherson and Zika, 1999). Sampling days with rough seas and poor visibility were avoided.

2.4. Study design and data analysis

To test the influence of the level of artificialization of the habitat on response variables describing juvenile assemblages, three different levels of artificialization were defined (in increasing order of modification and loss of 3D structure): natural sites (high structural complexity), which consist of unmodified rocky areas composed of small bays and small boulder beaches with shallow waters interspersed with steeper portions (for the SC such habitat is found at the northern most of the sampling area), CDS, and highly modified harbors. For the most abundant species, we analyzed the variability of response variables

Table 2
Sampled area, species richness and taxa-specific abundances in sampled natural sites, CDS and harbors in 2015 and 2016.

Sampled area in m ²	2015							2016							Total		
	Rocky coast			Sandy coast			Total	Total	Rocky coast			Sandy coast				Total	Total
	Natural	Harbor	Total	Natural	CDS	Harbor			Natural	Harbor	Total	Natural	CDS	Harbor			
	12324	589	12913	1695	1670	11550	14915	27828	9506	5289	14796	1484	1985	11598		15067	29863
Richness	5	4	6	3	5	5	5	7	6	3	5	3	4	4	5	7	8
<i>Dentex dentex</i>	–	3	3	–	1	2	3	6	–	–	–	1	5	3	9	9	15
<i>Diplodus cervinus</i>	–	–	–	–	1	1	2	2	3	–	3	–	–	–	–	3	5
<i>Diplodus puntazzo</i>	68	78	146	1	6	86	93	239	103	29	132	11	10	139	160	292	531
<i>Diplodus sargus</i>	1210	259	1469	976	1514	1857	4347	5816	4559	860	5419	3349	11026	8887	23262	28681	34497
<i>Epinephelus marginatus</i>	1	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	1
<i>Pagrus pagrus</i>	–	–	–	–	–	–	–	–	1	–	1	–	18	–	18	19	19
<i>Sphyrnaena viridensis</i>	213	30	243	85	50	34	169	412	29	13	42	–	17	17	59	471	
<i>Thalassoma pavo</i>	2	–	2	–	–	–	–	2	5	–	5	–	–	–	–	5	7
Total	1494	370	1864	1062	1572	1980	4614	6478	4700	902	5602	3361	11059	9046	23466	29068	35546

(species composition, taxa-specific densities and mean size) according to the following model with three fixed factors: “year” (with two levels: 2015 and 2016), “region” (with two levels: RC and SC) and “artificialization level” (with two levels on the RC (natural and harbor) and three levels on the SC (natural, CDS and harbor)). Replication units used for this model were the entire sites (i.e. the whole cove, CDS or harbor, with each site representing one continuous transect). Sites were replicated for each combination of the three forcing factors (year x region x artificialization, the total sampled area for each combination is given in Table 2). Abundance data was then divided by the sampling area of each site (ranging from 123 m to 4646 m) to obtain comparable densities (expressed in ind./10 m²).

The degree of openness of a bay is known to have an effect on juvenile fish densities (Cuadros et al., 2017a). Thereby, for our data sampled among habitats inside the harbors, the distance to the entrance of the harbor might affect the distribution of juveniles. Indeed, all habitats were not situated at equal distance from the entrance (see supplementary material 2), which might confound the results. Consequently, a second model was used to test the relative effect of distance from the entrance and habitat type within harbors on the same response variables. Replication units were transects of each habitat type with three to nine transects per habitat type per harbor (lengths between 14 m and 446 m) and the data was expressed in ind./10 m² as previously noted. Similar to the first model, we used three fixed factors: “year” (with two levels: 2015 and 2016), “region” (with two levels: RC and SC) and “habitat” (with five levels: outer jetty, inner jetty, natural, dock and riprap). In this model, we added distance from entrance as a covariate in order to disentangle the variability of the response variables due to both factors (habitat and distance). Distances were estimated (to the nearest meter) on Google Earth (version 7.1.2.2041) by tracing the shortest possible path between the entrance and the middle of each transect.

As our data did not follow normal distribution and our designs were unbalanced and contained interactions of factors, we used permutational MAN(C)OVAs, ANOVAs and AN(C)OVAs. Permutation tests were used because they can handle this kind of complex design and have no assumption on data distribution as long as observational units might be exchangeable (Anderson, 2001). Analyses were performed on Euclidian distance matrixes for the univariate total and taxa-specific densities and TL and on Bray-Curtis dissimilarity matrixes for the multivariate assemblage composition with the addition of a dummy variable. P-values were calculated by 999 random permutations of residuals under a reduced model and Type III sum of square (Anderson, 2001) for the first model. For the second model, Type I sum of square was used and covariate was introduced in the first place into the model (without

including the interaction terms between covariate and factor). It allowed the assessment of the variations in the response variable(s) that are due to variations in the covariate, prior to test the putative effects of other factors (Anderson et al., 2008). The order of factors was defined as follows: Distance (covariate), Habitat, Region, Year and their interactions Region*Habitat, Year*Habitat, Year*Region and Year*Region*Habitat. The Monte-Carlo test was used when less than 200 permutations were generated. Post-hoc pairwise tests were performed on all designs obtaining significant results from the global tests.

SIMPER analyses were conducted when PERMANOVAs on species composition were significant in order to determine the relative contribution of each taxa to differences between groups of samples. The significance level was consistently set at a level of 0.1 for all tests due to the intrinsic variability of ecological data. All statistical analyses were performed using PRIMER 6 software with the PERMANOVA add-on (Clarke and Gorley, 2006; Clarke et al., 2014) and R software (R version 3.0.3- Rstudio Version 0.99.486) using the ggplot library (Wickham, 2009).

3. Results

3.1. Effect of the artificialization level (natural, CDS and harbor sites)

Although all eight studied species were observed, there were large disparities in abundances with *Diplodus sargus* being by far the most numerous species while some others were very rare. This was the case of the dusky grouper (one surveyed individual), the zebra seabream (five individuals) and the ornate wrasse (seven individuals) (Table 2). A PERMANOVA on species composition showed there were significant differences in juvenile composition according to the three interactions Year*Region (p-value = 0.003), Year*Anthropization level (p-value = 0.001) and Region*Anthropization level (p-value = 0.003) and SIMPER analysis confirmed that *D. sargus*, was responsible for almost all the observed dissimilarity and similarities between and among the tested factors (always more than 80%). Accordingly, we present the results for this species as well as for *D. puntazzo* and *S. viridensis* as they were present in large enough number to run the analysis. Analyses were not run for the other five species since less than 20 individuals were observed for both years pooled. However, we noted that while *D. dentex* and *D. cervinus* were present both years in both regions, *P. pagrus* was observed only in 2016 and almost exclusively on the RC, *T. pavo* was observed only on the RC both years and the unique observation of *E. marginatus* happened in 2015 on the RC as well (Table 2).

Concerning *D. sargus* there was a significant Year*Artificialization level interaction (Table 3) with densities in harbors being the lowest for both years. Natural sites and CDS did not differ in 2015, but in 2016

Table 3

Results of the univariate 3-way PERMANOVAs tests performed to compare *D. sargus* and *S. viridensis* densities (ind./10 m²) between Years (2015, 2016), Regions (RC and SC) and Artificialization levels (natural, CDS and harbor). df and MS respectively degree of freedom and Mean square. Significance = *p ≤ 0.1; **p ≤ 0.05; ***p ≤ 0.01; ****p ≤ 0.001.

Source	df	MS	Pseudo-F	P(perm)	
<i>D. sargus</i> density					
Year	1	50.6650	51.549	0.001	
Region	1	9.15260	9.3123	0.008	***
Artificialization level	2	21.5000	21.875	0.001	**
Ye*Re	1	2.88460	2.9349	0.088	***
Ye*Art	2	12.3540	12.57	0.001	°
Re*Art	1	3.03460	3.0875	0.082	***
Ye*Re*Art	1	0.61258	0.45966	0.418	°
Res	80	0.98285			
Total	89				
<i>S. viridensis</i> density					
Year	1	0.01090	7.74	0.009	
Region	1	0.00508	3.60	0.077	**
Artificialization level	2	0.00523	3.71	0.053	°
Ye*Re	1	0.00575	4.08	0.060	°
Ye*Art	2	0.00506	3.59	0.056	°
Re*Art	1	0.00724	5.13	0.045	°
Ye*Re*Art	1	0.00809	5.74	0.043	*
Res	80	0.00141			*
Total	89				

CDS hosted significantly higher densities (Fig. 2-a). For all three artificialization levels, the densities in 2016 were significantly higher than in 2015 (pairwise tests, p-value = 0.002, p-value = 0.025 and p-value = 0.001 for natural, harbor and CDS respectively). The Region*Artificialization level interaction was also significant (Table 3), however this significant interaction might result from the absence of CDS on the RC as in both regions harbors hosted significantly lower densities than natural sites. On the SC natural sites and CDS did not differ one from the other (Fig. 2-b). The effect of region varied depending on the year with a significant Year*Region interaction (Table 3). *D. sargus* densities were higher on the SC than on the RC for both years but this difference was of a greater amplitude in 2016 (pairwise tests, p-value = 0.009 in 2015 and p-value = 0.026 in 2016) and they were significantly higher in 2016 than in 2015 for both regions (pairwise tests, p-value = 0.001 on the RC and p-value = 0.002 for the SC) (Fig. 2-c).

D. sargus mean TL was significantly different depending on the year and the artificialization level (PERMANOVA, p-value = 0.001 and p-value = 0.003 respectively). Individuals were bigger in 2015 than in 2016 (pairwise test, p-value = 0.001) and in harbors than in natural sites or CDS (pairwise test, p-value = 0.001 and p-value = 0.009 respectively) (supplementary material 3).

D. puntazzo was the second most abundant species but its contribution to dissimilarity between artificialization levels was very low and its densities differed only according to the year factor (PERMANOVA, p-value = 0.09) with higher densities in 2015.

As the second contributor to dissimilarity and the third most abundant species *S. viridensis* showed densities that varied significantly according to the triple interaction Year*Region*Artificialization level (Table 3). For both regions and either year, no significant difference was observed between artificialization levels. However, densities were significantly higher in 2015 than 2016 for the natural sites of the RC and the CDS of the SC. In 2015, the densities of natural sites were significantly higher on the SC than on the RC (pairwise tests, p-value = 0.037) while no significant difference was observed for the harbor sites. In 2016, there was no significant difference between the two regions for either the natural or harbor sites (Fig. 2-d).

The size of *S. viridensis* differed according to the Year*Artificialization level and Year*Region interactions (PERMANOVA, p-value = 0.001 and p-

value = 0.003 respectively). There was no significant difference in size between the different artificialization levels in 2015 but in 2016 observed individuals in harbors had a longer average TL than those of natural site (pairwise tests, p-value = 0.003) (no observations were made on CDS). Concerning differences between regions, there was no difference between regions in 2015 but juveniles were bigger on the RC in 2016 (pairwise tests, p-value = 0.001). Globally, individuals were longer in 2015 than 2016 but this difference was significant only for natural sites and the RC (pairwise tests, p-value = 0.03 and 0.041 respectively) (Supplementary material 4).

3.2. Focus on the inside of harbors: effect of habitat type

After looking at the effect of the artificialization level, we then focused on within harbor variations according to habitat type. In total, 12 species were observed, with a maximum of 10 species and a minimum of four per habitat, region and year (Table 4).

3.2.1. Species composition

Distance to the entrance of the harbor significantly influenced species composition. Moreover, independently from distance to entrance, composition varied significantly according to the triple interaction Year*Region*Habitat (Table 5). In both regions and for both years, the main differences in assemblages were observed for outer and inner jetties, which differed significantly from most of the other habitats, while those habitats showed only some differences between them that varied depending on the year and the region.

This variability in assemblages is corroborated by the SIMPER analysis, which showed a relatively low level of similarity (< 29%) among a same habitat and a relatively high level of dissimilarity (> 74%) between habitats. *D. sargus* was always the main contributor to dissimilarity between habitats (> 40%) followed by *D. vulgaris*, *Mullus* sp., *D. labrax*, *O. melanura* and *D. puntazzo* in different orders depending on the combination of tested habitats. Regions also showed a high level of dissimilarity (83.37%) mainly due to *D. sargus* (47.54%) and to a lesser extent to the above-cited species. Both regions exhibited relatively low levels of similarity (20.74% for the RC, 21.33% for the SC). The same pattern was observed between years with similarity being higher for 2016 than 2015 (25.89% and 14.77% respectively), and the same species were responsible for the dissimilarity, which was rather high (82.38%).

3.2.2. Taxa-specific densities

Since they were the main contributors to the dissimilarity between habitats, regions and years, variations in taxa-specific densities for *D. sargus*, *D. vulgaris*, *Mullus* sp., *D. labrax*, *O. melanura* and *D. puntazzo* were analyzed.

D. sargus and *O. melanura* showed similar patterns (Fig. 3-a and b) with densities that were significantly influenced by distance from the entrance and significantly differed according to the triple interaction Year*Region*Habitat (Table 5) once controlled for the effect of the covariate.

For *D. sargus*, the effect of habitat was different between the regions with densities being significantly higher on jetties and ripraps on the SC while on the RC the higher densities were hosted by natural habitats and ripraps (Fig. 3-a). As a mean of comparison, it should be noted that densities observed on outer jetties in 2016 were higher than those observed in natural sites outside of the harbors on the same coast (respectively 33.9 ± 11.3 ind./10 m² and 29.7 ± 11.1 ind./10 m², cf. above part about artificialization level). Densities on outer and inner jetties of the SC were significantly higher than on the RC and those on natural habitats significantly higher on the RC than on the SC. The effect of habitat and region was, however, relatively consistent between years (Fig. 3-a). Globally, densities were higher in 2016 than in 2015 (significantly for all habitats on the SC, for natural and docks only on the RC).

Densities of *O. melanura* were variable depending on the year and

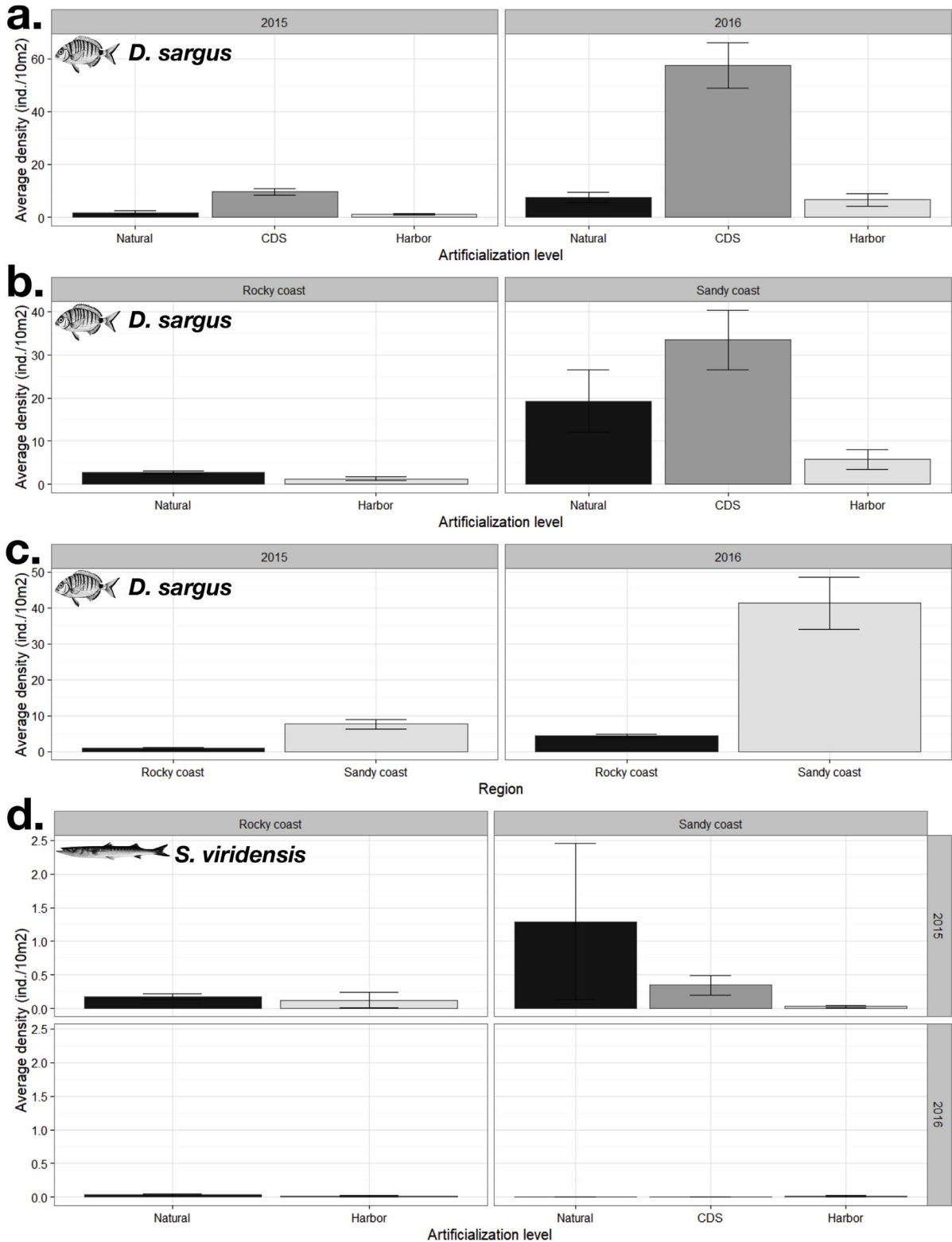


Fig. 2. Mean taxa-specific densities expressed in number of individuals per 10 m² for (a.) *D. sargus* according to Year and Artificialization level, (b.) Region and Artificialization level, (c.) Year and Region and for (d.) *S. viridensis* according to Year, Region and Anthropization level. Error bars = standard error. Lowercase characters give pairwise results: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs.

Table 4
Sampled area, species richness and taxa-specific abundances in sampled habitat type within harbours in 2015 and 2016 on the rocky and sandy coasts.

	2015										Total		
	Rocky coast					Sandy coast							
	Outer jetty	Inner jetty	Natural	Dock	Riprap	Total	Outer jetty	Inner jetty	Natural	Dock		Riprap	Total
Richness	702	404	1344	2469	371	5289	2238	1558	680	3962	2968	11409	16696
<i>Chromis chromis</i>	6	6	8	8	6	11	10	9	4	10	9	11	11
<i>Dentex dentex</i>	15	35	-	513	-	563	7	-	-	1	-	8	571
<i>Dicentrarchus labrax</i>	1	-	1	-	1	3	2	-	-	-	-	2	5
<i>Diplodus annularis</i>	-	-	-	8	31	39	3	81	3	91	431	609	648
<i>Diplodus puntazzo</i>	1	-	-	-	-	1	-	23	-	15	4	42	43
<i>Diplodus sargus</i>	10	2	20	36	10	78	57	12	-	9	8	86	164
<i>Diplodus vulgaris</i>	-	2	108	116	33	259	765	535	1	78	482	1861	2120
<i>Mullus sp</i>	17	18	53	32	39	159	309	221	4	33	135	702	861
<i>Oblada melanura</i>	-	2	2	6	11	21	146	283	19	98	149	695	716
<i>Sparus aurata</i>	11	210	93	45	-	359	642	82	-	10	6	740	1099
<i>Sphyræna viridensis</i>	-	-	6	24	-	30	11	15	-	1	7	34	64
<i>Spondylosoma cantharus</i>	-	-	-	-	-	-	-	-	-	-	-	-	0
Total	191	322	284	800	151	1748	2255	1276	27	348	1226	5132	6880

	2016										Total		
	Rocky coast					Sandy coast							
	Outer jetty	Inner jetty	Natural	Dock	riprap	Total	outer jetty	inner jetty	natural	dock		riprap	Total
Richness	702	404	1344	2469	371	5289	2238	1558	680	3962	2968	11409	16696
<i>Chromis chromis</i>	4	4	5	8	6	8	10	9	5	7	9	11	12
<i>Dentex dentex</i>	-	-	-	-	-	-	-	-	-	-	-	-	571
<i>Dicentrarchus labrax</i>	-	-	-	3	21	24	16	41	13	35	262	367	1039
<i>Diplodus annularis</i>	-	-	-	-	-	-	-	3	-	12	5	20	63
<i>Diplodus puntazzo</i>	3	4	9	6	7	29	21	18	1	45	57	142	335
<i>Diplodus sargus</i>	42	75	297	298	148	860	3302	2426	59	473	2628	8888	9748
<i>Diplodus vulgaris</i>	22	35	80	109	15	261	220	242	6	75	115	658	1780
<i>Mullus sp</i>	13	32	33	51	49	178	109	373	28	130	378	1018	1912
<i>Oblada melanura</i>	-	-	-	3	12	15	88	-	-	-	-	88	103
<i>Sparus aurata</i>	-	-	11	2	-	13	5	3	-	3	11	30	80
<i>Sphyræna viridensis</i>	-	-	-	2	-	2	17	-	-	-	17	30	94
<i>Spondylosoma cantharus</i>	-	-	-	2	-	2	7	5	-	1	14	16	16
Total	195	842	537	624	348	2546	4020	3551	107	800	3705	12183	21609

region. On the RC, in 2015, the highest densities were found on inner jetties followed by natural habitat, while there were found on ripraps in 2016. On the SC, in 2015 jetties hosted the higher densities and ripraps the lowest but there was no difference between habitats in 2016 (Fig. 3-b).

The densities of *D. vulgaris* were also significantly influenced by the covariate but varied significantly according to the double interaction Region*Habitat (Table 5). On the RC, densities were slightly different according to habitat type, one habitat always showing similar densities to at least two others. On the SC, jetties hosted the highest densities and docks the lowest with the other habitats being intermediate (Fig. 3-c). Concerning the differences between regions, outer and inner jetties hosted significantly higher densities on the SC, while natural habitats and docks of the RC hosted higher densities than those of the SC.

The distance from the entrance of harbor did not influence densities of *D. puntazzo*, which significantly differed only according to the Ye*Re interaction (Table 5). In 2015, densities were higher on the RC than on the SC, while there was no significant difference in 2016. On the RC, there was significantly more *D. puntazzo* in 2015 than in 2016, while it was the contrary for the SC with higher densities in 2016.

Similar to *D. puntazzo*, the distance to the entrance had no significant effect on *D. labrax* densities. Habitat was the only factor having a significant effect for this species (Table 5). Densities were significantly higher on ripraps than on docks, natural habitats and outer jetties (Fig. 3-d).

For *Mullus* sp., densities were significantly influenced by the distance to the entrance covariate and differed according to the Region*Habitat and Year*Habitats interactions (Table 5). On the RC, the pattern was similar to the one observed for *D. vulgaris* with densities which slightly differed according to habitat type, one habitat always showing similar densities to at least two others. On the SC, densities were the highest on inner jetties and the lowest on natural habitats and docks (Fig. 3-e). In 2015, densities on natural habitats and docks were significantly lower than those on inner jetties and ripraps. The same kind of pattern was observed in 2016 with significantly higher densities on inner jetties and ripraps than on natural habitats, docks and outer jetties (Fig. 3-f).

4. Discussion

Our results showed that human infrastructures such as harbors and CDS were used as juvenile habitats by certain coastal species typically settling on heterogeneous shallow rocky habitats, notably, during our sampling period, the white seabream *D. sargus*. The densities of juveniles were variable between regions and years but globally the highest on CDS (versus harbors and even natural sites). The densities found in harbors were lower than on CDS and natural sites but still not negligible as they represented between 50% and 90% of those in natural sites. They were also variable according to the type of habitat within the harbor with the least complex docks hosting the lowest densities.

4.1. Anthropogenic structures as a habitat opportunity for juveniles

This study showed contrasting densities of juveniles according to artificialization level but also a strong effect of the region factor with surprisingly higher mean densities on the SC. It would have been expected that the RC would host the highest densities as it displays more abundant natural habitat for the studied juveniles (shallow heterogeneous rocky habitat). However, this result is consistent with previous studies that found higher *D. sargus* densities on the SC or on CDS (Cheminée et al., 2017a; Pastor et al., 2013). Indeed, in this study, CDS hosted higher juvenile densities than natural and port sites, which might explain the differences between regions (CDS being absent of the RC). Nonetheless, Cheminée et al. (2017a) hypothesized that differences between regions were not due to what they named "habitat type" (here referred as artificialization level), because high densities were

Table 5

Results of the uni- and multi-variate 3-way PERMANOVAs tests performed to compare fish species composition, *D. sargus*, *D. vulgaris*, *O. melanura*, *D. puntazzo*, *Mullus* sp. and *D. labrax* densities (ind./10 m²) between Years (2015, 2016), Regions (RC and SC) and Habitat type within harbor (outer jetty, inner jetty, ripraps, natural and dock). df and MS respectively degree of freedom and Mean square. Significance = [°]p ≤ 0.1; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

Source	df	SS	MS	Pseudo-F	P(perm)	
Assemblages						
Distance	1	30862	30862	24.673	0.001	***
Habitat	4	48563	12141	9.7061	0.001	***
Region	1	21271	21271	17.005	0.001	***
Year	1	27406	27406	21.91	0.001	***
Re*Hab	4	49774	12444	9.9482	0.001	***
Ye*Hab	4	14552	3638.1	2.9086	0.001	***
Ye*Re	1	4806.9	4806.9	3.843	0.003	**
Ye*Re*Hab	4	7497	1874.2	1.4984	0.54	°
Res	245	3.06E+05	1250.8			
Total	265	5.11E+05				
Dicentrarchus labrax						
Distance	1	1.2864	1.2864	0.96816	0.347	
Habitat	4	46.194	11.548	8.6913	0.001	***
Region	1	3.6269	3.6269	2.7296	0.102	
Year	1	0.54425	0.54425	0.4096	0.571	
Re*Hab	4	2.8104	0.7026	0.52878	0.687	
Ye*Hab	4	1.1227	0.28066	0.21123	0.947	
Ye*Re	1	5.48E-02	5.48E-02	4.12E-02	8.49E-01	
Ye*Re*Hab	4	0.74955	0.18739	0.14103	0.97	
Res	245	325.54	1.3287			
Total	265	381.93				
Diplodus puntazzo						
Distance	1	1.07E-02	0.010690	0.20395	0.641	
Habitat	4	4.00E-02	0.009999	0.19077	0.951	
Region	1	0.23519	0.235190	4.4872	0.045	*
Year	1	2.59E-04	0.000259	4.95E-03	9.38E-01	
Re*Hab	4	0.37617	0.094043	1.7942	0.126	
Ye*Hab	4	0.30613	0.076532	1.4601	0.197	
Ye*Re	1	0.25845	0.258450	4.9309	0.033	*
Ye*Re*Hab	4	0.3219	0.081547	1.5558	0.184	
Res	242	12.684	0.052414			
Total	262	14.237				
Diplodus sargus						
Distance	1	1261.8	1261.8	9.2044	0.002	**
Habitat	4	3029.7	757.43	5.525	0.001	***
Region	1	1927.9	1927.9	14.063	0.001	***
Year	1	3351.1	3351.1	24.444	0.001	***
Re*Hab	4	3199.4	799.84	5.8344	0.002	**
Ye*Hab	4	2812.9	703.23	5.1297	0.001	***
Ye*Re	1	1152.9	1152.9	8.4095	0.004	**
Ye*Re*Hab	4	1931.5	482.87	3.5222	0.007	**
Res	243	3331.3	137.09			
Total	263	51980				
Diplodus vulgaris						
Distance	1	14.942	14.942	35.684	0.001	***
Habitat	4	12.336	3.084	7.37E+00	0.001	***
Region	1	0.77285	0.77285	1.8457	0.181	
Year	1	1.20E-02	1.20E-02	2.87E-02	0.854	
Re*Hab	4	11.844	2.961	7.0714	0.001	***
Ye*Hab	4	1.02	0.25499	0.60897	0.667	
Ye*Re	1	0.24587	0.24587	0.58719	0.459	
Ye*Re*Hab	4	1.1433	0.28583	0.68261	0.603	
Res	245	102.59	0.41873			
Total	265	144.91				
Mullus sp.						
Distance	1	4.2944	4.2944	5.8334	0.012	
Habitat	4	33.851	8.4629	11.496	0.001	***
Region	1	8.4396	8.4396	11.464	0.003	***
Year	1	8.3626	8.3626	11.36	0.001	***
Re*Hab	4	9.1139	2.2785	3.095	0.018	**
Ye*Hab	4	6.2626	1.5657	2.1267	0.072	
Ye*Re	1	1.6747	1.6747	2.2749	0.14	
Ye*Re*Hab	4	0.99414	0.24853	0.3376	0.859	

(continued on next page)

Table 5 (continued)

Source	df	SS	MS	Pseudo-F	P(perm)	
Res	245	180.36	0.73617			
Total	265	253.36				
Oblada melanura						
Distance	1	37.835	37.835	11.18	0.002	**
Habitat	4	50.963	12.741	3.7647	0.012	*
Region	1	2.532	2.532	0.74817	0.407	
Year	1	37.58	37.58	11.104	0.001	***
Re*Hab	4	75.172	18.813	5.559	0.004	**
Ye*Hab	4	72.172	18.043	5.3314	0.001	***
Ye*Re	1	2.4221	2.4221	0.71569	0.435	
Ye*Re*Hab	4	59.526	14.882	4.3972	0.002	**
Res	245	829.16	3.3843			
Total	265	1167.4				

observed for both CDS and natural sites on the SC. Their study was led on data surveyed only in 2015 and in the present study we also obtained no significant difference between CDS and natural sites for this year. However, there was a significant difference in 2016 suggesting that the effect of “habitat type” (i.e. artificialization level) might depend on settlement intensity, which was much higher in 2016. CDS would then be of a particular importance as nursery habitat in years of high settlement. It might be possible that when larval inputs are high, and natural habitats are saturated, CDS are then furnishing an alternative habitat. Even if they might be of lower quality (which is to be assessed), this anthropogenic structures may increase the adult stock by providing more juvenile habitat, especially in areas where nursery habitat is limited (such as the sandy coast) (Sundblad et al., 2014). The SC

is characterized by long stretches of sandy bottom; therefore a concentration of individuals on the smaller amount of available habitat might then explain such higher densities. Settlement would thereby be limited by the availability of suitable habitat (Holbrook and Schmitt, 2002; Holbrook et al., 2000; Sale et al., 2005; Schmitt and Holbrook, 2000). However, the study by Cheminée et al. (2017a) cited above demonstrated that when multiplied by the total area of available nursery and standardized by the total area of the region, densities are still higher on the SC. A better survival rate on CDS could also be an explanation for this discrepancy between coasts. The very high mortality rate of settlers and juveniles is essentially due to predation pressure and food availability (Houde and Hoyt, 1987; Macpherson et al., 1997; Planes et al., 1999; Vigliola et al., 1998). It is also known that adult fish and benthic assemblages on this kind of structure are different than those on natural rocky shores (Clynick et al., 2008; Fowler and Booth, 2013; Lam et al., 2009; Moschella et al., 2005; Perkol-Finkel and Benayahu, 2004; Rilov and Benayahu, 2000). Predation pressure as well as food availability and quality might then differ between the two coasts inducing differences in mortality rate. However, our sites were selected in areas with similar fishing regulation and thus similar fishing pressure on predators or competitors. Consequently, another hypothesis, and maybe the most likely, is a difference in larval flux, the input being much higher on the SC. Hydrologic conditions at the regional scale have a determinant effect on the settlement success of juveniles along the coast through the dispersal and survival of the planktonic larvae (Hindell et al., 2003; Pineda et al., 2010; Roy, 1998). In the studied area, the dominant current (liguro-provençal current) goes from the northeast to the southwest and might bring with it larvae (Guizien et al., 2006; Pastor, 2008), which could then first settle on the northern nurseries of the SC. This would lead to a higher larval input on the SC

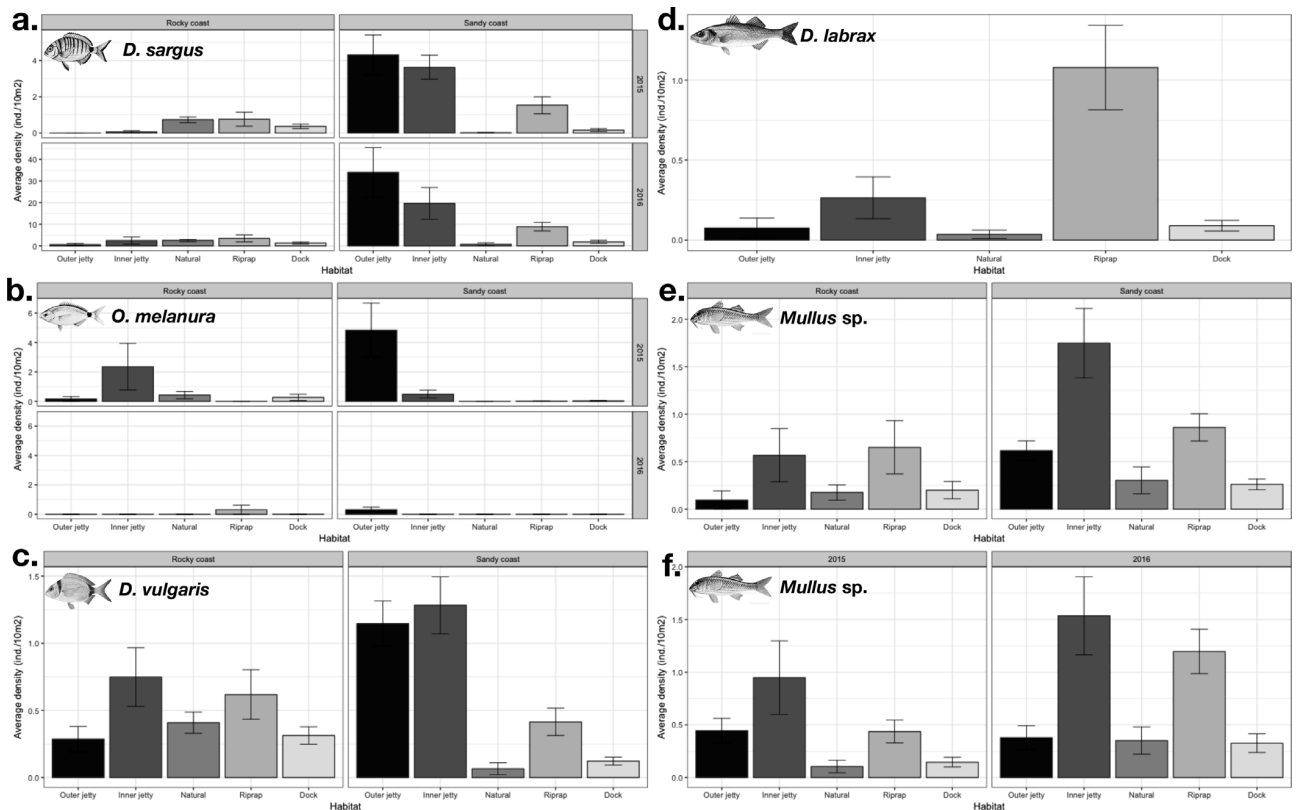


Fig. 3. Mean taxa-specific densities expressed in number of individuals per 10 m² for (a.) *D. sargus* and (b.) *O. melanura* according to Year, Region and Habitat type, (c.) for *D. vulgaris* according to Region and Habitat type, (d.) for *D. labrax* according to Habitat type and (e.) and (f.) for *Mullus sp.* according to Region and Habitat type and Year and Habitat type respectively. Error bars = standard error. Lowercase characters give pairwise results: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs and that presented densities are not corrected for the effect of the distance from the entrance of harbor, while the pairwise tests do.

and an impoverished larval flow to the RC (Pastor, 2008). CDS are also more “exposed” (-census (Cuadros et al., 2017a)) and so more accessible to the larvae, which can favor settlement. On the other hand, harbors are usually very enclosed, which might limit larval flow inside those infrastructures.

The presence of juvenile fish within harbors has already been documented (Bouchouca et al., 2016; Clynick, 2006, 2008; Dufour et al., 2009; Mercader et al., 2017) but comparison of the observed densities with nearby natural sites is very often lacking, preventing the assessment of their potential nursery role. Here, we compared the densities in harbors with those of natural sites and CDS and found that if juvenile fish do settle in harbors; the densities observed are lower than those of the other sites (CDS and natural). In 2015, *D. sargus* densities in harbors were about 50% of those of natural sites and 15% of those of CDS. In 2016, when settlement was much higher, those proportions were different with densities in harbors representing almost 90% of those of natural sites (although still significantly different) but an even smaller proportion of CDS (densities in natural sites representing only 13% of those on CDS). These results suggest that, like CDS, the use of harbors as juvenile habitat is in part dependent on the intensity of settlement. On years of important larvae flux, the number of larvae arriving at the coast might be significant enough to allow some of them to arrive inside harbors despite their low accessibility. Lower densities inside harbors could also be explained by post-settlement processes influenced by higher levels of anthropogenic pressures. Indeed, pollution potentially caused by the presence of hydrocarbons, organic pollutants, anti-fouling paint and heavy usage as well as sound pollution are known to have adverse effects on juvenile survival and growth rates (Kerambrun et al., 2012; Marchand et al., 2003; Nichols et al., 2015; Simpson et al., 2016). However, Bouchouca et al. (2018) showed that the concentrations of metallic trace elements in the muscles of juvenile *Diplodus* spp. settled in harbors were far below health safety thresholds. Also, their growth rate and condition were not different from those of juveniles settled outside the harbor. Another potential explanation, and maybe the most intuitive, for lower densities in harbors is the poor structural complexity and the relative homogeneity of the substrate. Indeed, it is known that the loss or reduction of complexity and/or heterogeneity leads to the reduced abundance and survival of organisms (August 1983; Brokovich et al., 2006; Cuadros et al., 2017b; Fisher et al., 2007). This point will be further discussed in the next section.

Although densities are lower in harbors, juvenile *D. sargus* tended to be bigger in those sites, which might suggest a faster growth rate. This is in concordance with the fact that *D. sargus* are known to have a preference for areas protected from strong swell and hydrodynamics (Harmelin-Vivien et al., 1995), conditions that are met inside harbors together with high productivity (more food) and higher temperatures, which are known to favor growth (Vigliola et al., 1998).

4.2. Effect of small-scale habitat variations within harbors

Most studies investigating the distribution of juveniles focus on only one spatial scale, however it has been shown that seascape attributes at different spatial scales might influence the densities of juveniles (Cuadros et al., 2017a). In our study, harbors in their totality (all habitats together) always show lower densities than other sites. However, when looking at a finer spatial scale within the harbors (habitat type), some habitats might host densities comparable to those observed in natural sites while others exhibit very low densities. Habitat choice could result from widely varying structural complexity since habitat complexity has an important effect on settlement and the abundance of juvenile fish with greater complexity supporting more species and individuals (Anderson and Millar, 2004; Cheminée et al., 2017b; Garcia-Charton et al., 2004; Horinouchi and Sano, 1999; Thiriet et al., 2014). It has been shown that a reduced tri-dimensional habitat complexity may reduce habitat quality, alter habitat choices and cause

differential mortality of juveniles (Cheminée et al., 2016). Harbors are composed of a mosaic of habitats with different complexity and our results showed that the contribution of each habitat type to the global amount of juveniles of a site is highly variable. In this study, relatively complex jetties and ripraps represented approximately 50% of the habitat, while featureless vertical docks the other 50% (this proportion being variable from one harbor to the other). Docks do not provide essential habitat for juvenile fish. They provide them with neither the protection nor the foraging opportunities that are essential for their growth and survival thereby explaining the very low densities observed on docks and the resulting globally low densities of harbor sites. Jetties and riprap, on the other hand, structurally simulate the essential habitat of juvenile fish and may provide suitable nursery habitat, which explains why some of them supported densities of juvenile *D. sargus* equivalent to those observed in natural sites. However, the effect of habitat is highly contrasted between the two regions. Although jetties hosted the highest densities for most sampled species on the SC, it is not the case on the RC. The presence of nearby natural habitat could explain this difference as juveniles are known to settle on the first suitable habitat they encounter (Shapiro, 1987). However, juveniles were found in relatively high densities within the harbors of the RC suggesting that the low densities on jetties might rather result from hydrodynamic conditions or the fact that they are much steeper and deeper on the RC than on the SC (Authors' unpublished data). Densities on natural habitats within harbors were also very different, being high on the RC and low on the SC, but this was consistent with the nature of the substrate, which is different between the two regions. On the RC it is composed of rocky bottom, which represents the preferential habitat of the studied species, while on the SC it consists of sandy or muddy bottom, which doesn't provide the complexity needed by the sampled species. Ripraps are the only habitat showing a consistent response on both coasts with intermediate densities probably due to their complex structure but their lower accessibility. Indeed, as mentioned in the above section, accessibility might be a determining factor for settlement success. This is corroborated by the significant effect of the covariate distance from the entrance of the harbor. With the exception of some species, densities decreased as distance increased, which sustains the hypothesis according to which settlement is favored in exposed areas if suitable habitat is available (Brown et al., 2005; Jenkins and Wheatley, 1998; Pastor et al., 2013). Larval supply would then represent a limiting factor in highly sheltered areas such as inner reefs (D'Alessandro et al., 2007), upper parts of estuaries (Bell et al., 1988; Martins et al., 2007), narrow coves (Cuadros et al., 2017a) and lagoons (Pastor et al., 2013), and here, on the most enclosed part of the harbor.

Even if global patterns in terms of habitat use and the effect of distance are consistent between species, some variations are observed suggesting they might have different requirements and preferences. This is in concordance with the fact that many fish species are known to have taxon-specific microhabitat requirements for settlement (Cheminée et al., 2013; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Macpherson and Zika, 1999; Vigliola and Harmelin-Vivien, 2001) which may evolve as juveniles grow (Dahlgren and Eggleston, 2000; Macpherson et al., 1997).

Within harbors and at the time of the survey (late July), *D. sargus* and *O. melanura* showed approximately the same distribution. They both tended to be more on jetties (which might be due to the above mentioned factors such as accessibility) but *D. sargus* uses ripraps more than *O. melanura*. This difference might be explained by the fact that ripraps are often located in very shallow areas and present a gentle slope (while it can be steeper on jetties) which might better correspond to the requirements of *D. sargus* than *O. melanura*. Indeed, in natural areas settlers of *D. sargus* are usually found in very shallow water close to the bottom, whereas those of *O. melanura* tend to be more on the surface even in habitat with deeper waters (Harmelin-Vivien et al., 1995).

D. vulgaris seemed to use the inside of the harbor more and a larger

variety of habitats. Since this species settles during winter, individuals are already at an intermediate developmental stage or even at a pre-dispersal stage during the sampling period. During these stages, juveniles use all suitable habitats available or are even ready to leave their nursery to join adult habitat (Bouchoucha et al., 2016; Ventura et al., 2014; Vigliola and Harmelin-Vivien, 2001). This less restrictive habitat requirement would explain the broader distribution of this species inside the harbors.

Supporting this hypothesis, the same pattern is observed for *D. puntazzo*, which is known to be more specialized than *D. vulgaris* and also settles during winter. It is to note that this species is not very abundant in the region and that densities observed in harbors are equivalent to those observed in natural sites, particularly in winter and spring when juveniles are at post-settlement and intermediate stages (authors unpublished data).

D. labrax are known to mainly settle in lagoons or estuaries (Cabral and Costa, 2001; Jennings and Pawson, 1992; Martinho et al., 2008), therefore the low hydrodynamic and high productivity found in harbors might furnish suitable conditions for settlement and development of this species. The highest densities of this species were observed in Port-Barcarès harbor, which is connected to a lagoon, and in Argelès harbor in which flows a small river, which supports this hypothesis. Surprisingly, within the harbors, juvenile *D. labrax* are mostly found on ripraps, a rocky habitat quite different from the usually soft bottom or meadow found in lagoons.

The last species found in harbors in relatively large densities were *Mullus* sp., which were mainly observed on inner jetties and ripraps. Those habitats composed of structurally complex rocky substrate usually surrounded by a large portion of soft bottom, correspond well to the natural nursery of the species (García-Rubies and Macpherson, 1995).

4.3. Implications for management

In the Mediterranean Sea, nursery grounds are still poorly taken into account in protection measures. Indeed, coastal management historically focused on adult fish and only a small proportion of nursery habitat benefits from protection (Cheminée et al., 2017a). It is also to note that, even in Marine Protected Areas, juvenile habitat may still be transformed and impacted by human activities. Most nurseries are located in areas of intense touristic activities and coastal development (beaches and coves), which makes the implementation of substantial protection measures particularly difficult. However, co-management (Granek and Brown, 2005; Pinkerton, 1989) could encourage alternative coastal use and management in order to help to reduce habitat transformation notably by limiting practices that lead to habitat homogenization (Cheminée et al., 2014; Cuadros et al., 2017a). Our results showed that man-made infrastructures and CDS in particular could serve as juvenile habitats for some species. Despite this potential, the ecological consequences resulting from the construction of these structures, such as the loss of habitat essential to other species or changes in courants and sediment loads, should always be evaluated and taken into consideration (Bulleri and Chapman, 2010). In cases where their construction doesn't destroy highly complex ecosystems (i.e. seagrass meadow, coral reef), they might be seen as little oases of biodiversity (Clynick, 2006; Guidetti, 2004; Ruitton, 1999) that can increase connectivity (Koeck et al., 2013). In light of their potential as juvenile habitat and the importance of this function in the replenishment of fish populations (Beck et al., 2001; Mumby et al., 2004), these kinds of structures should be taken into account in future management plans. However, this requires keeping in mind that the diversity of habitat among the seascape mosaic is crucial to provide suitable essential habitat to different species and allow a true renewal of coastal biodiversity.

Harbors also host juveniles but our results showed that the densities were highly dependent on the habitat considered. Given the amount of

featureless docks inside harbors and the fact that juveniles only poorly use them due to their lack of complexity, it could be interesting to consider ecological engineering approaches on those structures. Recent studies showed that the use of small artificial habitats could enhance juvenile densities on docks and under pontoons (Bouchoucha et al., 2016; Mercader et al., 2017) and that even the protected dusky grouper (*Epinephelus marginatus*) could settle inside harbors (Mercader et al., 2016). Also, since harbors are usually seen as having a negative environmental impact, eco-engineering and restoration ecology approaches coupled with pollution reduction measures could represent another and complementary way, along with natural habitat preservation, to favor the nursery function of the Mediterranean coast even in highly urbanized areas.

5. Conclusion

The results of this study showed contrasting densities of juveniles depending on the level of artificialization and the region. Despite the habitat modifications they may cause, CDS hosted higher densities of certain coastal species, notably *D. sargus*, than most natural sites and so may be considered as important potential juvenile habitats. This seems to be particularly true when settlement numbers are high. Although densities in harbors were lower than on CDS and natural sites, they still hosted some juveniles, and densities found on jetties and ripraps were equivalent to those in natural nurseries. The effect of the habitat type inside harbors seemed to be very dependent of the region, however, lower densities on featureless docks were a general pattern. These results suggest that despite their ecological impact, man-made infrastructures might represent alternative juvenile habitats, at least for some species whose juveniles usually settle on heterogeneous rocky bottoms. Taking them into account in management plans at the seascape scale is of prime interest for fish population maintenance. Ecological engineering in highly modified sites such as harbors could also represent an interesting complementary approach to conservation efforts particularly in the concerned coastal zone where protection isn't always possible.

Acknowledgements

This work was supported by the Total Foundation, the Fondation de France and the Conseil Départemental 66 in the frame of the e-Cate program (2014–2016), as well as the Agence de l'eau Rhône Méditerranée Corse for all sampling done in harbors. The authors would like to thank Gilles Saragoni, Quentin Thernon, as well as Amélie Foncuberta and Anaïs Gudefin from the Ecocean company for their help in fieldwork. We would also like to thank the MPAs' managers for facilitated access to the field and constructive exchanges. The authors also thank Marc Bouchoucha for constructive comments on the manuscript and are particularly grateful to Bob Clarke (PML – Primer-E) for his advises on data analysis. We also want to thank two anonymous reviewers for their constructive comments.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.marenvres.2018.02.030>.

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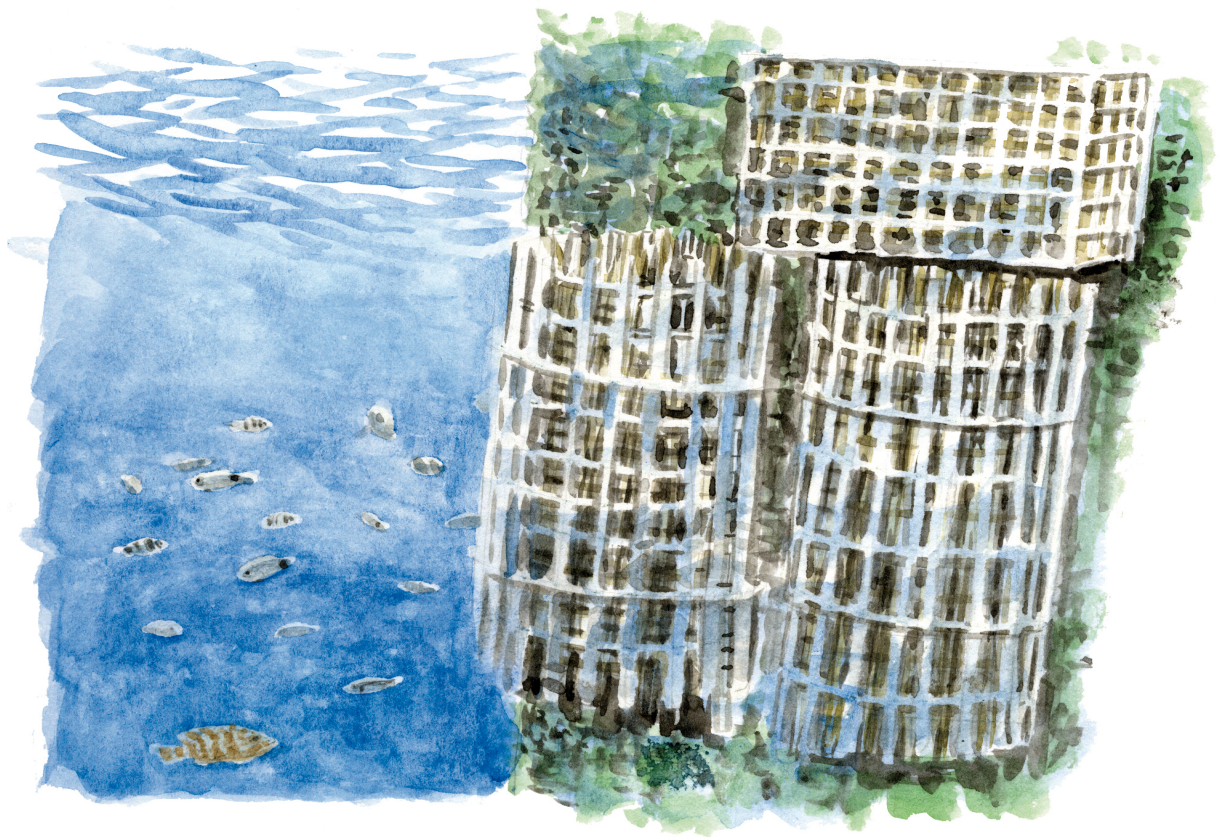
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2- Résumé du chapitre

Ce chapitre avait pour objectif d'évaluer le rôle potentiel des ports en tant qu'habitat juvénile en dehors de toute action de restauration. Pour ce faire, nous avons étudié la distribution spatiale des juvéniles sur un paysage sous-marin d'une centaine de kilomètres de côte, en se focalisant sur les habitats de type petits fonds rocheux hétérogènes et des infrastructures anthropiques susceptibles de servir de nurserie alternative à ces habitats naturels (brise-lames, épis, ports). Les résultats ont montré que, pour les espèces présentes dans les nurseries en période estivale, et particulièrement pour le sar commun *D. sargus*, les infrastructures de défense des côtes abritaient les densités les plus élevées, pouvant être jusqu'à six fois plus élevées que sur les habitats naturels. Les ports quant à eux abritaient les densités les plus faibles. Toutefois, ce résultat est à nuancer, car les densités moyennes observées dans ces écosystèmes urbanisés pouvaient tout de même représenter de 50 à 90% de celles relevées en milieu naturel. Aussi, étant donnée l'importance relative de ces ouvrages en terme de proportion d'occupation du trait côte, il est possible que leur contribution potentielle au stock adulte ne soit pas négligeable, au moins pour certaines espèces. La répartition des densités à l'intérieur des ports était également très variable en fonction du type d'habitat considéré. Les plus fortes densités étaient retrouvées sur les habitats les plus complexes (jetées et enrochements artificiels pour les ports situés en zone sableuse, enrochements artificiels et habitats naturels dans l'enceinte du port pour ceux situés en zone rocheuse) et les quais de complexité très restreinte abritaient les densités les plus faibles. Même si les densités présentes sur les jetées pourraient être aussi, voire plus, élevées que celles dans les habitats naturels en faisant de potentielles nurseries alternatives, le manque de complexité de la majorité des structures composant les ports semble être responsable des densités moyennes à faibles observées à l'échelle du site. Ces résultats confirment la nécessité d'accroître la complexité structurale de ces habitats artificiels dans l'optique d'augmenter la contribution relative des ports au maintien des ressources halieutiques.

Chapitre 5 :

Évaluation de la réhabilitation de la fonction de nurserie au sein d'infrastructures portuaires



**1- Evaluating the rehabilitation of coastal fish nursery function within
Mediterranean harbors (article en préparation)**

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Abstract

Habitat loss caused by urban sprawls has harmful consequences on marine biodiversity. However, the alternative habitats represented by anthropogenic infrastructures could nonetheless support ecological functions that can be essential for fish species, such as nurseries for whose juveniles settle on rocky habitats. Among these infrastructures, ports are responsible for most of the coastal artificialisation. With a view to maintain biodiversity and fish stocks, it may be worthwhile to restore some ecological features in these areas. The aim of this study was to evaluate the efficiency of artificial habitats as a way to rehabilitate Mediterranean harbors as nurseries for coastal fish. Densities of juvenile fish were analyzed using a BACI design coupled to semi-parametric contrast curves, which permitted to quantitatively evaluate the effect of restoration. Our results showed that, at the habitat scale, the use of artificial habitats proved efficient in increasing juvenile densities. However, the effect of rehabilitation at the site scale was not large enough to be detected, suggesting the proportion of restored habitat was not sufficient to increase the overall contribution of the harbors. Future initiatives should favor larger scale project, with the installation of more artificial habitat units in order to expect an overall increase in density, which could generate significant benefits in term of contribution to adult populations. From a methodological perspective, the approach we developed has proved adapted for environmental assessment studies at different spatial scales, even with complex design and highly variable data usually resulting from field surveys. This work should help the development of evaluation protocols for ecological restoration programs and in the broader field of conservation ecology.

Keywords: juvenile fish, nursery, artificial habitat, coastal urbanization, restoration ecology, port, BACI

Introduction

In the face of an ever-growing human population, anthropogenic impacts on ecosystems keep increasing on land and under the seas (McCauley et al., 2015). In this context, conservation approaches are being multiplied in order to maintain biodiversity. Conservation measures (i.e. protection of ecosystems from human impacts) are usually implemented in places of high ecological value, where natural habitats and populations are still well preserved. However, as increasing numbers of ecosystems are being degraded or replaced by urban areas, ecological restoration might represent an alternative and complementary tool to serve the common goal of preserving Earth's biodiversity (Wiens and Hobbs, 2015; Young, 2000). Indeed, even if complete ecosystem restoration (i.e. a lasting reestablishment of a self-maintaining ecosystem in its integrity and with all its functionalities (SER, 2004)) might not always be feasible in highly urbanized areas, rehabilitating some of their key ecological functions can help improve the health of deeply modified ecosystems (Aronson et al., 1993; Muller et al., 1998; Nienhuis et al., 2002; Xia, 2004).

While urban development is the highest in coastal areas, and has been causing dramatic changes to coastal seascapes (Bulleri and Chapman, 2010; Chapman et al., 2009), marine restoration and rehabilitation (i.e. the restoration of certain functions or services furnished by an ecosystem) are only starting to develop. In tropical regions, most restoration programs aim to restore coral reefs (by transplant or recruitment enhancement) or mangroves (Epstein and Rinkevich, 2001; Goreau and Hilbertz, 2005; Kamali and Hashim, 2011; Lewis, 2005; Rinkevich, 1995, 2008; Shaish et al., 2008). In temperate regions, most initiatives are led on oyster reefs (Coen and Luckenbach, 2000; La Peyre et al., 2014; Luckenbach et al., 2005), or intend to enhance benthic fauna and flora diversity and abundance on artificial structures (Brown and Chapman, 2014; Chapman and Blockley, 2009; Sella and Perkol-Finkel, 2015). Despite their high ecological and socio-economic importance (Holmlund and Hammer, 1999; Taylor, 2006), few projects directly devote to the maintenance or enhancement of fish populations. Although projects restoring marine habitats (e.g. reefs or mangroves) might have a beneficial impact on fish, fish communities associated to aforementioned habitats are rarely assessed as part of restoration evaluation protocols (but see Cabaitan et al., (2008) or Peterson et al., (2003)).

Most marine coastal fish species depend on shallow water habitats to accomplish their life cycle. After a pelagic dispersive phase (egg and larva stages), larvae may reach the shore and settle in their new benthic habitats where juveniles can grow to a size that allows them to avoid most predation and to recruit into the adult population (Di Franco et al., 2013; Jones, 1988; Mora and Sale, 2002; Vigliola and Harmelin-Vivien, 2001). Mortality during the juvenile stage is often high, and the number of individuals that will ultimately contribute to the renewal of adult population highly depends on availability and quality of adequate habitats for juveniles (Doherty, 1991; Doherty and Williams, 1988; Houde and Hoyt, 1987; Macpherson et al., 1997). Among diverse neighboring habitats for juveniles, nurseries are those that contribute a higher than average number of individuals to adult populations on a per-unit basis. The nursery value of a habitat is determined by the combination of four ecological processes, (1) initial density of juveniles (i.e. settlement rate), (2) survival rate, (3) growth rate, and (4) migration to adult population (i.e. recruitment) (Beck et al., 2001).

Despite the importance of coastal nurseries for the replenishment of adult fish populations (Bellwood and Hughes, 2001; Schmitt, 1999), few such habitats are presently located in Marine Protected Areas (MPAs) (Cheminée et al., 2017). This may be explained by the fact that marine reserves were first implemented to protect adults and so did not necessarily include suitable habitats for juveniles, but also because most of the nursery habitats occur in places of high socio-economical interest (e.g. beaches, bays, lagoons) which makes them difficult to protect. Coastal nurseries are also highly exposed to impacts from diverse human activities such as shore armoring, maritime traffic, coastal tourism, fishing, pollution... In this context, providing juvenile fish with alternative habitats that fulfill nursery functionalities in anthropogenized areas could surrogate the loss of natural nurseries and complement MPAs in the preservation of fish populations. Preliminary studies aimed at rehabilitating the nursery functions of coastal harbors by the use of artificial habitats gave encouraging results, with higher juvenile densities on artificial habitats than on control docks over a few years (Bouchoucha et al., 2016; Mercader et al., 2017a; Patranella et al., 2017). However, those studies did not include an initial assessment of the use of harbors by juveniles before rehabilitation, and a comparison with a natural habitat of reference, thereby preventing any estimation of the relative ecological benefits of rehabilitation. Moreover, the high temporal and spatial variability of juvenile fish settlement (Bradford and Cabana, 1997; Doherty, 1991;

Nagelkerken et al., 2015; Pineda et al., 2010) might represent a challenge in the evaluation of such projects.

A common approach to evaluate the impacts of natural or human-induced perturbations on ecosystems is a Before-After-Control-Impact (BACI) design which permits to distinguish the effect of treatment impact from background spatio-temporal variability when sampling is done simultaneously in control and treatment sites (also referred as paired BACI) (Downes et al., 2008; Stewart-Oaten et al., 1986; Underwood, 1992, 1994). Here we extended this approach to provide a quantitative evaluation of the performance of artificial habitats in rehabilitating coastal nursery functions within harbors at different spatial scales (habitat and site). The main objective of this study was to test whether temporal trajectories in the densities of juvenile coastal fishes, as a proxy of nursery value, varied as a function of the type of habitat and the implementation of restoration actions. We used field survey focusing on Mediterranean coastal species settling in shallow heterogeneous rocky habitats. Density data were then analyzed using GLMM under a paired BACI design, which we complemented with additional reference sites and habitats from the natural (untouched) environment. GLMM analysis were coupled with the semi-parametric contrast curve approach to compare complex ecological trajectories in a quantitative approach (Durban et al., 2005).

We here use this method for restoration impact assessment but this work should help the development of evaluation protocols for the broader field of conservation ecology and environmental assessment.

Methods

Case study

Since few years, several pilot initiatives of nursery function rehabilitation within harbors are being led on the French Mediterranean coast. Those initiatives are encouraged by the Agence de l'Eau (the French water agency), which provides financial support for the installation of artificial habitats that can serve as functional nurseries to harbors engaged in this kind of ecological enhancement approach. Nowadays, the most widely used artificial habitats for harbor rehabilitation in the Mediterranean are those conceived by a small French company, Écocéan, and commercialized under the

appellation Biohut® (hereafter referred to as Biohut). Thereby, our case study was led using Biohut as a mean to add structural complexity to diverse types of man-made structures within harbors (docks and pontoons) with the objective to enhance the nursery function of harbors. Several of those artificial habitats (dock Biohut and pontoon Biohut) have been used in previous studies (Bouchoucha et al., 2016; Mercader et al., 2017b) and a detail description of those used in this study is available in supplementary material 1.

The study was conducted on the southernmost French Mediterranean coast in the Gulf of Lion (NW Mediterranean). It included six geographical sites along 100 km of coastline; (i) two control harbors (Argelès-sur-Mer 42°32'29.80 N, 3°03'01.55 E, and Banyuls-sur-Mer 42°28'49.54 N, 3°09'09.74 E), (ii) two harbors benefiting from the installation of artificial habitats (Le Barcarès 42°47'57.07 N, 3°02'08.21 E and Port-Vendres 42°31'08.66 N, 3°06'40.22 E), and (iii) two natural rocky areas as reference (Criques de Portails 42°32'05.43 N, 3°04'22.10 E and Plages des Elmes 42°29'12.98 N, 3°09'31.79 E) (Figure 1). Sites were chosen to be representative of harbors and natural shallow rocky bottom of the northwestern Mediterranean, and are all included in the Gulf of Lion Natural Marine Park. The park is a 4010 km² large MPA, from the Spanish border to the town of Leucate. The harbor rehabilitation treatment consisted of the equipment of 60 m of dock and 60 m of pontoon with artificial Biohut habitats. However, the number and nature of the units differed between the two studied harbors due to logistical and technical reasons. In Port-Vendres, it consisted in the installation of 30 dock Biohut units and 60 kelp Biohut units for docks as well as 12 pontoon Biohut units. In le Barcarès, 20 dock Biohut units and 27 pontoon Biohut units were installed.

Data acquisition

All sites were sampled monthly from April to October in 2015 and May to October in 2016 (sampling could not be done in April 2016 due to poor meteorological conditions), rehabilitated harbors being equipped of artificial habitats only on the second year. This sampling period encompasses the settlement or post-settlement periods of many Mediterranean species (Crec'hriou et al., 2015; Garcia-Rubies and Macpherson, 1995; Raventos and Macpherson, 2001).

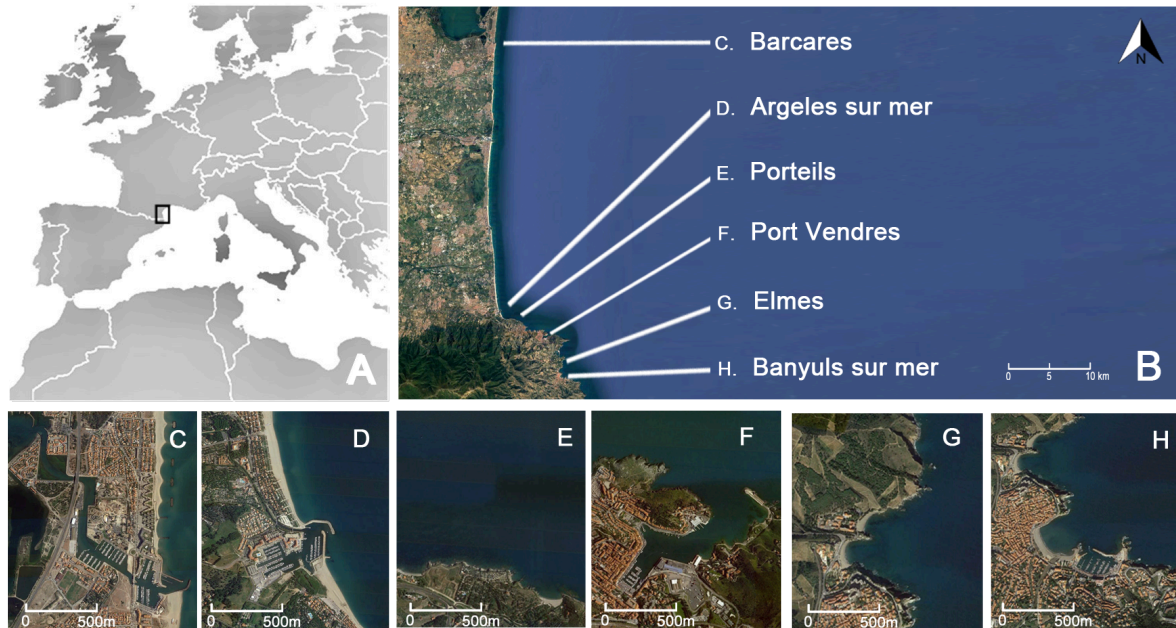


Figure 1: Localization of the study area (Gulf of Lion) in the Northwestern Mediterranean Sea (A). Localization of the six study sites on the 100 km of shoreline considered in this study (B) and a detailed view of those sites from north to south (C to H), rehabilitated harbor of Le Barcares (C), control harbor of Argelès (D), reference site of Porteils (E), restored harbor of Port-Vendres (F), reference sites of Les Elmes (G) and control harbor of Banyuls (H).

The density of juvenile fish was estimated by 9 to 13 replicates of 60 per 1 m transects for each site. In natural sites, transects were positioned randomly in heterogeneous rocky habitats (rocky cliffs, boulders or pebbles beaches) with varying slopes, orientations and depths (from 0 to -4 m below the surface). Because the harbors exhibited diverse structures (hereafter referred as habitat), transects were haphazardly distributed within each habitat type, which included (1) outer jetties (seaward side), (2) inner jetties (landward side), (3) ripraps, (4) docks and (5) pontoon.

Surveys were performed by Underwater Visual Census (UVC) (Harmelin-Vivien et al., 1985). The same diver performed all surveys in order to minimize observer bias, except at few occasions when another trained and previously inter-calibrated observer was used as substitute. The diver snorkeled parallel to the coastline at a slow and steady pace while identifying, counting and estimating the size of each juvenile fish encountered. Observations were recorded on a waterproof map. Only Young of the Year (YoY or y_0 individuals) were taken into account. As species settle at different time period, depending on month and the species considered, YoY include fish from newly settled individuals to individuals ready to recruit into the adult population but are still living in their juvenile habitat. In order to re-sample the same exact transect each month, visual cues marking the beginning of each transect were determined. In natural

sites, sixty meters were measured directly underwater by the use of a retractable measuring tape. Within harbors, a surface observer accompanied the diver to help prevent boats from approaching the immersed person as well as to help measure transect length from the surface, as the depth and accessibility of some areas did not permit the diver to do it directly in the water.

Study design and Statistical approach

The effect of restoration on juvenile densities was assessed within a Before-After-Control-Impact (BACI) design. Given the high spatial and temporal variability of juvenile settlement, a design including reference and control sites as well as pre-treatment data was critical to accurately evaluate restoration outcomes. In this kind of analysis, a significant BA term would indicate a difference between pre- and post- restoration, but those differences can result from a true effect of restoration or rather be attributable to natural inter-annual variations. Similarly, a significant CI term would indicate a difference between treatments (i.e. restored, control or reference), but again this can either be a result of the restoration treatment or of natural spatial variations. Only a significant BA-CI interaction would reflect a significant change imputable to the restoration treatment. Following advice from the Society for Ecological Restoration (SER) regarding restoration evaluation procedures, we compared our restored sites to reference sites (natural nurseries) as well as to non-restored harbors (control sites), in order to capture any significant departure from a degraded state even when nursery values remained below that provided by natural habitats. In order to evaluate the effects of habitat restoration at different scales, we ran separated analyses to test for the effects of treatments among habitats at both the site scale and across multiple sites combined.

We analyzed data using Generalized Linear Mixed effect Models (GLMM) at two different spatial scales, that of ecological habitats (pooling across multiple sites) and that of the sites (pooling across multiple habitats). For the first model at the scale of habitats, density trajectories of juvenile fish were regressed against the co-variable *Month* according to the fixed factor *Year* (BA-design) with two levels (before restoration in 2015, and after restoration in 2016), the fixed factor *Habitat* (CI-design) with eight levels (natural, outer jetty, inner jetty, riprap, dock, restored-dock, pontoon, and restored-pontoon) and their interaction, and with *Site* as a random factor. Similarly for the second model at the scale of sites, densities trajectories were regressed against the

co-variable *Month* according to the fixed factor *Year* (BA-design), and the fixed factor *Site* (CI-design) with three levels (restored, reference, control), and with *Habitat* treated as a random factor. All analyses were led on log transformed data ($\ln((\text{ind}/60\text{m}) + 1)$). Model diagnostics indicated this transformation was more appropriate to reach residual normality and heteroscedasticity than when using GLMM with Poisson or Negative binomial distributions on raw data.

Juvenile fish density trajectories were estimated using a semi-parametric approach that combines GLMM and penalized splines to account both for the spatio-temporal structure of observations (repeated measures in time on multiple, individually-distinct transects in space) and deviations from linearity in a statistically optimized fashion (Bolker et al., 2009; Ruppert et al., 2003). The semi-parametric contrast curve technique (Durban et al., 2005; Kayal et al., 2015) was then used to compare juvenile fish trajectories between restored habitats and sites and control and reference treatments in a pairwise fashion. This approach calculates the difference between two curves along a co-variate (here time in months) while also accounting for data complexity and non-linearity, allowing to identify portions of the co-variable where the response variable (juvenile density) significantly differs between the two groups. This method enabled us to quantitatively evaluate the effect of restoration through time despite the highly variable nature of fish settlement and recruitment in time and space. Methodological details and programming code for the contrast curve approach are available in Durban et al., (2005) and Kayal et al. (2015). All statistics and graphing were performed in R (R Development Core Team) complemented with the NLME package (Pinheiro et al., 2008) at a risk level of 5%.

Results

A total of 121,678 observations of juveniles from 23 fish species were made across the six sites and over the two years of this survey. However, large disparities existed between species and sites. Some species forming large schools, such as *Sarpa salpa* (Salema), *Atherina boyeri* (Big-scale sand smelt) or members of the Mugilidae family (Grey mullets), were particularly abundant at all sites. Beside these, the most abundant species were *Diplodus sargus* (White sea bream), *Diplodus vulgaris* (Two-banded sea bream), *Dicentrarchus labrax* (Sea bass), *Oblada melanura* (Saddled sea bream), *Pagellus* spp. (Pandoras), *Diplodus puntazzo* (Sharpsnout sea bream), and *Mullus* spp. (Mulletts).

These species were present on both years in all survey sites, with however large variations in their relative abundance among sites. In contrast, some species were only encountered at a few sites, such as *Sparus aurata* (Gilthead sea bream), which was observed exclusively in the control harbor of Argelès, and *Lithognathus mormyrus* (Striped sea bream), which was only found at the les Elmes (natural) reference site. Details on the repartition of each species between years, sites and habitats are given in supplementary material 2.

Effect of restoration at the scale of habitats

Juvenile fish densities showed different trajectories across habitats (p-value < 0.001 and years (p-value < 0.001) (Figure 2). Densities were generally higher in 2016 than 2015 and variable through the sampling period, with higher average values observed in June and July. Densities were highest on ripraps and jetties, intermediate for natural habitats and the lowest on docks and pontoons (no individuals were observed during most surveys on the latest). No significant effect of restoration was detected with parametric tests (GLMM, interaction *Year* × *Habitat*, p-value = 0.07), though semi-parametric contrast curves revealed a significant effect of habitat restoration for docks but not for pontoons (Figure 2). Indeed, before restoration was performed (2015), juvenile fish density was found in similar levels at focal (to be restored) docks and control (unmanipulated) docks (Figure 3-A), with density values significantly below those observed in riprap (Figure 3-B) and natural reference habitats (Figure 3-C). After restoration was performed (2016), restored docks hosted significantly higher juvenile fish densities than control docks over the entire sampling period (up to six-folds higher once back-transformed (i.e. $\exp(Y)-1$) (Figure 3-A), with density levels that did not significantly differ from ripraps (Figure 3-B) and natural habitats while they were approximately twice lower before restoration (Figure 3-C). In contrast, no effect of restoration was observed for pontoons, with densities on restored pontoons being on both years lower than on ripraps, natural habitats, and even control pontoons (Figure 3-D to F).

Similar patterns in juvenile fish density were observed at the two restored sites, the effect of dock restoration being only slightly more marked at Le-Barcarès than in Port-Vendres.

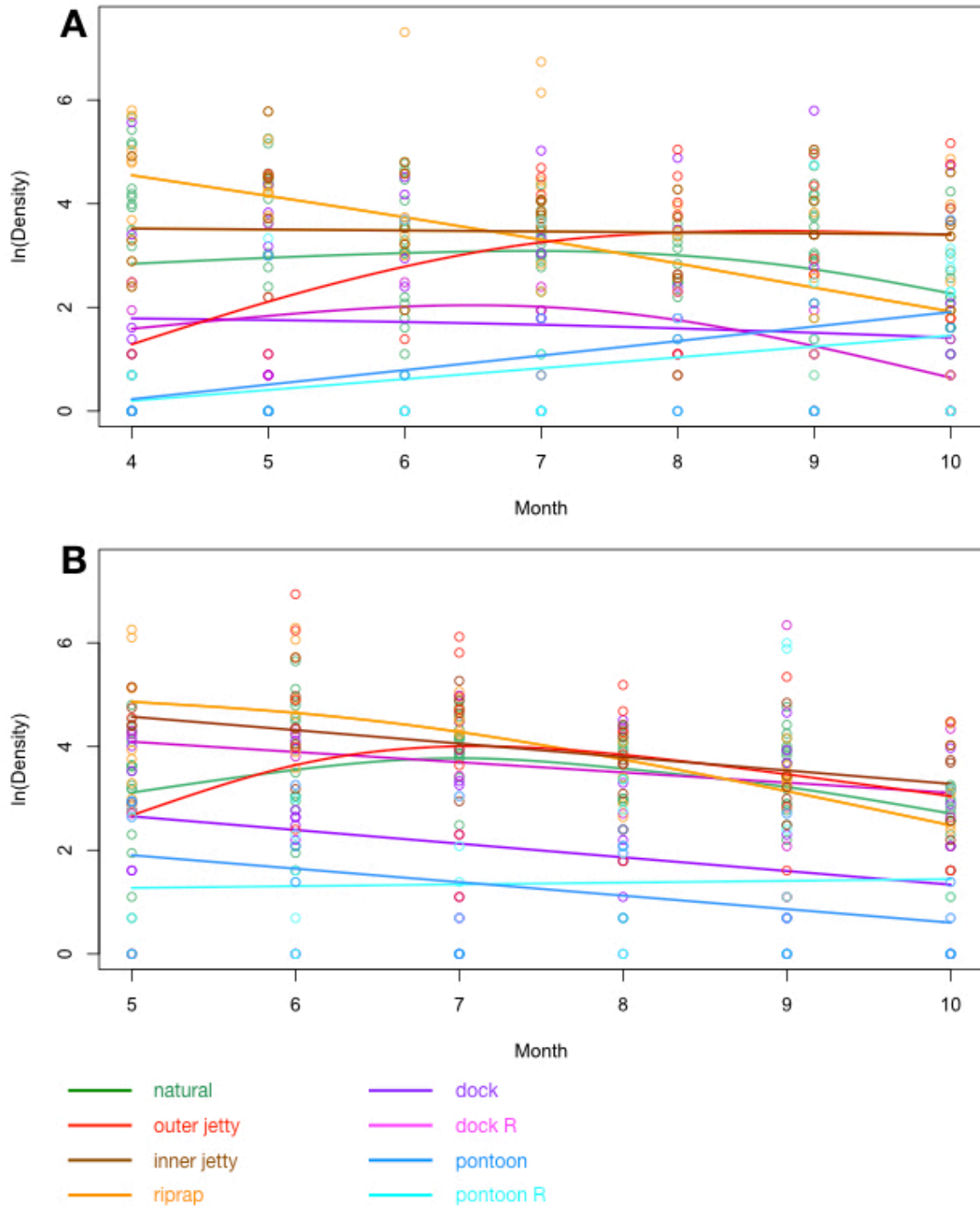


Figure 2: Juveniles fish density through time (x-axis, note that this axis starts in April for 2015 (A) and May for 2016 (B)) according to habitat (different colors) and year before (A) and after (B) restoration was performed on some docks (*dock R*) and pontoons (*pontoon R*). Trajectories (lines) were estimated using semi-parametric regression (Ruppert et al., 2003). Points represent observed densities which are expressed as $\ln((\text{ind.} / 60 \text{ m}) + 1)$. Note how the curve for dock R (magenta) is closer to more complex habitats (jetties, riprap and natural) after restoration (B) than before (A), while this is not the case for pontoons.

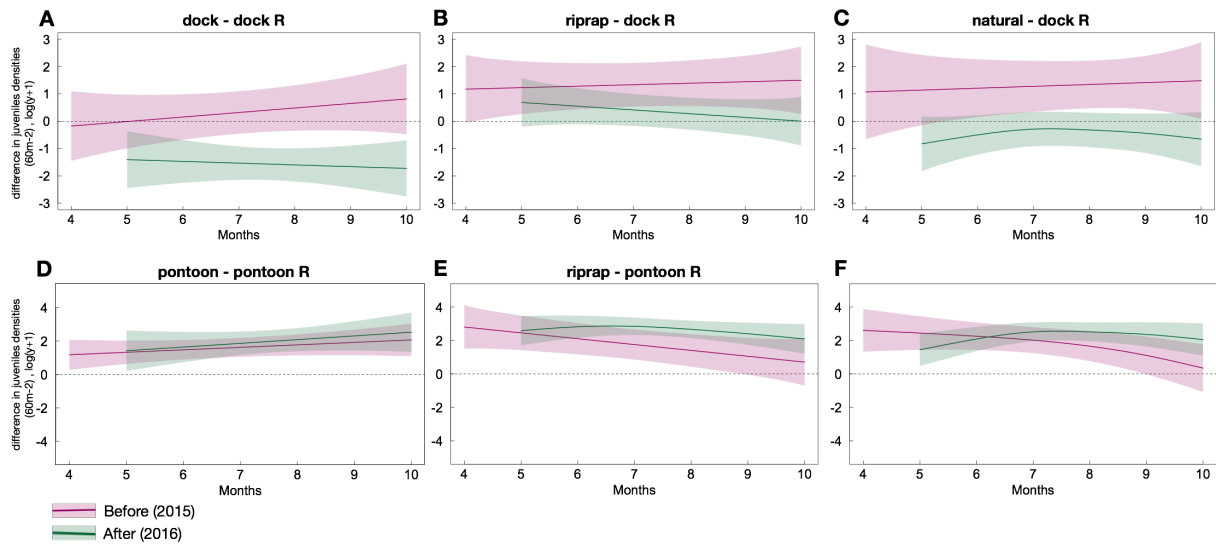


Figure 3: Contrast curves identifying periods (month) of significant differences in juvenile densities between restored (*dock R* (A-C) and *pontoon R* (D-F)) and non-restored habitats (*dock* (A), *pontoon* (D), *riprap* (B and E) and *natural* (C and F)). The contrast curves represent temporal variations (x-axis) in the differences between habitats before (in red) and after (in green) restoration was performed. Significant differences are identified as portions of the x-axis for which the 95% confidence interval of the contrast curves (shaded areas) does not cross the no-difference threshold ($y=0$, horizontal dashed line). Differences being calculated as *other habitat* – *restored habitat*; portions of the curves below the no-difference threshold indicate higher densities for the restored habitat (and conversely). When confidence intervals of contrast curves for before and after restoration do not overlap, it indicates that the periods of difference between the two tested habitats differed between the two years.

Effect of restoration at the scale of sites

At the scale of the site (all habitat pooled) juvenile fish density trajectories varied significantly only as a function of year (p -value < 0.001). No significant *Year* × *Site* interaction was detected despite a *Month* × *Year* × *Site* interaction was close to significance (p -value = 0.08), however no significant difference was detected by post hoc contrast curve analyses indicating the effect of restoration observed at the habitat scale was not large enough to be detectable at the site scale.

When running the analysis for each restored site separately the results obtained for Port-Vendres harbor were similar to those of the global analysis. Whereas a significant *Month* × *Year* × *Site* interaction was detected for the le Barcarès harbor (p -value = 0.02), indicating restoration induced variations in densities but only for some months (Figure 4). Contrast curves showed significantly higher densities at this restored site than at the control sites (Argelès and Banyuls) from May to August (Figure 5-A). When compared to reference sites this improvement was significant only in May (Figure 5-B).

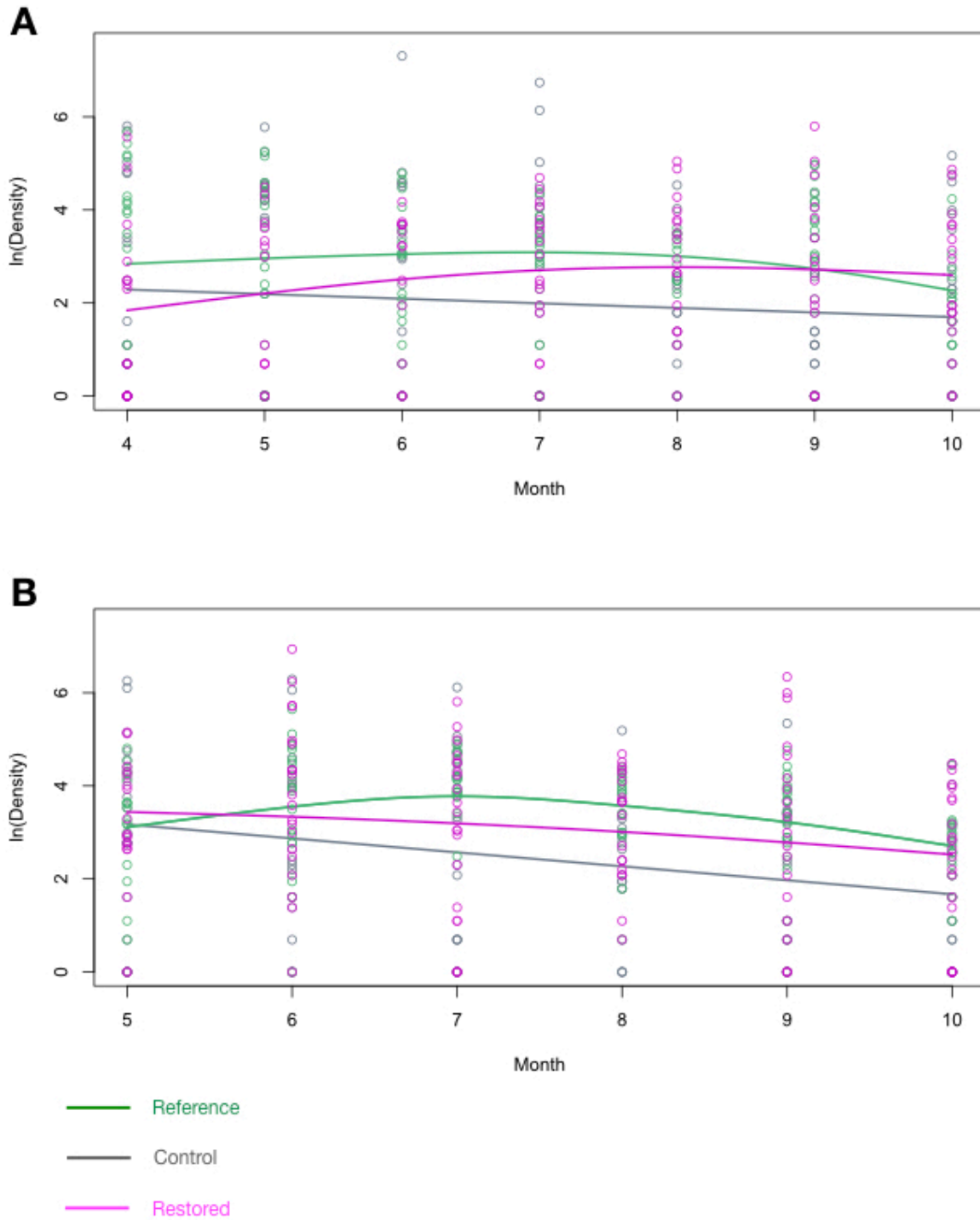


Figure 4: Juveniles density through time (x- axis, note that this axis starts in April for 2015 (A) and May for 2016 (B)) according to site type (different colors) and year Before (A) and after (B) restoration was performed. Trajectories (lines) were estimated using semi-parametric regression (Ruppert et al., 2003). Points represent observed densities which are expressed as $\ln(\text{ind.} / 60 \text{ m} + 1)$.

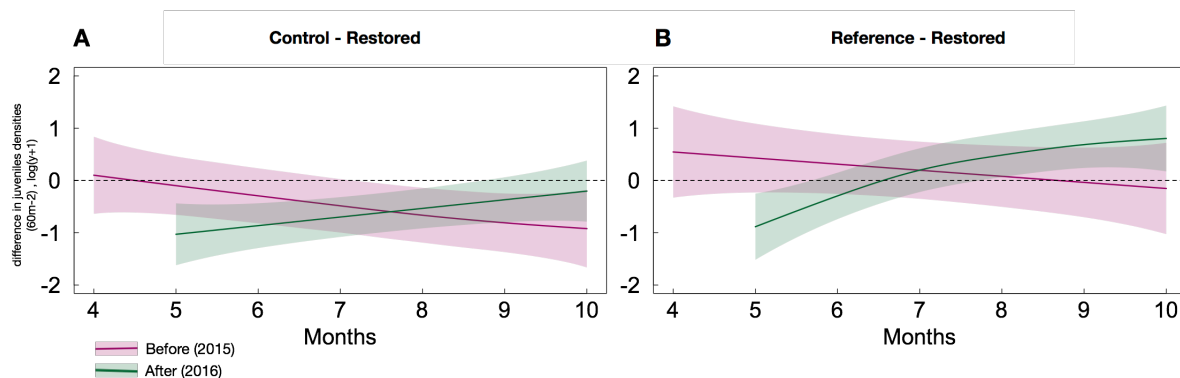


Figure 5: Contrast curves identifying periods (months) of significant difference in juvenile densities between the restored Le Barcarès harbor and control (A) and reference (B) sites. The contrast curves represent temporal variations (x -axis) in the differences between sites before (in red) and after (in green) restoration. Significant differences are identified as portions of the x -axis for which the 95% confidence interval of the contrast curves (shaded areas) do not cross the no-difference threshold ($y=0$, horizontal dashed line). Difference being measured as *other sites – restored sites*, portions of the curves below the no-difference threshold indicate higher densities for the restored habitat (and conversely). When confidence intervals of contrast curves for before and after restoration do not overlap, it indicates that the periods of difference between the two tested habitats differed between the two years.

Discussion

The results showed that the use of artificial habitats within harbors could, in some cases, enhance juvenile fish density. Indeed, at the habitat scale, the rehabilitation of docks significantly increased juvenile density compared to untouched control docks, this densities being comparable to those of natural habitats or ripraps. However, no significant effect was observed for pontoon. Likewise, our analysis at the scale of the whole harbor did not detect any significant effect of rehabilitation, suggesting the benefits at the habitat scale were not large enough to lead to an overall better contribution of the harbors. Nonetheless, when both sites were analyzed separately a slight increase in the density of juvenile was observed in May in the le Barcarès harbor. At the habitat scale these results are consistent with those of previous study, which evidenced higher densities on artificial habitat than on control docks or pontoon using a C-I design (Bouchoucha et al., 2016; Mercader et al., 2017a; Patranella et al., 2017). Under our full BACI design and using the contrast curves as a mean to compare the habitats, we evaluated the increase in density to be approximately six-folds for docks. Indeed, before restoration control and to be restored docks did not show any differences in juvenile densities while after restoration, densities on restored docks were approximately six time higher than on control ones. What was particularly interesting was that this increase in density was also significant when comparing restored docks to

reference habitats such as natural habitats or riprap within harbors. Before restoration densities on the aforementioned reference habitats were more than twice as high as on to be restore docks, however, after restoration those densities were equivalent. This result suggest that the use of artificial habitats on docks permits those structures to perform as well as more complex within harbor habitats but also as unmodified natural habitats. Surprisingly, we did no detected any beneficial effect of restoration on pontoon, while this was the case in the study by Bouchoucha et al., (2016). Different hypothesis might explain the discrepancy. First their study concerned only four *Diplodus* species, while the set of species considered here is more diverse. Each species has specific habitats requirements at settlement and might also follow different ontogenic shifts in term of habitat use as they grow (Biagi et al., 1998; Bouchoucha et al., 2016; Bussotti and Guidetti, 2011; Harmelin-Vivien et al., 1995; Macpherson, 1998; Vasconcelos et al., 2014; Vigliola and Harmelin-Vivien, 2001). Also, it is possible that the species taken into account in this study do not all use the under pontoon habitats as much as *Diplodus* spp. The second hypothesis is linked to the localization of the sampled pontoons. Indeed, pre-restoration comparison of control and to be restored pontoons revealed a difference in juvenile densities in favor of control pontoons. Transects were chosen randomly, but it happened that the restored portions were more distant from the entrance of the harbor and so might host lower densities as there are more enclosed (Cuadros et al., 2017; Mercader et al., 2018). Some pontoons were parallel to the coast while others were perpendicular, which might also affect the number of larvae settling on those habitats. If larvae never reach the habitat, restoration might be useless. Finally, on all pontoons many survey resulted in zero juvenile observation, the zero inflation of the data might also have make it very difficult to detect any potential effect of the artificial habitats. Also, reanalyzing separately the pontoon data under a different statistical model taking into account for zero inflation in the data (Fletcher et al., 2005) could help determine which of the above hypothesis are more plausible.

The effect of restoration at the habitat scale was consistent between the two restored sites although they were very different one the other. Port-Vendres harbor is a commercial and fishing port built on natural rocky bottom, while le Barcarès is a marina built on a sandy coast and connected to a lagoon. Two sites is not enough to conclude on a general efficiency of the rehabilitation method for all harbors, and it is possible it

might not work for some of them (Bouchoucha et al., 2016), but still this is an encouraging result for future projects.

At the site scale no effect of restoration was detected, except for a small improvement in May for the le Barcarès harbor. The proportion of rehabilitated docks and pontoons was small compared to the overall sampling array; also the unchanged relative densities on other habitats may have masked the increase in density observed on restored docks. However, our model accounted for variations due to habitat types (more juveniles on riprap than pontoon for example) and the sampling was representative of habitat repartition within harbors suggesting that the proportion of restored habitat was not sufficient to increase the overall contribution of the harbors. Future initiatives should favor larger scale project, with the installation of more artificial habitat units in order to expect an overall increase in density, which could generate significant benefits in term of contribution to adult populations. All projects should also include a pre-restoration assessment of the distribution of juveniles within the harbors. Indeed, this does not only contribute to an accurate evaluation procedure if analyzed under a BACI design (Mahlum et al., 2017; Underwood, 1992), but also permits to identify where artificial habitats should be placed in priority by avoiding areas where juveniles may never settle (e.g. inappropriate orientation, too enclosed, local detrimental physico-chemical conditions). Doing so should permit to gain in efficiency, particularly when financial resources are limiting the number of artificial habitats that can be installed.

The natural reference sites and habitats gave important information on the relative performance of harbors as juvenile habitats and on the benefits that can result from their rehabilitation. Indeed, while an increase in the density of juvenile on restored habitats compared to control non-restored habitat is already an encouraging results, it does not provide information on how restoration performs compared to non-degraded habitats. This makes it difficult to estimate the actual benefits it can generate, which can sometimes lead to reluctance in restoration, to which protection will probably be preferred (Benayas et al., 2009; Holl and Aide, 2011; Palmer and Filoso, 2009). Nevertheless, MPAs do not always fully protect habitat or species from degradation (Gaston et al., 2008; Joppa et al., 2008). Moreover, protection reduces the risk of increased habitat loss but does not create any novel habitats, which might sometimes not be sufficient to reinforce certain ecological functions or maintain endangered species (Dobson, 1997; Kuussaari et al., 2009; Wilson et al., 2006). Concerning nursery

habitats, only a small proportion is under protection and it seems protection as no significant effect on juvenile densities (Cheminée et al., 2017). Also, creating new alternative juvenile habitat in places where no habitat is available might have a greater impact on population renewal than conservation measures. For that matter, within harbors artificial habitats have proved to be used by endangered species, which are rarely observed in natural habitats (Claassens et al., 2018; Mercader et al., 2017b).

Natural reference is an important element for the accuracy of evaluation procedures. Pre-human impact should be considered as a baseline for assessing degradation and restoration effectiveness (Jackson et al., 2011; McClanahan and Omukoto, 2011). Nevertheless, choosing this reference can be problematic, particularly for nurseries as those are located in various habitats for different species (D'agata et al., 2016; Ellis et al., 2012; Sheaves et al., 2015). In this study, untouched heterogeneous shallow rocky habitats were selected as reference because they represent the known nursery for many coastal species and because harbors are mainly composed of hard structures. However, harbors also hosted species settling in other natural habitats, such as lagoons and estuaries for *D. labrax* and *S. aurata*, or meadows for *D. annularis* and *S. cantharus* for instance (Costa et al., 1994; Dufour et al., 2009; Harmelin-Vivien et al., 1995; Tournois, 2013). Thereby, the chosen reference was not adapted for those species and may lead to some bias in evaluation. Depending on the objective, (i) enhancing the population of one particular species or (ii) enhancing the populations of a variety of species, future studies should respectively (i) include multiple habitats as reference or (ii) focus only on the target species and its habitat.

Temporal variations in density of juvenile and in their response to restoration probably result from taxa-specific differences in settlement periods and habitat preferences. Also studying the trajectory of each species separately would give relevant information on how restoration performs for each of them. This would provide a better understanding of the global patterns observed and give insights on how those habitats are used by juveniles (i.e. are they used only by some developmental stages or by all of them, how long are they used...). Eventually, this might help to improve artificial habitats design or localization within the harbor.

As settlement intensity exhibits high inter-annual variations that are often inconsistent among species (Cuadros et al., 2018; Macpherson and Zika, 1999) the assessment of the rehabilitation of the nursery function would gain to be led on several years post-

rehabilitation to consider the effect those variations might have on the efficiency of the actions undertaken. Indeed, even if BACI design remains one of the best option for environmental effects assessment, caution should be taken when interpreting the results particularly when time replication is limited (Smokorowski and Randall, 2017). Also, when possible, sampling should be done on multiple years pre- and post-restoration and attention should also be paid to the adequation between the spatio-temporal scale of monitoring and this of the ecological processes being assessed.

Spatio-temporal calibration is also an issue for restoration planning. Indeed, the scale at which restoration actions are undertaken should match this at which populations might function. For instance, adult populations renewal might be dependent on few events of intense settlement every several years and the intensity of settlement seems to influence the relative importance of harbors as juvenile habitats (Mercader et al., 2018). For this reasons restoration projects should be thought as lasting measures to expect for substantial ecological benefits.

Finally, we here extended the BACI approach by using additional comparisons and modern quantitative statistical methods to account for as much as possible of the natural variability. Other approaches using Bayesian Markov Chain Monte Carlo (MCMC) or power analysis have already worked in that sense (Baldigo and Warren, 2008; Conner et al., 2016). Even if logistically demanding, accounting for natural variability by including spatio-temporal controls and robust statistical approaches will limit the chances of inaccurate conclusions in restoration assessment and should then be favored.

Acknowledgements

This work was financially supported by the Agence de l'eau Rhône Méditerranée Corse. The authors would like to thank Alexandre Mercière, Quentin Thernon, Jérémy Pastor, Nicolas Tapia, Alan Brazo and Gilles Saragoni, for they help in fieldwork. We also thank the managers of the different harbors for giving the authorization to sample in those restricted areas and for facilitated access. We are grateful to the Ecocean® company for the installation and maintenance of the Biohut® throughout the whole study period.

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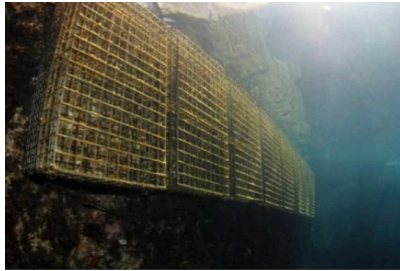
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Supplementary material

Supplementary material 1: description of the Biohut® artificial habitats



Biohut® quai

Size: 80 * 50 * 24 cm

Outer grid mesh: 5 * 5 cm

Inner grid mesh: 2.5 * 2.5 cm

Material: steel and oyster shells



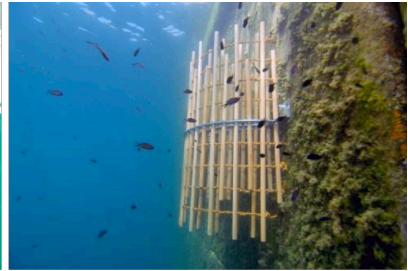
Biohut® ponton

Size: 80 * 50 * 36 cm

Outer grid mesh: 5 * 5 cm

Inner grid mesh: 2.5 * 2.5 cm

Material: steel and oyster shells



Biohut® kelp

Size: 98 * 94 * 41 cm

Material: steel, wood and coconut fiber

Supplementary material 2: Number of juvenile observation made for each species by site, year and habitat. * indicates to be restore (before) or restored (after) habitats.

Number of observations	Atherinidae		Pomacentridae		Moronidae		Mugilidae		Mullidae		Serranidae		Sparidae		Sparidae		Sparidae	
	<i>A. boyeri</i>		<i>C. chromis</i>		<i>D. labrax</i>	Gen. sp.	<i>Mullus</i> spp.	<i>S. cabrilla</i>	<i>S. scriba</i>	<i>D. dentex</i>	<i>D. annularis</i>	<i>D. cervinus</i>	<i>D. puntazzo</i>	<i>D. sargus</i>				
After	dock	50	-	6	15	-	1	-	-	-	-	-	2	77				
	inner jetty	2	-	51	-	-	80	-	-	-	1	-	95	180				
	outer jetty	-	-	-	-	-	44	5	-	-	-	-	17	457				
	pontoon	-	-	6	3	-	-	-	-	-	-	-	17	2				
Argelès	riprap	300	-	786	55	-	69	-	-	-	25	-	116	231				
	dock	-	-	154	391	-	1	-	-	-	-	-	7	-				
	inner jetty	-	-	99	93	-	11	-	-	-	-	-	148	53				
	outer jetty	50	15	10	110	-	7	2	-	-	-	-	39	116				
After	pontoon	-	-	-	151	-	-	-	-	-	-	-	9	-				
	riprap	-	-	2980	200	-	2	-	-	-	-	-	105	46				
	dock	150	1	1	217	-	50	-	-	-	-	-	6	144				
	outer jetty	110	1	-	25	-	15	-	-	-	-	-	-	65				
Banyuls	pontoon	765	-	-	-	-	-	-	-	-	-	2	32	-				
	riprap	585	-	8	5	-	50	-	-	9	-	-	10	237				
	dock	83	-	9	822	-	2	-	-	1	-	-	46	9				
	outer jetty	195	135	-	1	-	-	-	-	-	-	-	15	7				
Before	pontoon	150	-	-	-	-	-	-	-	-	-	-	4	-				
	riprap	-	2	17	80	-	1	-	-	5	-	-	61	22				
	dock	435	-	-	-	-	4	-	-	-	-	-	-	99				
	dock *	3040	2	11	-	-	23	-	-	12	-	-	-	294				
After	inner jetty	75	-	16	-	-	39	-	-	1	-	-	54	1015				
	outer jetty	15	-	-	20	-	101	1	-	-	-	-	63	1861				
	pontoon *	-	-	-	-	-	-	-	-	1	-	-	86	-				
	riprap	1050	1	306	-	-	45	-	-	-	-	-	23	556				
Barcares	dock	-	-	25	-	-	14	-	-	-	-	-	5	-				
	dock *	-	-	-	-	-	14	-	-	-	-	-	-	1				
	inner jetty	780	-	22	-	-	18	-	-	-	-	-	16	205				
	outer jetty	101	-	-	-	-	15	-	-	-	-	-	1	241				
Before	pontoon *	-	-	-	-	-	-	-	-	-	-	-	-	20				
	riprap	68	-	39	-	-	24	-	-	-	-	-	15	94				
	natural	1983	3	8	78	-	142	-	-	1	-	-	118	1144				
	natural	1454	1	67	55	-	56	-	-	1	-	-	84	360				
Portells	natural	1426	-	44	1	-	44	10	1	1	-	-	77	1805				
	natural	965	-	11	80	-	13	-	-	-	-	-	338	521				
	dock	30	15	1	83	-	15	1	1	-	-	-	30	117				
	dock *	2	2	4	70	-	-	-	-	12	-	-	19	234				
After	inner jetty	-	-	-	-	-	7	2	-	-	-	2	6	25				
	outer jetty	-	-	-	30	-	2	-	-	-	-	-	2	-				
	pontoon	215	-	-	1	-	12	-	-	-	-	-	18	33				
	pontoon *	-	-	-	1	-	-	-	-	-	3	-	1	1				
Port-Vendres	riprap	-	13	-	1	-	7	2	1	-	-	-	10	53				
	dock	30	191	110	38	-	2	-	1	-	-	-	68	8				
	dock *	200	-	-	30	-	-	-	-	-	-	-	19	3				
	inner jetty	105	-	-	-	-	4	1	-	-	-	-	-	1				
Before	outer jetty	-	-	-	-	-	-	-	-	-	-	-	2	-				
	pontoon	9300	-	-	2000	-	-	-	-	-	-	-	44	6				
	pontoon *	-	-	-	-	-	-	-	-	-	-	-	6	-				
	riprap	400	41	1	-	-	1	1	-	-	-	-	84	7				
Total	24112	423	4748	4655	935	25	4	71	2	4	1801	4	10470					

Supplementary material 2: (suite)

Number of observations	Sparidae										Total	
	<i>D. vulgaris</i>	<i>L. mormyrus</i>	<i>O. melanura</i>	<i>P. pagrus</i>	<i>Pagellus</i> spp.	<i>S. salpa</i>	<i>S. aurata</i>	<i>S. maena</i>	<i>S. cantharus</i>	<i>Sphyrænidae</i> <i>S. wifidensis</i>		Triglidæ Gen. sp.
Argèlès	dock	9	-	-	-	-	350	-	-	-	-	510
	inner jetty	228	-	32	-	-	146	48	-	-	-	863
	outer jetty	143	-	93	-	529	2936	-	3	15	-	4242
	pontoon	1	-	1	-	-	-	-	-	-	-	30
riprap	519	-	-	-	1	1274	984	-	-	-	4360	
Banyuls	dock	2	-	-	-	-	1173	-	-	-	-	1728
	inner jetty	427	-	11	-	-	942	190	-	-	-	1974
	outer jetty	321	-	219	-	1	2273	-	-	8	-	3171
	pontoon	-	-	-	-	-	350	-	-	-	-	510
riprap	481	-	-	-	-	2031	423	-	1	-	6269	
Barcarès	dock	61	-	8	-	-	669	-	-	-	-	1307
	outer jetty	20	-	29	-	69	227	-	-	-	-	561
	pontoon	10	-	31	-	-	348	-	-	-	-	1188
	riprap	61	-	-	-	3	1008	-	-	-	-	1976
Elmes	dock	236	-	10	-	-	5298	-	-	-	-	6516
	outer jetty	21	-	196	-	-	1193	-	-	-	-	1763
	pontoon	3	-	30	-	-	709	-	-	-	-	896
	riprap	380	-	1	-	-	1688	-	-	-	-	2257
Porteils	dock	8	-	-	-	-	-	-	-	-	-	546
	dock *	5	-	6	-	10	30	-	1	-	-	3434
	inner jetty	71	-	10	-	132	98	-	4	-	-	1515
	outer jetty	15	-	45	-	119	817	-	1	-	-	3058
Port-Vendres	pontoon *	-	-	12	-	-	-	-	-	-	-	99
	riprap	59	-	4	-	-	62	-	-	-	-	393
	dock	6	-	-	-	-	-	-	-	-	-	50
	dock *	8	-	11	-	-	-	-	-	-	-	34
Total	inner jetty	281	-	191	-	-	422	-	-	1	-	1936
	outer jetty	26	-	174	-	2	77	-	-	-	-	637
	pontoon *	4	-	48	-	-	-	-	-	1	-	73
	riprap	118	-	2	-	-	31	-	-	2	-	6809
Elmes	After natural	465	7	70	-	344	2444	-	-	2	1	6809
	Before natural	1609	3	159	-	130	2757	-	-	10	-	6746
Porteils	After natural	160	-	338	-	-	1283	-	-	1	-	5147
	Before natural	741	-	372	-	-	5282	-	-	4	-	8329
Port-Vendres	dock	62	-	228	-	95	510	-	-	-	-	1188
	dock *	125	-	51	3	500	1651	-	7	-	-	2678
	inner jetty	27	-	49	-	-	17	-	-	-	-	135
	outer jetty	9	-	-	-	3	223	-	-	-	-	269
Total	pontoon *	26	-	55	-	725	8655	-	-	-	-	9740
	riprap	89	-	52	-	20	2515	-	-	-	-	2762
	dock	236	-	397	-	-	2091	-	-	-	-	3173
	dock *	63	-	20	-	-	2282	-	-	-	-	2617
Total	inner jetty	31	-	154	-	-	187	-	-	-	-	483
	outer jetty	2	-	16	-	-	157	-	-	-	-	177
	pontoon	81	-	144	-	-	4345	-	15	-	-	15935
	pontoon *	-	-	-	-	-	2	-	-	-	-	8
riprap	32	-	92	-	1	806	-	-	-	-	1466	
Total	7282	10	3363	3	2884	59359	1645	15	16	45	1	121673

2- Harbors rehabilitation and endangered species: Observation of juvenile dusky groupers (*Epinephelus marginatus*) in artificial habitats of North-Western Mediterranean harbors (article publié)

Depuis 2013 et sur toute la durée de cette thèse, un suivi de l'installation des juvéniles de poissons est réalisé dans plusieurs ports de Méditerranée française. Ce réseau de surveillance de l'installation des juvéniles de poissons (RESPIRE), est financé par l'Agence de l'eau Rhône Méditerranée Corse et consiste en l'installation de 9 modules Biohut® ponton dans les zones d'avant port. Ces modules ont été suivis 3 fois par an pour la majorité d'entre eux et de façon bi-mensuelle pour les sites de suivi « haute fréquence » dont Port-Vendres et Le Barcarès faisait parti. Ces suivis ont permis l'observation de plusieurs juvéniles de mérrou brun (*Epinephelus marginatus*) installés dans les habitats artificiels. Les juvéniles de cette espèce classée « en danger » par l'IUCN ne sont que très rarement observés dans le Golfe du Lion. Bien que des programmes à large échelle semblent être une meilleure option pour induire un réel gain sur la contribution globale des ports, ces observations suggèrent que l'installation de quelques modules peut déjà engendrer certains bénéfices.

Observation of juvenile dusky groupers (*Epinephelus marginatus*) in artificial habitats of North-Western Mediterranean harbors

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Received: 21 October 2015 / Revised: 22 February 2016 / Accepted: 14 April 2016
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The dusky grouper, *Epinephelus marginatus* (Lowe, 1834) is an emblematic species of the Mediterranean Sea (Pastor et al. 2009). However, the species is classified as endangered by the International Union for the Conservation of Nature (IUCN); NW-Mediterranean stocks having suffered drastic decline, with remaining individuals being found almost exclusively in Marine Protected Areas (MPA) (Zabala et al. 1997). Since the early 1990's an increasing number of groupers is being reported along the shores of the NW-Mediterranean sea including an increasing proportion of small individuals (under 40cm) (Bodilis et al. 2003a). Despite the observation of few Young Of the Year (YOY) (under 10cm) on the eastern French coasts and Corsica, only one observation had been made in the Gulf of Lions (Bodilis et al. 2003b).

Grouper's juveniles have a cryptic behavior and a preference for crevices, shelter availability being the determining factor for habitat suitability (La Mesa et al. 2002). They appear in shallow coastal waters, which makes them sensitive to littoral habitat degradation. The loss of coastal nursery habitat is of major concern for fish juveniles. Lately, the development of ecological restoration led, among other actions, to the deployment of artificial microhabitats (Biohut®) (Fig. 1a) along the French Mediterranean coast. Placed in harbors, they aim at restoring nursery function through habitat complexification. The settlement of juveniles (all species) on these structures has been monitored since 2013.

During this monitoring, four juvenile groupers were observed, making it the first record of settlement of this species on artificial structures and in harbors. Two first observations were that of a 5cm individual and a 7cm individual in Le Bruscat harbor on October 2013 and 2014 (Fig. 1b). Since then, two other groupers of 6cm have been seen in the Gulf of Lions, one in Marseillan (October 2014) and one in Port-Vendres (June 2015) (Fig. 1c).

A key element in the assessment of local population recovery is the presence of YOY in an area where only very scarce observations were made. Also, the use of artificial habitats should be seen as a promising tool to complement protection measures like MPAs and moratoriums for the conservation of endangered coastal fish to increase their recovery.

Communicated by R. Thiel

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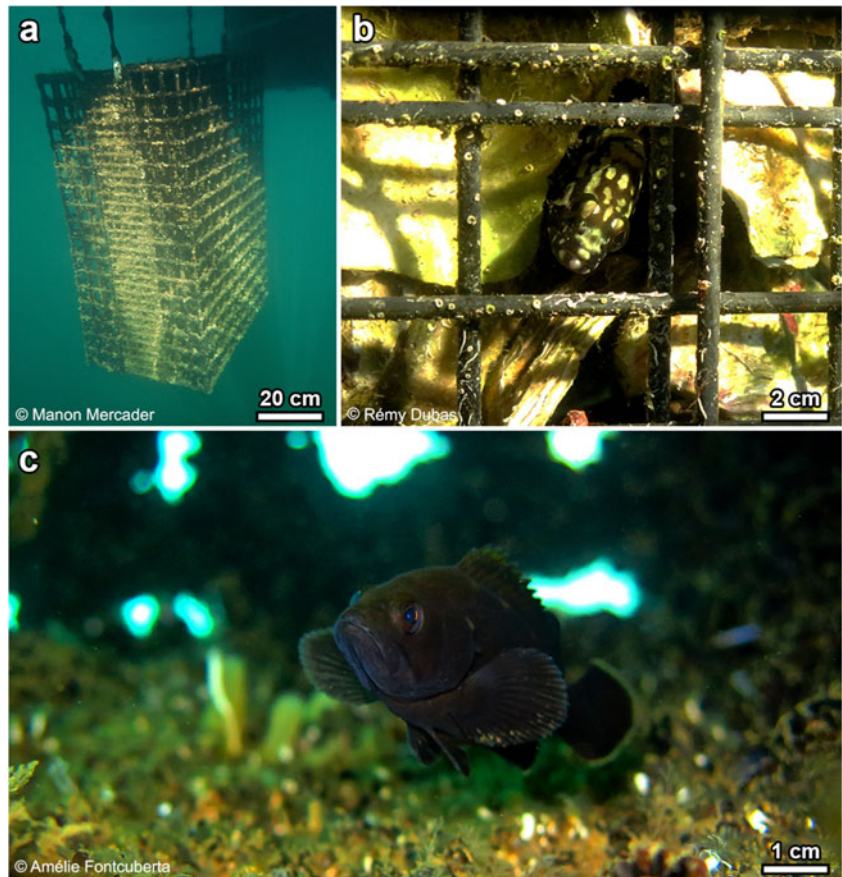
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Fig. 1 Artificial microhabitat fixed under pontoon (a) and juvenile groupers inside the habitats in Le Brusac (2014) (b) and Port-Vendres (2015) (c)



Acknowledgments We thank the Agence de l'Eau for financial support of the settlement network (RESPIRE).

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3- Résumé du chapitre

L'objectif de ce chapitre était d'évaluer la réhabilitation des ports dans leur rôle de nurseries. Cette évaluation a été menée lors de deux cas concrets de programmes de réhabilitation dans les ports de Port-Vendres et de Port-Barcarès dans les Pyrénées-Orientales sur la base d'estimations des densités en juvéniles de poissons réalisées par comptages visuels. Le protocole d'évaluation se basait sur des comparaisons entre ports restaurés, ports témoins non restaurés et zones naturelles de référence dans le cadre d'un design de type Before-After-Control-Impact (BACI) à deux échelles spatiales, celle de l'habitat et celle du site dans sa totalité. Afin d'intégrer au maximum la variabilité naturelle de la répartition des juvéniles, les données issues des comptages ont été analysées suivant une approche semi-paramétrique couplant des modèles linéaires généralisés mixtes (GLMM), et des courbes de contrastes permettant la comparaison de trajectoires écologiques complexes. À l'échelle de l'habitat, les résultats montrent un bénéfice significatif de la mise en place d'habitats artificiels sur les quais. En effet, quand comparée aux quais témoins, la réhabilitation des quais a permis une augmentation d'un facteur six des densités en juvéniles qui étaient alors comparables à celles observées sur les habitats naturels. Toutefois, à l'échelle du port dans sa globalité, la réhabilitation ne paraissait pas avoir d'effet significatif suggérant que les actions menées n'étaient pas suffisantes pour engendrer un gain quantifiable de la contribution des ports à l'approvisionnement en juvéniles. Malgré tout, même un nombre restreint de modules a permis d'observer des juvéniles d'une espèce classée comme « en danger » par l'IUCN, le mérrou brun, alors que leur observation est rare en milieu naturel. Ces résultats sont encourageants et confortent l'idée que les futurs projets de réhabilitation devraient être menés à plus large échelle pour escompter augmenter la contribution globale des ports au maintien des populations de poissons.

D'un point de vue méthodologique, l'approche développée dans ce chapitre s'est révélée adaptée aux évaluations environnementales à différentes échelles spatiales sous contraintes de design expérimentaux complexes et de la nature souvent très variable inhérente aux données issues d'approches de terrain. Aussi, ce travail devrait bénéficier au développement de protocoles d'évaluation des programmes de restauration écologique mais également à toutes autres mesures de gestion environnementale.

Chapitre 6 :

Discussion générale et perspectives



Ces travaux de thèse s'organisaient autour de deux objectifs principaux: (i) déterminer le rôle joué par les infrastructures portuaires en tant qu'habitat pour les juvéniles de poissons côtiers (Chapitre 4) et (ii) évaluer le potentiel de la réhabilitation de la fonction de nurserie en zone portuaire en tant qu'outil pour le maintien des populations de poissons (Chapitre 5). Répondre à ces deux objectifs a également nécessité une étape préalable d'estimation du taux de survie sur les habitats artificiels utilisés (Chapitre 3). Les approches choisies combinaient des expérimentations *ex-situ*, qui ont consisté en des études de terrain à plusieurs échelles spatiales et en l'instauration de sites ateliers de restauration écologique des ports. Elles ont permis de mettre en évidence (i) la relative importance des infrastructures portuaires en tant qu'habitat juvénile dans un paysage sous-marin de plus en plus façonné par les activités humaines et (ii) les bénéfices pouvant être engendrés par la mise en place d'actions de réhabilitation dans ces zones. Ces résultats soulèvent ainsi la pertinence de la prise en compte des zones artificialisées dans les stratégies de gestion du milieu marin ainsi que celle de la complémentarité des actions de restauration écologique avec d'autres mesures de conservation telles que les AMP ou encore les récifs artificiels de protection (anti-chalutages) ou de production.

Ce dernier chapitre a ainsi pour objectif d'intégrer les résultats issus de cette thèse dans un contexte plus large afin de proposer un cadre conceptuel de gestion des zones côtières incluant la prise en compte des zones urbanisées et des améliorations écologiques pouvant y être menées.

1- Synthèse et limites des travaux

1.1 Les infrastructures portuaires en tant qu'habitat juvénile pour les poissons côtiers

Les résultats des chapitres 4 et 5 ont montré, qu'en Méditerranée, les juvéniles de différentes espèces de poissons marins côtiers étaient capables de s'installer et se maintenir en zones portuaires. Des études antérieures avaient déjà reporté la présence de juvéniles de poissons dans ces zones, notamment pour des espèces ayant été observées durant cette thèse, telles que les sars (*Diplodus* sp.) (Bouchouca et al., 2016; Clynick, 2006; Mercader et al., 2017) ou le loup (*Dicentrarchus labrax*) (Dufour et al., 2009). Toutefois, le nombre de sites échantillonnés pour ce travail de thèse ainsi que la

fenêtre temporelle d'échantillonnage couvrant la période d'installation de nombreuses espèces ont permis de mettre en évidence l'utilisation des ports comme habitat juvénile par un plus grand nombre d'espèces que supposé, notamment par des espèces à fort intérêt commercial comme la dorade (*Sparus aurata*) et le rouget (*Mullus* spp.), ou rarement observées en milieu naturel sur la zone d'étude, comme le sar tambour (*Diplodus cervinus*), le denti (*Dentex dentex*), le canthare (*Spondyllosoma cantharus*) ou encore le mérrou brun (*Epinephelus marginatus*). Cependant, toutes les espèces observées étaient des espèces dont les juvéniles s'installent naturellement en zone rocheuse. Le fait de ne pas avoir observé d'espèce s'installant sur fond meuble s'explique à la fois par (i) un protocole de suivi qui n'était pas adapté à ces espèces (pas d'échantillonnage sur les fonds meubles au milieu des ports) et (ii) des modifications de l'habitat engendrées par la construction des ports (remplacement du substrat meuble par du substrat dur, plus grande profondeur...) ne permettant plus leur installation.

Si d'une façon générale, les juvéniles utilisent bien les ports, de fortes variations spatio-temporelles ont été observées au cours des deux ans d'échantillonnage. Comme en milieu naturel, les densités de certaines espèces (e.g. *O. melanura*, *S. viridensis*) étaient plus élevées en 2015 qu'en 2016, ou à l'inverse en 2016 qu'en 2015 pour d'autres (e.g. *D. sargus*). Des disparités ont également été observées entre sites (Chapitres 4 et 5) comme cela avait déjà été le cas dans une précédente étude (Bouchouca et al., 2016), ces disparités étant particulièrement marquées en fonction de la localisation géographique des ports (côte rocheuse au sud de la zone d'étude versus côte roche au nord) (Chapitre 4). Certaines études suggèrent que l'installation et le recrutement sont des processus stochastiques (Doherty, 1987, 1991; Doherty and Williams, 1988; Sale, 1991). Toutefois la cohérence dans les patrons observés suggère l'implication de processus déterministes à large échelle (Cowen, 1985; Fowler et al., 1992; Victor, 1983, 1986). Par exemple, des processus pré-installation peuvent influencer la reproduction ainsi que la survie et la dispersion des larves et de ce fait déterminer le nombre de larves arrivant à la côte, conditionnant lui même les densités initiales lors de l'installation (Asplin et al., 1999; Pineda et al., 2010; Watson and Munro, 2004; Zhang et al., 2014). Ces processus peuvent inclure des facteurs tels que l'hydrodynamisme (courants, vents) et la température ou encore la disponibilité en nourriture. La construction d'un port, ou de toute autre structure anthropique en mer, modifie profondément les courants locaux (Martin et al., 2005; 2007) pouvant ainsi avoir des

conséquences sur l'installation benthique (Munday et al., 2008). Cette importance des courants locaux dans le succès de l'installation (Hindell et al., 2003; Pineda et al., 2010; Roy, 1998) pourrait en partie expliquer les différences inter-sites observées. En effet, sur la zone d'étude considérée dans cette thèse il semblerait par exemple que le flux larvaire de *D. sargus* soit 30 fois plus important pour la côte sableuse que pour la côte rocheuse (Pastor, 2008). Ces différences peuvent également résulter de processus post-installation (i.e. survie et croissance des juvéniles) (Doherty, 2002; Macpherson and Raventos, 2005; Munday et al., 2008; Öhman et al., 1998) essentiellement liés à la qualité des habitats présents (Planes et al., 1998) mais également aux éventuelles différences dans l'abondance et la nature des prédateurs (Cowan et al., 2016). Les résultats obtenus dans les chapitres 4 et 5 vont d'ailleurs dans le sens de l'hypothèse selon laquelle la qualité de l'habitat conditionne pour beaucoup les densités en juvéniles (approximation du succès de l'installation ainsi que de la valeur de nurserie de l'habitat en question). En effet, les densités recensées sur les jetées et les enrochements à l'intérieur des ports étaient comparables voire supérieures à celles des habitats naturels. Alors que les quais et pontons, dont la complexité est quasi nulle, présentaient des densités beaucoup plus faibles. Ainsi, si les jetées, au même titre que les épis et brise-lames peuvent être considérées comme des nurseries (*sensu* Beck et al. (2001)), cela n'est pas le cas pour les ports dans leur globalité qui abritent des densités relativement faibles par rapport aux autres habitats. Cependant, ces infrastructures occupent souvent une part non négligeable du linéaire côtier. Par exemple dans la zone d'étude, les ports s'étendent sur environ 20 km de linéaire, soit l'équivalent de la côte rocheuse naturelle, représentant ainsi une large proportion de paysage sous-marin. Il est donc possible que leur contribution absolue soit élevée en faisant des habitats pour juvéniles efficaces, c'est à dire des habitats dont la contribution par unité de surface n'est pas forcément élevée mais dont la prépondérance dans le paysage sous-marin peut résulter en une forte contribution globale à la population adulte (Dahlgren et al., 2006). Bien que la densité entre installation et recrutement soit une approximation du nombre d'individus qui rejoindra la population adulte, une évaluation de la quantité de juvéniles y contribuant réellement représenterait une mesure plus pertinente et intégrative (i.e. prenant en compte les quatre critères de Beck et al. (2001)) du rôle des infrastructures portuaires (mais aussi des autres habitats) dans le maintien des populations. Toutefois, à l'heure actuelle, cette évaluation représente un réel verrou méthodologique. En effet,

cela nécessiterait de suivre les juvéniles afin d'estimer leur taux de mortalité et leur capacités migratoires pour *in fine* évaluer leur contribution relative au stock adulte. Cependant aucune méthode de marquage interne ou externe n'est aujourd'hui suffisamment miniaturisée pour permettre le marquage de juvénile de l'année (YoY). Seuls les Passive Integrated Transponder (PIT tags), qui sont notamment beaucoup utilisés en milieux dulçaquicole (Aarestrup et al., 2003; Achord et al., 1996; Gries and Letcher, 2002), pourraient éventuellement représenter une option, mais la portée de détection en eau salée est extrêmement réduite (moins d'un mètre) en eau salée du fait de la conductivité. L'utilisation de la microchimie des otolites pourrait être une autre option. Cependant il semblerait qu'il n'y ait pas de signature multi-élémentaire caractéristique de l'ensemble des ports (Bouchoucha, 2017), une alternative serait alors de travailler à l'échelle d'un seul site. Afin d'estimer la contribution relative d'un port, cela nécessiterait au préalable de caractériser les signatures de l'ensemble des habitats juvéniles potentiels, ce qui représente tout de même un investissement considérable (en terme de temps et de coût).

1.2 Augmenter la complexité structurale de l'habitat pour réhabiliter la fonction de nurserie en zone portuaire

En milieu naturel, la qualité de l'habitat conditionne pour beaucoup l'installation des juvéniles de poissons (Mellin, 2007; Ventura et al., 2014), cela est également le cas en zone portuaire, les densités les plus élevées étant retrouvées sur les habitats les plus complexes (enrochements, jetées) (chapitres 4 et 5). De même, les densités en juvéniles sont plus importantes sur les ouvrages portuaires équipés de petits habitats artificiels que sur leurs homologues non équipés (chapitre 5) (Bouchoucha et al., 2016; Mercader et al., 2017) bien que ces différences soient minimes pour les pontons (chapitre 5). Le potentiel des ports en tant qu'habitat pour juvéniles semble donc être essentiellement limité par le manque de complexité de la majorité des structures qui les composent (quais et pontons). Le confinement (distance à l'entrée du port) de certaines zones peut également être un facteur limitant (chapitre 4). Dans sa thèse, Marc Bouchoucha (Bouchoucha, 2017) souligne que les plus fortes densités observées sur les ouvrages complexifiés peuvent résulter d'une réelle « production » via un taux de survie supérieur sur les habitats artificiels (Bulleri and Chapman, 2010) ou d'une concentration des juvéniles sur ces habitats (Ammann, 2004). Cette question est largement discutée dans

la littérature concernant les récifs artificiels (Osenberg, 2002; Pickering and Whitmarsh, 1997; Tessier et al., 2014). Les résultats obtenus dans cette thèse ne permettent pas de trancher en faveur de l'une ou l'autre de ces hypothèses. Ils suggèrent plutôt, comme pour les récifs artificiels (Pickering and Whitmarsh, 1997; Svane and Petersen, 2001), qu'il est fortement probable que les densités observées résultent d'une combinaison des deux phénomènes. Les quais et pontons n'ayant pas été équipés la deuxième année abritaient des densités relatives (par comparaison aux enrochements intra-portuaires ou aux habitats naturels) semblables à celles reportées la première année (chapitre 5). Cela suggère que les individus présents sur ces habitats ne les auraient pas particulièrement désertés pour s'installer sur les zones équipées. Toutefois, les différents transects étaient relativement éloignés les uns des autres, limitant certainement les migrations entre zones de comptage, du moins pour les individus les plus jeunes, les individus plus grands ayant eux des capacités dispersives plus importantes (Di Franco et al., 2013a). De plus, à l'échelle du site dans sa globalité, l'effet de la réhabilitation n'était pas significatif (chapitre 5), aussi il n'est pas possible d'affirmer que la contribution globale du port soit accrue par le déploiement des habitats artificiels (le fait de ne pas détecter d'effet peut également être lié à la méthodologie employée, ce point est discuté dans la section suivante 1.3). Cependant, il est peu probable que la mortalité des juvéniles en zones portuaires soit totalement indépendante de la disponibilité en refuges. En effet, la mortalité post-installation des juvéniles semble être essentiellement causée par la prédation, celle-ci dépendant du nombre et de la nature des prédateurs mais surtout de la complexité structurale de l'habitat qui influence donc directement la survie des juvéniles (Bulleri and Chapman, 2010; Cheminée et al., 2016; Holbrook and Schmitt, 2002; Mellin, 2007; Schmitt and Holbrook, 2000). En effet, Thiriet (2014) a par exemple montré que la mortalité de petits labridés était plus faible dans les forêts de cystoseires que sur des habitats moins complexes bien que l'abondance et la diversité des prédateurs y soient plus élevée. La disponibilité en nourriture n'intervient que peu sur la mortalité (Cuadros et al., 2017; Macpherson et al., 1997; Vigliola et al., 1998) et il est peu probable que l'influence de facteurs environnementaux (e.g. température, pollutions chimiques, pathogènes) diffère entre des habitats adjacents (e.g. un quai et des enrochements situés l'un à côté de l'autre dans la même zone d'un port). Aussi, il est fort probable que le taux de survie des juvéniles soit accru sur les habitats artificiels. D'ailleurs, bien qu'insuffisants pour

pouvoir généraliser cette hypothèse, les résultats du chapitre 3 vont dans ce sens. Ainsi, les plus fortes densités observées sur les portions équipées résultent certainement d'une combinaison entre installation préférentielle et meilleur taux de survie par comparaison aux portions non équipées. Les mêmes processus peuvent être avancés pour expliquer les densités observées sur les enrochements intra-portuaires. Les études précédentes ont montré une variabilité taxa-spécifique de la réponse à l'augmentation de complexité structurale des ouvrages portuaires. Certaines espèces présentaient des abondances nettement supérieures sur les portions équipées que sur les témoins (e.g. *D. puntazzo*, *D. annularis*), alors que d'autres ne semblaient que peu influencées par la mise en place des habitats artificiels (e.g. *D. sargus*) (Bouchoucha et al., 2016; Mercader et al., 2017). Dans le chapitre 5, des variations temporelles de l'effet de la réhabilitation ont été mises en évidence. Les périodes d'installation des espèces observées étant différentes, il est possible que la variabilité de la réponse globale soit en partie due à des disparités dans la réponse de chaque espèce, les préférences en terme d'habitat étant variables d'une espèce à l'autre (DeMartini et al., 2010; Freitas et al., 2016; Harmelin-Vivien et al., 1995; Wiederholm, 1987). Ce dernier point, déjà soulevé dans le chapitre 3 amène à penser que la réhabilitation des ports gagnerait à se faire via une multitude d'habitats différents utilisés sur des périodes assez longues, voir sur l'ensemble de l'année. Ceci ne pourra se faire qu'avec un développement de la filière du génie écologique marin. Toujours dans un souci d'efficacité, des projets à large échelle impliquant l'équipement d'une grande proportion des quais et pontons présents dans un port, seraient à privilégier. En effet, si la présence d'habitats plus complexes sur quelques mètres linéaires d'ouvrages portuaires permet l'installation d'un plus grand nombre de juvéniles que sur les ouvrages nus, celle-ci ne semble pas suffisante pour induire un gain quantifiable à l'échelle du port dans sa globalité. Bien que cela reste à démontrer, les résultats obtenus dans cette thèse laissent supposer que l'installation d'un plus grand nombre et d'une plus grande diversité d'habitats, surtout dans les zones d'avant port pourrait potentiellement mener à une contribution plus importante des ports au maintien des populations de poissons côtiers. Étant donné la forte variabilité inter-annuelle de l'installation des juvéniles, et le fait que celle-ci semble influencer la contribution relative des ports (chapitre 4), des programmes de restauration à long terme sont à envisager pour escompter un gain substantiel.

1.3 Méthodes de suivi et d'évaluation

Un protocole d'évaluation de la réhabilitation de la fonction de nurserie a été mis au point durant cette thèse. Il intègre la variabilité naturelle malgré les contraintes liées à l'échantillonnage en milieu portuaire (autorisations, accessibilité, visibilité) et naturelles (accessibilité, conditions météorologiques) ainsi que la durée limitée du projet, représentait un vrai challenge. Premièrement, il fallait intégrer la variabilité temporelle à différentes échelles, (i) au fil des mois d'une même année pour couvrir la période d'installation d'un maximum d'espèces ainsi que l'évolution de leurs effectifs, (ii) entre les années connaissant la possibilité de fortes variabilités inter-annuelles (Di Franco et al., 2013b; Vigliola et al., 1998). S'ajoutait à cette variabilité temporelle une variabilité spatiale de la répartition des juvéniles en milieu naturel (Cheminée et al., 2017) et également entre zones portuaires (Bouchoucha et al., 2016). Notre choix s'est ainsi porté sur l'utilisation d'une procédure de type BACI incluant de multiples « témoins » et permettant une évaluation à deux échelles spatiales. Celle de l'habitat, à laquelle nous nous attendions à détecter un effet des habitats artificiels (à minima quand comparé au même habitat non équipé) étant donné les résultats des études précédentes (Bouchoucha et al., 2016; Mercader et al., 2017; Patranella et al., 2017), et celle du site réhabilité dans sa globalité à laquelle l'effet de la réhabilitation n'avait encore jamais été évalué. Suivant les recommandations de la SER ce protocole incluait la comparaison avec une/des référence(s) mais également avec un témoin afin de pouvoir détecter un changement vers un état fonctionnel mais également s'éloignant de l'état dégradé. Ce protocole s'est révélé efficace sur plusieurs points mais comportait également un certain nombre de limites qu'il serait à l'avenir judicieux de prendre en compte afin d'améliorer les procédures d'évaluations.

Concernant les points positifs, l'utilisation d'un protocole BACI s'est avérée primordiale pour intégrer la variabilité spatio-temporelle, et ainsi éviter des conclusions erronées quant à l'efficacité de la réhabilitation (Mahlum et al., 2017). En effet, sans la prise en compte de l'interaction BA*CI, un effet marqué du facteur BA du fait d'une installation beaucoup plus importante en 2016 (After) (chapitre 4) aurait par exemple amené à conclure trop rapidement à un impact considérable de la mise en place des habitats artificiels s'il n'était couplé à une comparaison entre sites ou habitats. Au contraire, sans la prise en compte de la répartition des juvéniles avant réhabilitation, il aurait pu être interprété un effet négatif de l'ajout d'habitats sous les pontons (les pontons témoins

abritant en fait naturellement plus d'individus). Un autre avantage d'un tel protocole est qu'il procure un état initial du site à restaurer permettant par exemple de pouvoir adapter la localisation des habitats artificiels en fonction de la distribution des juvéniles (les données collectées durant cette thèse ont par exemple permis de choisir l'emplacement d'habitats artificiels ayant été installés dans le port d'Argelès en 2017).

L'utilisation couplée de témoins « négatifs » (ports non-réhabilités) et de références « positives » (zones naturelles) s'est aussi avérée pertinente, permettant d'une part de mettre en évidence le « gain » potentiellement engendré par la mise en place des habitats artificiels par rapport à un ouvrage non restauré mais également la contribution relative des ouvrages restaurés ou non par rapport aux habitats naturels. Le choix de la référence nous mène cependant à une limite majeure de ce protocole. En effet il a ici été choisi d'échantillonner exclusivement des petits fonds rocheux hétérogènes. Toutefois certaines espèces observées en zones portuaires sont connues pour utiliser d'autres habitats comme nurseries. Cela est notamment le cas pour la dorade (*Sparus aurata*) et le loup (*Dicentrarchus labrax*) dont les habitats nurseries sont généralement localisés dans les estuaires et les lagunes (Dufour et al., 2009; Jennings and Pawson, 1992; Tournois, 2013) ou du sparailon (*Diplodus annularis*) qui s'installe dans les herbiers de posidonie (Harmelin-Vivien et al., 1995). Aussi, la référence devrait être redéfinie pour inclure une plus grande diversité d'habitats naturels. Ce type de problème aurait pu être évité en n'étudiant que certaines espèces mais cela aurait été réducteur car l'objectif des programmes de réhabilitation de zones portuaires réalisés durant la thèse n'étaient pas de favoriser une/des espèce(s) particulières mais plutôt la plus grande diversité d'espèces possible. Une autre limite de ce protocole réside dans le fait qu'il est difficile de déterminer si l'effet non significatif de la restauration à l'échelle du site est (i) réellement lié au fait que l'équipement d'une seule portion de quai et ponton ne suffit pas pour générer un gain assez conséquent pour engendrer une contribution globale plus élevée à l'échelle du site, (ii) résulte du plan d'échantillonnage prenant en compte une multitude d'habitats dans l'enceinte du port. En effet, dans chaque port restauré, les portions équipées ont été échantillonnées de concert avec les portions non équipées, les enrochements et les jetées, le nombre de transects de chaque habitat étant variable en fonction des caractéristiques du site. Aussi, il est possible que ce design ait eu une influence sur les résultats. Un échantillonnage exhaustif du site (comme dans le chapitre 4) ou un système de pondération par le type d'habitat (bien

que ce facteur ait déjà été pris en compte dans le modèle sous la forme d'un facteur aléatoire) permettrait peut-être une meilleure représentativité. Toutefois l'hypothèse selon laquelle la proportion de linéaire équipée n'est pas suffisante pour engendrer une meilleure contribution du site dans sa globalité reste plausible.

Bien qu'efficace ce protocole d'évaluation reste lourd à mettre en place et extrêmement chronophage. Le traitement des données générées nécessite également des outils statistiques complexes ce qui rend difficile le transfert de la méthode utilisée vers des gestionnaires par exemple. Aussi, il serait bénéfique de simplifier et de standardiser la méthodologie afin de faciliter et démocratiser son utilisation.

1.4 Intégrer restauration et conservation pour une gestion adaptative des zones côtières

Bien que le maintien de la biodiversité marine et des stocks de poissons soit défini comme une priorité à l'échelle internationale (CBD, 2011; Watson et al., 2014), les ressources financières (et humaines) restent restreintes (McCarthy et al., 2012). Face à cette contrainte de taille, gestionnaires et financeurs sont confrontés à une question récurrente : mieux vaut-il protéger des écosystèmes encore préservés ou restaurer des sites dégradés ? Mais, est-ce-là la bonne question ? Ne serait-il pas plus judicieux de se demander comment combiner ces deux approches afin de garantir une utilisation la plus « productive » possible des ressources allouées au maintien des habitats et des espèces ? Il y a de cela seulement quelques années, il était généralement préconisé de favoriser la protection des habitats en bon état écologique. Cette mesure paraissait garantir un meilleur rapport coûts/bénéfices, sauvegarder une plus grande biodiversité et générer plus de services écosystémiques par unité de surface que la restauration (Benayas et al., 2009; Dodds et al., 2008; Hobbs and Harris, 2001; Possingham et al., 2015; Williams et al., 2005; Young, 2000). Toutefois ces dernières années, plusieurs études prônent l'utilisation d'une combinaison des deux approches pour un maximum d'efficacité (Possingham et al., 2015; Wiens and Hobbs, 2015). En effet, la protection ne s'avère pas toujours efficace, surtout en milieu marin (Agardy, 1994; Costello and Ballantine, 2015; Cox et al., 2017; Edgar et al., 2014; Halpern, 2003). Concernant les habitats juvéniles, l'implémentation de mesures de protection est difficile d'un point de vue socio-économique du fait qu'ils occupent souvent les mêmes zones (e.g. plages, criques) que les activités touristiques et le développement côtier. Ainsi, sur une zone transfrontalière

France-Espagne incluant la zone d'étude de cette thèse, seulement 11% des nurseries identifiées bénéficiaient d'un statut de protection. De plus, le statut de protection paraissait n'avoir aucun effet sur les densités en juvéniles certainement du fait que les mesures réglementaires implémentées dans les AMP de la zone d'étude ont essentiellement vocation à protéger les adultes (Cheminée et al., 2017). A contrario, la restauration d'habitats dégradés peut engendrer des bénéfices sociétaux conséquents et nombre de services écosystémiques (De Groot et al., 2013) pouvant résulter en une meilleure acceptation du projet que dans le cas d'une réglementation à des fins de protection. Dans ce contexte, et au vu des résultats obtenus dans cette thèse et celle de Bouchoucha (2017), réhabiliter une fonction de nurserie en zone portuaire afin d'augmenter l'approvisionnement en juvéniles paraît être un outil potentiellement bénéfique pour le maintien des populations de poisson. Le PNMGL représente un outil privilégié pour le développement d'une gestion intégrée de la zone côtière prenant en compte le paysage sous-marin dans son intégralité et pas comme une multitude d'habitats déconnectés les uns des autres. Le concept de « nurserie paysagère » émerge d'ailleurs depuis quelques années suggérant qu'une prise en compte d'une multitude d'habitats ainsi que la connectivité entre ces habitats est la clé du maintien des stocks de poissons et de la biodiversité en zone côtière (Colloca et al., 2015; Nagelkerken et al., 2015). Les ports pourraient ainsi non seulement représenter des « habitats juvéniles efficaces » (Dahlgren et al., 2006) voire des nurseries alternatives, mais également accroître la connectivité du paysage (Glasby and Connell, 1999; Hoegh-Guldberg et al., 2008; Rudnick et al., 2012). De plus, ces socio-écosystèmes, à l'interface terre-mer représentent des lieux favorisant l'échange entre usagers de la mer, gestionnaires, scientifiques et décisionnaires. Des actions de communication et sensibilisation autour des programmes de restauration sont facilement envisageables (certaines existant déjà) et permettent une prise de conscience écologique chez les gestionnaires de zones portuaires comme chez les usagers, ce qui ne peut être que bénéfique sur le long terme. Bien qu'il ne s'agisse là que d'un ressenti personnel, le simple fait de voir les habitats artificiels et de pouvoir échanger avec les scientifiques lors des suivis, semble déjà générer une certaine appropriation du programme par de nombreux plaisanciers qui veillent à ce que leurs « crèches à poissons » ne soient pas dérangées. Utilisés en complément des mesures de protection, les programmes de réhabilitations des ports pourraient ainsi présenter nombre de bénéfices écologiques et sociétaux. Ils ne doivent

toutefois en aucun cas se substituer ou primer sur le principe de non-dégradation, sous prétexte de représenter une quelconque mesure compensatoire donnant « droit à détruire » des zones encore préservées.

2- Perspectives

2.1 Mieux appréhender le fonctionnement écologique des zones portuaires

Ce travail s'est focalisé sur le rôle des ports en tant qu'habitat juvénile pour les poissons côtiers. Bien que certaines questions subsistent encore quand à la contribution globale des ports au recrutement (e.g. les juvéniles quittent-ils bien les ports pour rejoindre les populations adultes ?), les résultats obtenus dans cette thèse et celle de Marc Bouchouca (Bouchouca, 2017) ont prouvé que ces infrastructures peuvent bien jouer un rôle de nurserie alternative pour certaines espèces de poissons côtiers. Toutefois, seuls les juvéniles ont été considérés dans ces études. Pourtant les ports semblent être également utilisés par les adultes de nombreuses espèces (Clynick, 2006; Clynick et al., 2008), il est donc probable qu'ils puissent jouer d'autres fonctions que celle de nurserie. Il serait ainsi intéressant d'étudier les patrons d'abondances et de diversités des adultes, ainsi que leurs périodes de résidence dans ces zones, ce qui pourrait renseigner sur une éventuelle utilisation des ports en tant que zone de frayère ou de nourrissage. Les infrastructures portuaires représentent des zones riches en nourriture (Acton, 2012) dans lesquelles les prélèvements sont restreints du fait de leur interdiction. Elles pourraient ainsi être considérées comme des *no-take zones* jouant un rôle de protection pour de nombreuses espèces.

Il serait également intéressant d'étudier la connectivité entre zones portuaires et naturelles. En effet, plusieurs études ont montré un certain niveau de connectivité entre AMP à différentes échelles spatiales (Andrello et al., 2013; Jonsson et al., 2016; Roberts et al., 2001; Rodrigues et al., 2004). En milieu marin, la connectivité est généralement réalisée par la dispersion au stade larvaire. En permettant l'installation des juvéniles, les ports pourraient accroître la connectivité entre AMP. Cela pourrait être particulièrement le cas pour les espèces de substrats rocheux, cet habitat étant généralement morcelé à l'échelle du paysage par de grandes étendues sableuses. Pourtant, à l'heure actuelle, aucune étude n'a pris en considération la possibilité d'un relais entre les AMP via les infrastructures anthropiques.

Mis à part les rôles pouvant être potentiellement joués par les ports dans le maintien des populations de poissons, il est probable que ces écosystèmes urbains fournissent les mêmes types de fonctions écologiques pour de nombreux autres taxa, notamment d'invertébrés benthiques largement présents dans ces zones.

Bien qu'un risque de contamination accrue soit possible dans les ouvrages portuaires, les conditions à l'intérieur de certains ports paraissent se rapprocher de celles trouvées en lagune, notamment en terme de productivité. Par conséquent, un export de matière organique depuis le port vers les eaux côtières environnantes est envisageable. Étudier ces processus et leurs éventuelles répercussions sur la structure trophique des écosystèmes adjacents peut s'avérer intéressant afin de mieux appréhender le fonctionnement des zones face à l'urbanisation croissante du littoral.

2.2 Améliorer l'évaluation des programmes de restauration de la fonction de nurserie en zones portuaires

Le protocole d'évaluation mis en place dans ces travaux a pu permettre de détecter les effets de la réhabilitation, tout du moins à l'échelle de l'habitat, tout en prenant en compte la variabilité spatio-temporelle naturelle. Toutefois, cette évaluation pourrait être améliorée.

Premièrement une analyse par taxa permettrait une vision plus précise de l'efficacité des habitats artificiels, et de déterminer les mécanismes sous-jacents aux variations de trajectoires observées (i.e. différence dans l'intensité de l'installation ou dans le taux de résidence sur tel ou tel habitat, différence dans la composition en espèces, dans les périodes d'arrivées des larves...). Une analyse de la répartition des classes de tailles permettrait également d'obtenir des informations quand à la dynamique d'utilisation des habitats artificiels par les juvéniles.

Afin de mieux appréhender la part des processus de concentration et production dans l'observation des plus fortes densités observées sur les habitats artificiels, il pourrait être envisagé une étude de la répartition des juvéniles suivant un gradient d'éloignement à ces habitats. Une évaluation globale (à l'échelle du site entier comme dans le chapitre 4) analysée sous un design BACI (comme dans le chapitre 5) pourrait également permettre de déterminer si l'effet de la restauration engendre un réel gain à l'échelle du port dans sa totalité et donc une réelle production.

Étant donné les variabilités inter-annuelles dans l'intensité de l'installation, la mise en place de suivis à long terme serait un moyen d'estimer l'impact de ces variations sur l'efficacité des habitats artificiels. Les abondances relatives des juvéniles entre zones naturelles et structures anthropiques pouvant différer en fonction de l'intensité de l'installation (chapitre 4) il est possible que cela ait également un effet sur le rôle joué par les habitats artificiels qu'il serait pertinent de prendre en compte.

Seuls les aspects écologiques ont été pris en compte dans ce travail, toutefois une évaluation des aspects socio-économiques liée aux projets de restaurations fournirait une vision plus intégrée des potentiels bénéfiques pouvant résulter de tels projets.

Sur la base de ces données empiriques, l'utilisation de simulations pourrait fournir des prédictions de la réponse du système à différents scénarios de restauration. Ce type d'approche pourrait être mené à l'échelle d'un port mais également à échelle plus large afin d'estimer les effets de la restauration d'un réseau de port sur les populations de poissons. Bien que les modèles ne soient qu'une représentation simplifiée de systèmes beaucoup plus complexes, les informations en résultant peuvent représenter une base d'aide à la décision afin de mettre en place les stratégies de gestion les plus appropriées possibles (Hussein et al., 2011a, 2011b).

Enfin, il serait intéressant de proposer un protocole d'évaluation simplifié et standardisé utilisable directement par les gestionnaires. Les procédures d'évaluation pourraient ainsi être menées sur un plus grand nombre de sites et à une échelle de temps plus longue donnant ainsi une vision plus représentative.

2.3 Vers un schéma territorial de gestion intégrée des zones côtières

Afin de garantir un maximum d'efficacité, les mesures de conservation des eaux côtières et de leur biodiversité doivent être planifiées et coordonnées. Il est également important que cela soit fait à une échelle spatiale et temporelle adaptée permettant d'intégrer les processus biologiques et écologiques tout en restant en cohérence avec les politiques territoriales existantes. A l'image du plan de gestion d'une AMP, la mise en place d'un outil de définition, de partage, de programmation et de mise en œuvre des actions de conservation à l'échelle d'un territoire permettrait certainement un gain d'efficacité considérable. Cela doit passer par l'intégration des mesures (i) de réduction des pressions (e.g. lutte contre la pollution), (ii) de maîtrise des activités maritimes (e.g.

mouillage, pêche, plongée sous-marine), (iii) de protection d'habitats et d'espèces (e.g. AMPs, moratoires) et (iv) de restauration de zones dégradées (e.g. réhabilitation des ports, transplantation d'herbier) au sein d'un même plan d'action. Une planification à moyen, voire long terme, ainsi que des procédures d'évaluation devraient également être prévues, notamment afin de pouvoir réajuster si nécessaire les mesures mises en place.

Tester la mise en place d'un tel outil de gestion pourrait éventuellement se faire à l'échelle du PNMGL. En effet, elle pourrait bénéficier d'un contexte de coopération déjà établi entre les différents acteurs (scientifiques, gestionnaires, élus, usagers, maîtres d'ouvrages...) ainsi que de la base d'un plan de gestion déjà existant (PNMGL, 2014).

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Annexes

Annexe 1

Article supplémentaire 1 : Mercader, M., Mercière, A., Saragoni, G., Cheminée, A., Crec’hriou, R., Pastor, J., Rider, M., Dubas, R., Lecaillon, G., Boissery, P., et al. (2017c). Small artificial habitats to enhance the nursery function for juvenile fish in a large commercial port of the Mediterranean. *Ecol. Eng.* 105, 78–86.

Annexe 2

Article supplémentaire 2 : Cheminée, A., Rider, M., Lenfant, P., Zawadzki, A., Mercière, A., Crec’hriou, R., Mercader, M., Saragoni, G., Neveu, R., Ternon, Q., et al. (2017a). Shallow rocky nursery habitat for fish: Spatial variability of juvenile fishes among this poorly protected essential habitat. *Mar. Pollut. Bull.* 119, 245–254.

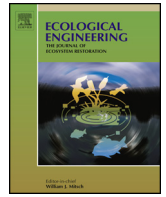
Annexe 3

Fiches produit des habitats artificiels Biohut® utilisés dans la thèse.



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Small artificial habitats to enhance the nursery function for juvenile fish in a large commercial port of the Mediterranean



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ARTICLE INFO

Article history:

Received 9 February 2017

Received in revised form 24 March 2017

Accepted 24 March 2017

Keywords:

Juvenile fish
Nursery
Artificial habitat
Coastal urbanization
Restoration ecology
Port

ABSTRACT

The concentration of human activities along the shoreline induces high levels of pressure, notably seascape urbanization caused by the proliferation of coastal and marine infrastructures such as ports, harbors, marinas and coastal defense structures. Because they are localized in sheltered and shallow coastal areas, these infrastructures inevitably lead to the loss of natural essential habitats once used as nursery ground by juvenile fish. Some studies have reported the presence of high juvenile densities on breakwaters and jetties suggesting those infrastructures could support the nursery function. However, ports seem unlikely to be used by juveniles due to their vertical and featureless docks. Here we explored the feasibility of using small artificial habitats to enhance the ecological value of ports. We set up a total of 108 artificial habitats in three different locations of the large commercial port of Marseille in the north-western Mediterranean. We then surveyed juvenile fish on the artificial habitats and control docks on 7 different occasions between June and September 2014. Average species richness and densities were higher on the artificial habitats but displayed high spatial and taxa-specific variations. Hence, small artificial habitats are promising ecological engineering tools to enhance the nursery function inside ports and thus reduce the ecological footprint of those infrastructures.

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1. Introduction

Coastal areas represent less than 15% of the planet's land surface but they concentrate more than 60% of the human populations (EEA, 1999), and this proportion is expected to reach 75% by 2025 (Airoldi and Beck, 2007; Creel, 2003; EEA, 2006; Gray, 1997). The land–sea interface undergoes high levels of human activities (fishing, transportation, industry and recreation) leading to increased pressure through resource overexploitation, pollution, and habitat modification (Airoldi and Beck, 2007; Crain et al., 2009; Dugan et al., 2011). Habitat conversion, fragmentation and loss are considered one of the greatest threats to marine biodiversity and ecosystems (Airoldi and Beck, 2007; Coll et al., 2010; Dafforn et al.,

2015; Gray, 1997; Halpern et al., 2008; Lotze et al., 2006; Seaman, 2007). The situation is particularly severe for coastal environments as a consequence of the growing number of man-made structures (ports, marinas, seawalls, breakwaters, groines, etc.) triggered by urbanization, commerce, industry, tourism and the need to protect the coast from erosion and flooding (Bulleri and Chapman, 2010; Gerland et al., 2014; Halpern et al., 2008; Scyphers et al., 2015). Some of the main characteristics of human-made coastal infrastructures are that it destroys, transforms or homogenizes the natural seascape mosaic: the intrinsic patchiness of the heterogeneous subtidal environment is replaced by homogeneous and less complex artificial habitats. It has been proven that the reduction of complexity (absolute abundance of individual structural components) and heterogeneity (relative abundance of different structural components) in terrestrial or marine environments leads to reduced abundances and survival of organisms (August, 1983; Brokovich et al., 2006; Fisher et al., 2007).

One of the essential functions offered by coastal habitats is their nursery role for marine organisms: during their life cycle, the het-

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erogeneity and complexity offered by the coastal seascape mosaic provide a wide range of habitat providing food and shelter suitable and essential for the juvenile stage of many different species (Beck et al., 2001). In the case of fishes for example, habitat homogenization and simplification may alter their “habitat quality” (sensu Dahlgren and Eggleston (2000)) and therefore ultimately impair their ecological function (Cheminée et al., 2016; Connell and Jones, 1991; Piko and Szedlmayer, 2007). If modifications of the native habitats and the functions they support are unavoidable (Airoidi and Beck, 2007; Airoidi et al., 2005; Martin et al., 2005) the creation of alternative habitats might support new ecological functions.

In this study we focused on the fish nursery function, which is of particular importance for population maintenance. Among man-made structures, it has already been shown that breakwaters host high densities of juvenile fish (Dufour et al., 2009; Pastor et al., 2013; Pizzolon et al., 2008; Ruitton et al., 2000) and adult fish species richness and abundances inside marinas seemed to be close to those found on natural rocky habitats (Clynick, 2008). Therefore, port and marina jetties might provide suitable nursery ground for juvenile fish (Dufour et al., 2009). However, ports are mainly characterized by vertical, featureless structures, such as docks and pontoons that seem unlikely to provide suitable habitat for juveniles.

The need to reduce the impact of man-made infrastructures and even to enhance their ecological value is becoming urgent since coastal hardening is predicted to increase in order to counter the foreseen global sea level rise and increasing frequency of large storms (Bray and Hooke, 1997; Michener et al., 1997; Thompson et al., 2002) and because of the high demand in marine transportation (e.g.: extension on Panama canal) and offshore energy.

However, combining ecological principles to urban infrastructure is a rather new concept (Bergen et al., 2001; Mitsch, 1996), especially in marine environments. Although ecological engineering has become a common practice in terrestrial and freshwater environments, it has just started to emerge over the last few years in marine environments (Browne and Chapman, 2011; Chapman and Blockley, 2009; Perkol-Finkel et al., 2006, 2008; Sella and Perkol-Finkel, 2015). Still, this kind of approach is rarely applied in the development of ports (Bouchoucha et al., 2016; Hellyer et al., 2011; Paalvast et al., 2012).

In a recent study, Bouchoucha et al. (2016) explored the potential role of marinas as habitat for juvenile seabreams (*Diplodus* spp.) and the used off small artificial units to increase habitat complexity. The habitats in large commercial ports are even more heavily transformed than in marinas, with much deeper waters, wide openings onto the sea and higher levels of human activities. Consequently, in the present study, we tested if a similar ecological engineer-

ing approach of marinas was implementable in a large commercial port and what benefit it could have on the assemblage of juvenile fish. We hypothesized that increasing habitat complexity would enhance the diversity (Browne and Chapman, 2011, 2014) and density of juvenile fish by furnishing shelter against predators (Bulleri and Chapman, 2010), thereby boosting the port’s nursery value (sensu Beck et al. (2001), a habitat with greater contribution to adult population through higher juvenile densities, better growth and survival rates, and facilitated migration toward adult habitat). Furthermore we explored if the response to habitat complexification would be consistent through space or depend on the localization of the artificial units within the port.

2. Material and methods

2.1. Study area

The “Grand Port Maritime de Marseille” (GPMM) is the busiest port in France and the 2nd in the Mediterranean (behind Algeciras, Spain) (AAPA, 2014), with 78 million tons of goods and over 2 million travellers passing through in 2014. It covers 10,000 ha between the cities of Fos and Marseille, in southern France, and is composed of two main basins: the western harbors located in Fos and the eastern harbors in Marseille. The study was led in the interconnected eastern harbors that are protected from the dominating wind generated waves by a 7 km breakwater (Digue du large) (Fig. 1a and e) constructed more than a hundred years ago. All the harbors undergo high levels of activity due to the navigation of container and cruise ships, but minimal fishing and diving pressure, as the site is a restricted area with limited access. The experimental model was conducted on three different docks, referred to as areas A, B and C (Fig. 1b–d). Each area exhibited different characteristics as described in Table 1.

2.2. Artificial experimental units and set up

Our study included two treatments in each area: normal docks (as controls) and equipped docks with increased complexity. In order to increase habitat complexity, we used Artificial Experimental Units (AEU) provided by the Ecocean[®] company (dock Biohut[®]) composed of a pair of stainless steel alloy cages (50 cm × 80 cm × 25 cm) (as used in Bouchoucha et al., 2016). The inner cage has a 2.5 cm mesh and is filled with a biogenic component (oyster shells) to promote colonization by benthic fauna and flora, as well as to increase the structure complexity. The outer cage has a 5 cm mesh and is left empty; the use of a larger mesh enables juveniles fish to go in and out without any inconvenience and offers a predator free zone (Fig. 2). AEU were attached to the initial substratum of the docks between the surface and –1 m by drilling superficial small holes permitting the fixation of the trellis to which the units are then attached.

A total of 108 AEU were installed in the port of Marseille over three days (14–16 May 2014). They were spread over 30 m of dock in each of the three different areas. An additional 30 m long stretch of unequipped dock was randomly selected as a control treatment in each area. Depending of physical constraints (presence of tires and wooden logs used as dock defense) docks were equipped with between 30 and 35 AEU spaced approximately 40 cm apart (always keeping to the 30 m of equipped dock).

2.3. Sampling procedure

Juvenile fish assemblages were monitored during seven separate surveys by an Underwater Visual Census (UVC) between June and September 2014 (June 23, July 8 and 31, August 7 and 20,

Table 1
Characteristics of the three sampling zones according to Bourgogne and Blin (2015).

Area	A	B	C
Depth (m)	3.5	12.5	8.5
Distance to the sea (m)	2400	2374	1820
Relative opening	Open	Open	Close
Presence of fenders	No	Yes	Yes
Bottom type	Mud	Mud	Mud
Rock proximity	No	No	Yes
Exposition to current	High	High	Low
Presence of macro-waste	High	Low	Low
Presence of hydrocarbons	Medium	Low	Low
Freshwater discharge	High	Low	Low
Terrestrial activity level	Low	Low	Low
Maritime activity level	Low	High	Low
Metallic trace elements levels	Very high	Medium	Medium
Rare earths levels	Very high	Low	High
Organic contaminants levels	High	Medium	Medium
Bacteriological contamination levels	High	Medium	Low

2.4. Data analysis

Statistical analyses were performed using the PRIMER 6 software with the PERMANOVA add-on (Clarke and Gorley, 2006; Clarke et al., 2014) and the R software (R version 3.0.3 – Rstudio Version 0.99.486). Uni- or multi-variate analyses of variance by permutations (PERMANOVAs) were performed to analyze the patterns of the following response variables: the univariate juvenile species richness, global juvenile density and taxa-specific density of species and the multivariate juvenile assemblage composition. As this method handles complex multiple factor designs, considers interactions of factors and does not require normal distribution of errors (Anderson, 2001), it was particularly suitable for our data. Response variables were modeled according to the following model with 3 factors: factor “treatment” has two levels (AEU, docks) and is fixed; factor “area” has 3 levels (A, B, C) and is random; factor “survey” has 7 levels (survey 1–7) and is fixed. Analyses were based on Bray–Curtis dissimilarity matrixes generated on square-root transformed data. p -Values were calculated by 999 random permutations of residuals under a reduced model and Type III sum of square (Anderson, 2001). The Monte-Carlo test was used when less than 200 permutations were generated. Post hoc pairwise tests were performed when relevant.

Furthermore, trends in multivariate data (juvenile fish assemblages) were graphically represented using the Principal Component Analysis (PCoA) on a Bray–Curtis dissimilarity matrix. This ordination method is well adapted to our data as it is applicable on a non-Euclidian distance matrix. It also presents the advantage of representing the data without distorting distances as it is based on eigenanalysis (Gower, 1966; Legendre and Legendre, 2012). SIMPER analyses were also conducted in order to determine which species would be responsible for differences between groups of samples.

3. Results

3.1. Species richness and total density

Overall, more than 16 species were observed (Table 2) with a maximum of 6 species per transect and survey. Sparids were the most represented fish families with 6 different species among which *Diplodus annularis* was the most abundant. For mean species richness, the interaction term between treatment and areas was significant (PERMANOVA, $F = 17.38$, $p = 0.001$). For two of the three areas (B and C), species richness was higher on AEU than on docks (2.62 ± 1.07 and 3.57 ± 1.40 species on AEU, 0.43 ± 0.68 and 1.14 ± 1.24 on docks respectively, pair-wise test, $p = 0.001$) (Fig. 3A). Total juvenile density trends were similar to those of species richness: a significant interaction between treatment and areas was detected (PERMANOVA, $F = 14.65$, $p = 0.001$). The mean total densities of juveniles were higher on AEU than on docks for two of the three areas (12.90 ± 2.36 and 18.14 ± 3.18 individuals/10 m on AEU and 2.57 ± 0.78 and 11.57 ± 5.40 individuals/10 m on control docks for area B and C respectively, pair-wise tests, $p = 0.001$) (Fig. 3B).

3.2. Assemblages and taxa-specific densities

Similar trends were observed for assemblage composition (relative abundance of species). Assemblages differed significantly according to combinations of the interaction survey \times area \times treatment (PERMANOVA, $F = 1.36$, $p = 0.047$). The effect of the treatment (AEU vs docks) varied according to the spatial position (area) or survey (Fig. 4). Those variations are also displayed on the PCoA plot, with most of the dock samples concentrated at the very left of the x -axis for areas A and B or at the top of the y -axis

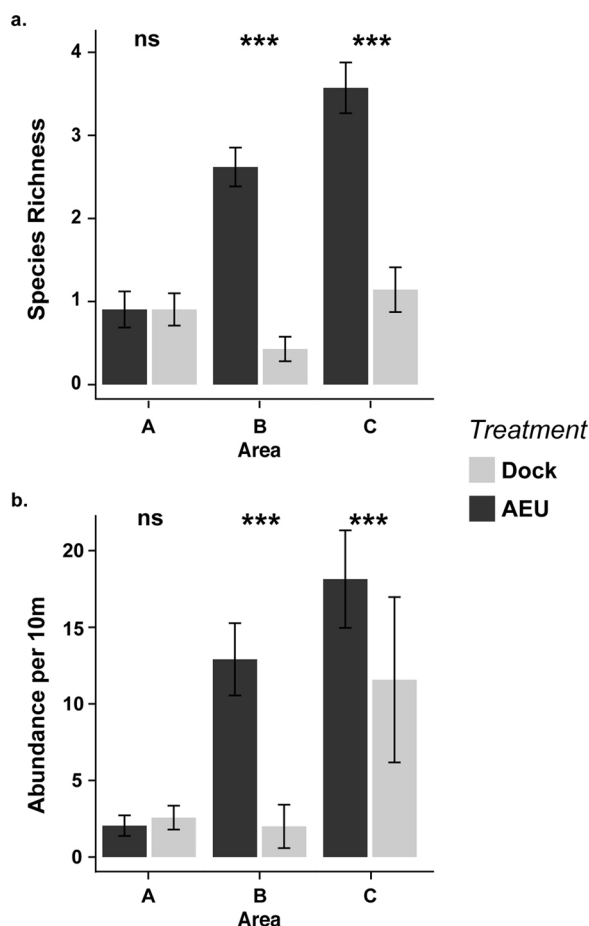


Fig. 3. (a) Mean (\pm SE) species richness by treatment and area. (b) Total mean density (\pm SE) (all species pooled) by treatment and area expressed in number of individuals per 10 m. Significant p -value: * <0.05 ; ** <0.01 ; *** <0.001 , ns = non significant.

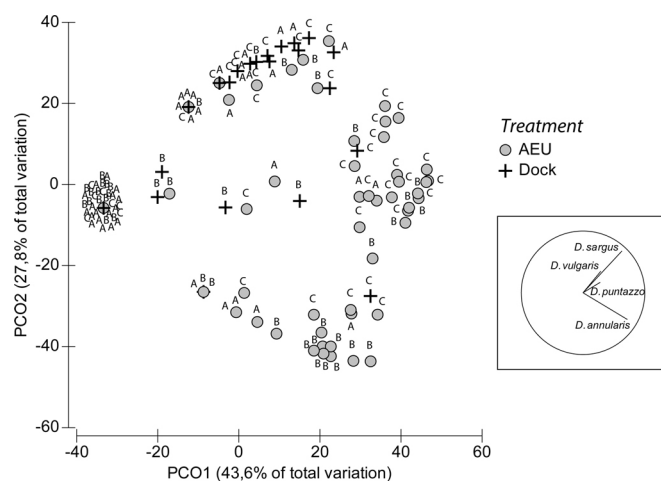


Fig. 4. PCoA plot for fish assemblages on AEU (gray circles) and control docks (black cross) for area A, B and C (labels). The dominant species correlated to similarity between the samples (Pearson coefficient >0.2) are shown as vectors beside the plot.

for samples from area C. AEU samples segregate according to both axes being dispatched on the left diagonal of the plot with samples from area C being mainly on top and samples from area A and B being more dispersed. According to the vectors, *D. sargus* and *D. annularis* are the main contributors to the differentiation between treatments and areas.

Table 2
Fish species found on the AEU and control dock for the three areas with all surveys pooled.

Family	Species	Common name	Area A		Area B		Area C	
			AEU	Control	AEU	Control	AEU	Control
Atherinopsidae	<i>Atherina</i> sp.	Sand smelt				+		+
Blenniidae	Blenniidae	Blennies	+		+			+
Gobiidae	Gobiidae	Gobies	+	+	+			+
Labridae	<i>Ctenolabrus rupestris</i>	Goldsinny wrasse						+
	<i>Symphodus roissali</i>	Five-spotted wrasse			+			+
	<i>Symphodus</i> sp.	Wrasses			+			+
Mugilidae	Mugilidae	Grey mullets						
Mullidae	<i>Mullus</i> spp.	Red mullets						+
Sparidae	<i>Diplodus annularis</i>	Annular seabream	+		+	+		+
	<i>Diplodus cervinus</i>	Zebra seabream						
	<i>Diplodus puntazzo</i>	Sharpnout seabream	+	+	+			+
	<i>Diplodus sargus</i>	White seabream	+	+	+	+		+
	<i>Diplodus vulgaris</i>	Common two-banded seabream		+		+		+
	<i>Oblada melanura</i>	Saddled seabream						+
	<i>Sarpa salpa</i>	Salema porgy		+	+	+		+
Tripterygiidae	<i>Trypetergion</i> sp.	Threefin blenny			+			+

Table 3
SIMPER analysis showing the contribution of the different fish species to dissimilarity between (A) treatments and (B) areas. Av.Abund: average abundance (in number of individuals by 10 m), Av.Diss: average distance, Diss/SD: dissimilarity/standard deviation Contrib%: contribution percentage, Cum.%: cumulative contribution percentage. Cut for low contributions was fixed at 90% cumulated contribution.

(A) SIMPER table of results habitat groups						
Av.Diss = 87.25	Group Biohut	Group Dock				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>D. annularis</i>	1.18	0.09	28.01	1.12	32.10	32.10
<i>D. sargus</i>	0.74	0.60	25.21	0.90	28.90	61.00
<i>Symphodius</i> sp.	0.39	0.00	10.01	0.51	11.47	72.47
<i>S. salpa</i>	0.18	0.18	6.54	0.40	7.50	79.97
<i>D. vulgaris</i>	0.10	0.15	3.94	0.47	4.51	84.49
Gobies	0.15	0.00	3.16	0.41	3.62	88.11
Blennies	0.13	0.00	2.34	0.37	2.68	90.79
(B) SIMPER table of results zone groups						
Av.Diss = 79.35	Group 160	Group 123				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>D. sargus</i>	1.12	0.34	31.15	0.92	39.26	39.26
<i>D. annularis</i>	0.91	0.75	13.00	0.71	16.39	55.65
<i>S. salpa</i>	0.30	0.20	7.81	0.44	9.84	65.50
<i>Symphodius</i> sp.	0.02	0.57	7.68	0.68	9.68	75.18
<i>D. vulgaris</i>	0.26	0.04	7.16	0.49	9.02	84.20
<i>Atherina</i> sp.	0.15	0.08	3.63	0.26	4.57	88.77
Gobies	0.17	0.02	2.39	0.49	3.01	91.78
Av.Diss = 77.34	Group 160	Group 108				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>D. sargus</i>	1.12	0.55	34.50	1.07	44.60	44.60
<i>D. annularis</i>	0.91	0.26	16.14	0.75	20.87	65.47
<i>D. vulgaris</i>	0.26	0.07	6.61	0.60	8.55	74.03
<i>S. salpa</i>	0.30	0.04	4.93	0.36	6.38	80.41
Gobies	0.17	0.04	4.00	0.44	5.17	85.58
Blennies	0.16	0.02	2.76	0.49	3.57	89.15
<i>Symphodius</i> sp.	0.13	0.00	2.38	0.40	3.08	92.23
Av.Diss = 79.35	Group 123	Group 108				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>D. sargus</i>	0.34	0.55	33.01	0.95	37.71	37.71
<i>D. annularis</i>	0.75	0.26	18.49	0.81	21.13	58.83
<i>Symphodius</i> sp.	0.57	0.00	14.56	0.68	16.63	75.46
<i>S. salpa</i>	0.20	0.04	8.07	0.41	9.22	84.68
<i>D. vulgaris</i>	0.04	0.07	4.79	0.32	5.47	90.15

This result is corroborated by the SIMPER analysis, which revealed high levels of dissimilarity between treatments and areas, in both cases mainly due to *D. annularis* and *D. sargus* (Table 3).

Symphodus sp. also contributes to the dissimilarity between treatments and between area A and B, while *S. salpa* and *D. vulgaris* are

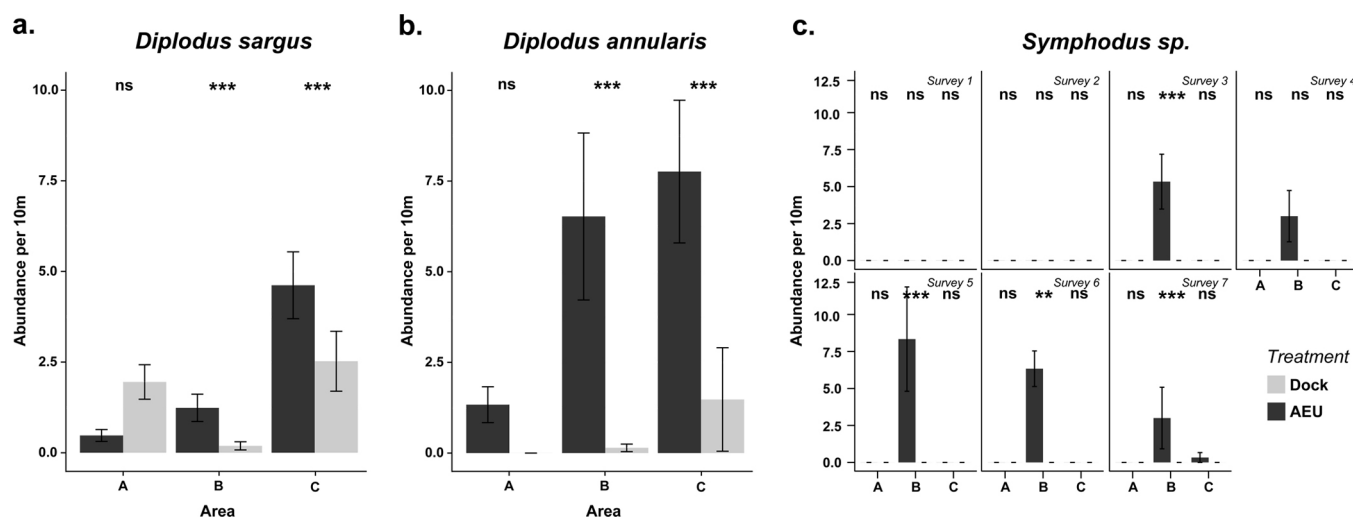


Fig. 5. Mean (\pm SE) taxa-specific densities according to significant interaction factor. (a) *Diplodus sargus* by area and treatment, (b) *Diplodus annularis* also by area and treatment and *Symphodus sp.* for all seven survey by area and treatment. Significant p -value: * <0.05 ; ** <0.01 ; *** <0.001 , ns = non significant.

the third contributors to dissimilarity between areas C and B, and C and A respectively (Table 3).

As *D. annularis*, *D. sargus* and *Symphodus sp.* are the main contributors to dissimilarity between treatments and areas (Table 3), they represent good indicators to assess the effect of the different factors on assemblage variability. Analysis of the variations in taxa-specific density of those species showed contrasting patterns according to species (Fig. 5). For instance, for *D. sargus* the interaction of the factors treatment and area was significant (PERMANOVA, $F = 7.25$, $p = 0.002$) with higher densities on AEU for area B (1.24 ± 0.38 individuals/10 m against 0.19 ± 0.11 on docks, pair-wise test = 0.007), no difference for area C and higher densities on docks for area A (1.95 ± 0.48 against 0.48 ± 0.16 for AEU, pair-wise test = 0.002) (Fig. 5A). *D. annularis* showed the strongest answer to treatment. Similar to *D. sargus*, a significant interaction between treatment and area was detected (PERMANOVA, $F = 4.73$, $p = 0.009$) but with significantly higher densities on AEU for the three areas (1.34 ± 0.49 , 6.52 ± 2.30 and 7.76 ± 1.97 individuals/10 m against 0, 0.14 ± 0.10 and 1.48 ± 1.43 for areas A, B and C respectively) (Fig. 5B). Densities of *Symphodus sp.* were significantly different according to the interaction factor survey \times area \times treatment (PERMANOVA, $F = 5.14$, $p = 0.001$) with individuals present exclusively on the AEU as of the third survey on area B and only on the last one for area C (Fig. 5C).

In addition to their response to treatment, total taxa-specific densities (all areas and all treatments pooled) showed taxa-specific variation throughout the surveys. Densities of *D. sargus* and *Symphodus sp.* were relatively constant throughout the whole sampling period while *D. annularis* exhibited densities which reached a peak on the second survey and then decreased until the end of sampling (Fig. 6).

4. Discussion

This study proved the feasibility of implementing the small artificial units approach to a large commercial port and its role as a tool to improve the nursery value of such infrastructures. By complexifying habitat structure, these infrastructures can support greater juvenile fish densities and higher species richness, with however large spatial variations.

4.1. Ports as juvenile fish habitats

The presence of juvenile fish has already been recorded on breakwaters, jetties (Clynick, 2006, 2008; Pastor et al., 2013; Ruitton et al., 2000) and more recently inside marinas (Bouchoucha et al., 2016; Clynick, 2006, 2008; Dufour et al., 2009), but this is the first study to focus on the potential use of a large commercial port by fish during early life stages. Although the characteristics of such infrastructures cause us to think of them as poor candidates for successful settlement, our results suggest that at least some locations may host juveniles, particularly on the artificial habitats that we tested. The species observed during this study are typical to shallow water habitats known as nurseries, such as rocky bottoms, but also, and more surprisingly, *Posidonia oceanica* meadows and *Cystoseira*. Most *Diplodus* spp. are known to recruit in very shallow rocky bottoms (<2 m) with gentle slopes with the exception of *Diplodus annularis* whose settlement preferentially occurs in *Posidonia oceanica* meadows between 5 and 8 m depth (Harmelin-Vivien et al., 1995). As for *Symphodus sp.*, they usually settle in macro algae forests, from 2 to 4 m depth (Cheminée et al., 2013; García-Rubies and Macpherson, 1995). The settlement of the *D. annularis* and *Symphodus sp.* on the port's hard structures suggests a higher than expected plasticity in juvenile habitat requirements, a result also found by Bouchoucha et al. (2016) who observed juvenile *D. annularis* in different Mediterranean marinas. One of their hypotheses was that as pelagic larvae often settle on the first suitable habitat encountered (Shapiro, 1987), the presence of juveniles in the port could result from lacking nearby suitable habitat, however, in our case, *Posidonia oceanica* meadows are present right at the entrance of the port. Therefore, an active selection of anthropogenic structure by the post-larvae cannot be excluded. High productivity and relatively low wave action could represent favorable conditions for post-larvae settlement (Clynick, 2006; Romer, 1990), which might explain juvenile presence in the port. Additionally, strong light intensity generated by the city may attract the larvae during the night (Longcore and Rich, 2004; Munday et al., 1998) resulting in a greater number of them reaching the shore in urbanized areas and especially inside ports.

Densities display high spatial variations. Such variations were also observed by Bouchoucha et al. (2016) between marinas, with the hypothesis being that differences in location and physico-chemical conditions explain the success or failure of *Diplodus* settlement. In the case of the Marseille port, the same hypothesis

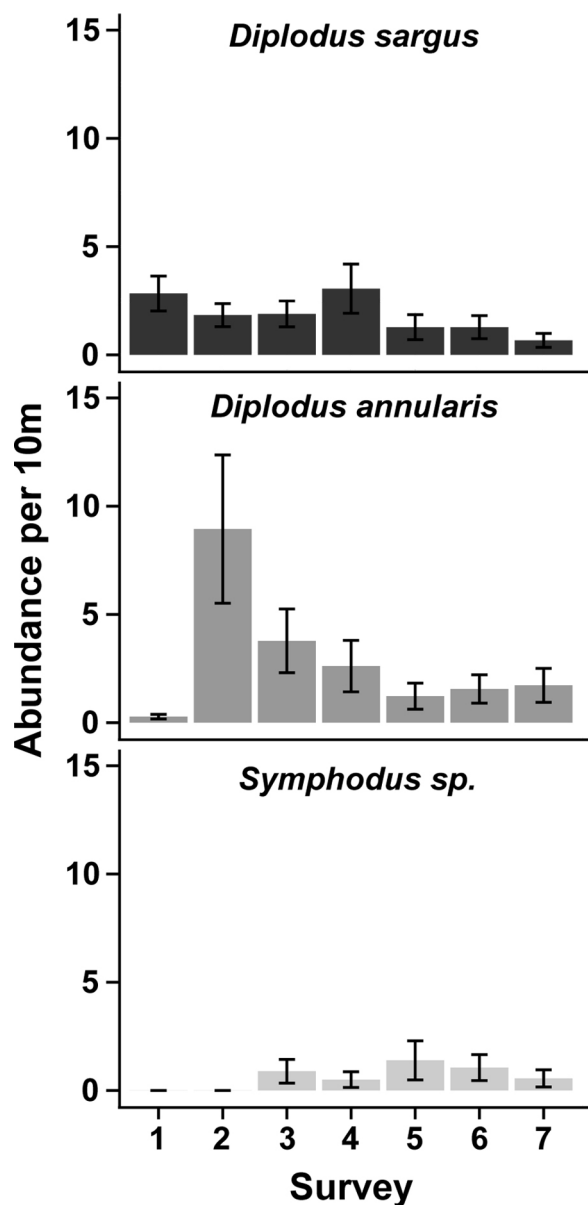


Fig. 6. Mean (\pm SE) taxa-specific densities per survey (from June to September) for all treatments and areas pooled, (a) *Diplodus sargus*, (b) *Diplodus annularis*, and *Symphodus sp.*

might be put forward to explain the observed disparity. The port is so large that each harbor composing it may have its own level and nature of anthropic pressures leading to particular structural and physico-chemical characteristics. Some locations submitted to frequent large ship traffic (e.g. area B) might undergo higher wave and current exposure, which could influence the arrival of the juveniles as well as their survival. Low densities (such as for area A) may be due to other factors such as pollution or higher salinity variations, as this area is exposed to high freshwater discharge and exhibits the highest concentrations of all contaminants (Table 1). Chemical pollution is known to have adverse effects on fish physiology and may affect juvenile growth and survival (Kerambrun et al., 2012; Marchand et al., 2003). Contamination levels in ports and their impact on juvenile fitness should be investigated in order to determine the real potential of urban ecosystems as nursery grounds for fish. The depth of the port (between 6 and 8 m for the studied areas) would have been expected to be a limiting factor for successful settlement, preventing the presence of most juveniles in such

environments. However, juveniles were observed in the 3 sampling areas despite the depth.

Sampling was done during the summer months which is a time period covering the settlement of most coastal fish species (Crec'hriou et al., 2015; Ventura et al., 2014). Indeed, the arrival peak of *D. annularis* was clearly observed in this study (survey 2), followed by a decrease in densities, which might be due to mortality (caused by predation and/or competition for food and space) but also by their potential displacement to adjacent habitats (Macpherson, 1998; Ventura et al., 2014; Vigliola and Harmelin-Vivien, 2001). *D. sargus* were also well represented in the port but no peak was observed suggesting that settlement had occurred before the beginning of sampling. This hypothesis is corroborated by the observation of numerous small juveniles at the end of May on adjacent habitats (authors personal observations). Other species that settle in summer were observed such as *Symphodus sp.*, *Mullus sp.* or *O. melanura* but in low densities suggesting poor larvae supply or inadequate habitat for those juveniles. Species settling during fall or winter, such as the highly commercially valued gilt-head sea bream *Sparus aurata* or the sea bass *Dicentrarchus labrax*, might also use ports as juvenile habitat. Extending the sampling period to study the use of such infrastructure as potential nurseries for those species could be of good interest.

4.2. Nursery value enhancement by the use of small artificial units

Our results showed that increasing habitat structural complexity by the use of small artificial units proved efficient in augmenting juvenile fish abundance, which could minimize the detrimental effect of the infrastructure on the nursery function. Indeed, greater species richness and juvenile densities were observed on the AEU compared to bare dock. This study is comparable to Bouchoucha et al. (2016) results obtained in five marinas using this kind of rehabilitation approach. Even if our results support the working hypothesis according to which habitat complexification would enhance the port's nursery value, some points need to be qualified. High spatial variation in the juvenile response to habitat complexification is one of them. In fact, in certain locations the addition of artificial habitats seemed to have no effect (e.g. Area A), while in others they supported greater abundances (e.g. Areas B and C). This spatial variations might be linked to the one mentioned above for settlement. Comprehending the factors that may lead to successful settlement (larvae supply and juvenile survival) in urbanized ecosystems should be a priority in future studies in order to target rehabilitation efforts on the most appropriate sites. Undoubtedly, determining which parts of each port would benefit most from being equipped by AUE would help to increase the cost-efficiency of rehabilitation programs.

Additionally, we need a better understanding of the processes behind the higher abundances recorded on the AEU. This result could be explained by two hypotheses. AEU are designed to provide higher complexity habitats with appropriate cavity sizes, which could increase juvenile survival by providing more places for refuge and thereby limit predator induced mortality (Ammann, 2004; Bulleri and Chapman, 2010; Hixon, 1991; Vigliola et al., 1998). Nonetheless, the concentration of juveniles on the AEU could also be an explanation since hard complex structures are known to attract fish in a pelagic environment (Ammann, 2004). Similar to artificial reefs studies, determining the contribution of each process, production through reduced mortality on one hand and concentration through thigmotaxis on the other, is challenging but essential to evaluate the efficiency of these structures in their role as nurseries and in long-term fish population maintenance (Grossman et al., 1997). These questions could partly be answered through the study of growth rates on different habitats (AEU, dock, riprap, nat-

ural rocky habitats, etc.) by following size class evolution through time (Bouchoucha et al., 2016) or using otoliths.

The observed patterns were different for the three most abundant species found in the port suggesting taxa-specific variations in the responses to habitat complexification through the use of small artificial units. *D. annularis* showed the strongest positive answer to the presence of AEU with higher abundances in all areas. However, the individuals observed were young settlers, and following them over a longer period of time would have been interesting in order to know if this tendency remains until recruitment into the adult population. As mentioned above, the observation of this species on hard structures was surprising and raises new questions concerning its behavioral plasticity. The inconsistent response of *D. sargus* makes it hard to conclude on the efficiency of the method for this species. However, the absence of temporal variation in its abundance might imply that post-larvae settlement occurred outside the sampling window and that we missed the abundance peak usually observed during the settlement phase which occurs in June for this species (Crec'hriou et al., 2015). Also, younger (and so smaller) individuals are known to be strongly associated with their preferential sheltered habitat but they extend their territory as they grow bigger as they are less vulnerable to predation (Houde and Hoyt, 1987; Macpherson, 1998; Vigliola et al., 1998). This could explain the lack of a clear pattern in *D. sargus* habitat use, which might have been more distinct for earlier stages. Indeed, inside marinas, the youngest juveniles of this species have been found to have a stronger association to AEU than older life stages (Bouchoucha et al., 2016). *Symphodus* sp. were present almost exclusively on area B's AEU, but more data is needed to be able to make accurate conclusions on the effect of the rehabilitation procedure on this taxon. The youngest individuals of this genus are hard to observe, even in natural habitats. An adaptation of the sampling procedure might be required for their study.

Usually, the goals of a restoration project are defined in regards to a reference, an ecosystem or a set of various attributes from different ecosystems, which would serve as target when planning and evaluating a restoration or rehabilitation program (Balaguer et al., 2014; SER, 2002). In this rehabilitation project, the objective was above all to give a nursery function to the port by complexifying habitat structure through the use of small artificial habitats. In order to test the effect of the artificial habitats on juvenile fish, we only compared our complex docks to the degraded state represented by bare featureless vertical docks. It was the original and novel aspect of this approach that was targeted, and this study represents the first step toward more integrated rehabilitation projects of port infrastructures. Forthcoming projects concerning nursery function rehabilitation should incorporate the study of nearby natural nursery grounds in order to evaluate the relative value of rehabilitated habitat and the efficiency of the tools and methods used.

5. Conclusion

Even though our study is lacking comparison with natural habitats and was conducted over a short period of time, our results demonstrate the clear role of the AEU to support juvenile fish through habitat complexification. Further studies would be useful to quantify the ecological gain provided by these infrastructures, and to gain a better understanding of the functioning of urbanized ecosystems in order to manage and restore them in the best possible way.

This kind of rehabilitation program is now possible thanks to the efforts by port managers to increase water quality by limiting all sorts of pollution (i.e. reject from boat fairing areas, gray and black water discharges, etc.). They also help to determine the presence and diversity of marine organisms within ports and marinas and

are increasingly committed to the preservation of marine life. This is particularly true in the case of fish for which the improvement of survival and growth rates by means of good water conditions is seen as a way to sustain local fisheries. Recently, the French National Water Agency has integrated these kinds of actions into the French program proposal to the Marine Strategy Framework Directive, which should promote ecological restoration programs in coastal areas and particularly in ports, harbors and marinas.

Although eco-conception should be favored when building new structures or undertaking maintenance, the small artificial habitat approach can be used as a good complementary tool for existing hard coastal structures. Their potential should not be underestimated. Indeed, their easy installation and non-permanent character are more easily accepted by port managers and users and therefore might help to create good environmental dynamics or even to initiate bigger restoration projects.

Acknowledgements

The authors are grateful to the managers of the Grand Port Maritime de Marseille for their help in obtaining authorizations for the installation of the Biohut[®] and the realization of the monitoring by Underwater Visual Census. We also want to thank Ecocean for the installation and maintenance of the Biohut[®] as well as the French Water Agency for financial support (GIREL program). We are thankful to two anonymous reviewers who helped improve the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.03.022>.

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Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Shallow rocky nursery habitat for fish: Spatial variability of juvenile fishes among this poorly protected essential habitat



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ARTICLE INFO

Article history:

Received 18 December 2016
Received in revised form 6 March 2017
Accepted 25 March 2017
Available online 13 April 2017

Keywords:

Nursery
Juvenile fish
Key habitat availability
MPAs
Coastal management
Mediterranean

ABSTRACT

Coastal nursery habitats are essential for the renewal of adult fish populations. We quantified the availability of a coastal nursery habitat (shallow heterogeneous rocky bottoms) and the spatial variability of its juvenile fish populations along 250 km of the Catalan coastline (France and Spain). Nurseries were present in 27% of the coastline, but only 2% of them benefited from strict protection status. For nine taxa characteristic of this habitat, total juvenile densities varied significantly between nursery sites along the coastline, with the highest densities being found on the northern sites. Recruitment level (i.e. a proxy of nursery value) was not explained by protection level, but it was moderately and positively correlated with an anthropization index. Patterns of spatial variations were taxa-specific. Exceptional observations of four juveniles of the protected grouper *Epinephelus marginatus* were recorded. Our data on habitat availability and recruitment levels provides important informations which help to focus MPA management efforts.

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1. Introduction

Due to an ever growing global population and a general migration to coastal areas, oceans and seas are experiencing an unprecedented variety and magnitude of anthropogenic pressures. The Mediterranean, a semi-enclosed basin surrounded by inhabited land, is particularly susceptible to the effects of human induced pressures (Coll et al., 2010). This translates into a greater use of resources and increased modification of natural habitats, just to name a couple of the many consequences. In this context, coastal areas represent great stakes: they contain habitats essential for species life cycles as well as concentrating a maximum of anthropogenic disturbances.

Many coastal fish have a complex life cycle composed of a pelagic and a benthic stage. For many Mediterranean necto-benthic coastal species, eggs are released into the water column and generally hatch after two days, producing larvae that develop in pelagic waters for more than a month before migrating towards the shore (Di Franco et al., 2013). At the shore, post-larvae undergo “settlement”, i.e. the transition from the pelagic larval habitat and establishment to the benthic juvenile habitat. Among juvenile habitats, nursery habitats are the one(s) that, for a

particular species, have a greater “nursery value”, i.e. contributes a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other habitats. The “nursery value” of a habitat results from a combination of four parameters: (1) the initial density of juveniles (“settlers”), (2) their survival rate, (3) their growth rate within these habitats and (4) their ability to move from the juvenile habitat and recruit into the adult habitat at the end of the post-settlement phase (Beck et al., 2001). The settlement period and juvenile nursery habitat can vary depending on the species to avoid inter-specific as well as intra-specific competition (Harmelin-Vivien et al., 1995).

In the Mediterranean, various Sparidae species of commercial and ecological importance use nurseries characterized as shallow coastal areas comprised of a heterogeneous rocky and sandy substrate (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). In the case of *Diplodus* species, after about 4 to 6 months, when the juveniles have reached about 6 to 8 cm of total length (TL), the recruitment stage occurs. The now sub-adults (“recruits”) leave the nursery habitat and disperse into the different and/or more diverse adult habitat(s) where they are integrated into shoals of older individuals (Macpherson, 1998; Vigliola and Harmelin-Vivien, 2001). The number of juveniles remaining in a nursery area before recruitment, at a given time, can be used to assess the nursery settlement success and final recruitment “level” (Macpherson and Zika, 1999), as a proxy of its nursery value, and can be compared between sites.

The alteration or transformation (let alone destruction) of a nursery habitat directly affects the life cycle of many species of fish by reducing

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its nursery value, and ultimately is detrimental to conservation efforts (Cheminée et al., 2016; Harmelin-Vivien et al., 1995). Because nursery habitats are essential in the life cycle of fish and the renewal of adult populations, protecting them should be a priority. Nevertheless, data on nursery habitat localization and site nursery value are often missing, preventing coastal managers from efficiently focusing their conservation efforts (Cheminée et al., 2014).

We studied one type of Mediterranean nursery habitat for fish, consisting of shallow (0 to 2 m depth) heterogeneous rocky bottoms made of blocks, pebbles and sand. We aimed to assess at a large spatial scale (>200 km long stretch of coastline) (1) the availability of this key habitat, (2) the spatial variation of juvenile fish population descriptors among this habitat (i.e. between sites displaying this given habitat) and (3) their response to anthropization and protection levels. The

overall goal was to better understand nursery habitat efficiency and provide key data and proposals to coastal managers.

2. Materials and methods

2.1. Study sites and sampling strategy

The sampled area spans 238.3 km of Mediterranean coastline from Leucate, France (FR) to Roses, Spain (ES). First, nursery sites were identified using aerial images and confirmed in situ (in a subset of sites) during surveying. Nurseries are defined as portions of the coast displaying suitable habitat according to the following criteria: protected from strong swell, shallow (0–2 m depth), gently sloping heterogeneous bottoms of mixed substratum composed of blocks, pebbles and sand

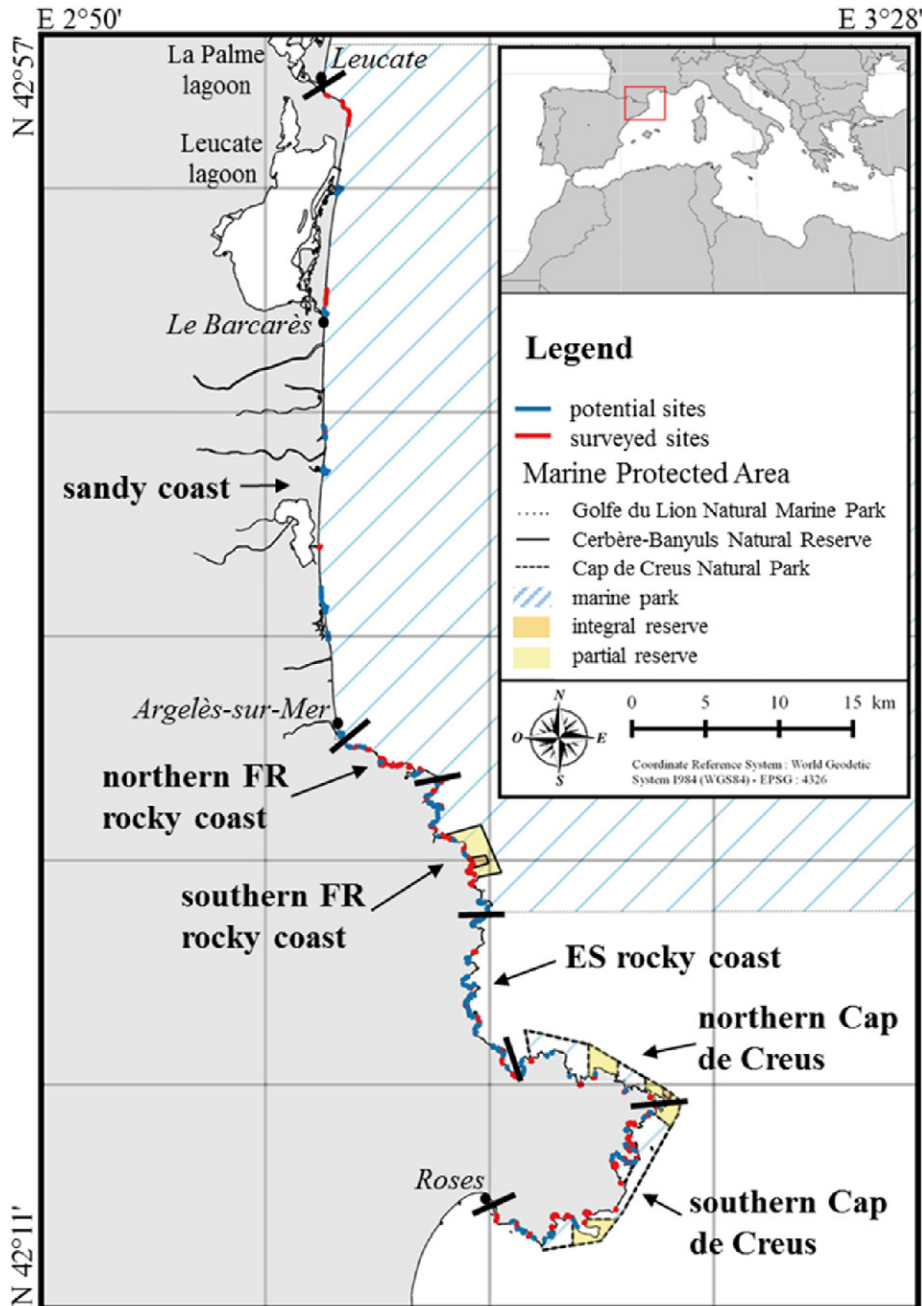


Fig. 1. Study area and all nursery sites that were identified along the coastline (red and blue stretches). Presented data comes from surveyed sites (in red). Other non-surveyed nurseries are indicated (in blue). Coastline was divided into 6 sectors for analysis (black arrows). Protection levels (Marine Protected Area zones) are identified.

Table 1

Length, percentage of nursery habitats and juvenile abundance by sector. Taxa: dc = *Diplodus cervinus*; dd = *Dentex dentex*; dp = *Diplodus puntazzo*; ds = *Diplodus sargus*; em = *Epinephelus marginatus*; pa = *Pagellus* spp.; pp = *Pagrus pagrus*; sv = *Sphyræna viridensis*; tp = *Thalassoma pavo*.

Sector	Length (km)	Surveyed nurseries (km) (number of sites)	Other potential nurseries (km) (number of sites)	Total nurseries (km)	% of coastline that is nursery (number of sites)	Number of juvenile individuals surveyed per taxa									
						ds	pa	sv	dp	em	dd	dc	pp	tp	Total
Sandy coast	56.7	3.4 (16)	8.3 (24)	11.7	21% (39)	2499	1878	135	7	0	1	1	0	0	4521
Northern FR rocky coast	16.7	4.8 (10)	1.8 (4)	6.6	39% (14)	620	26	112	63	0	0	0	0	0	821
Southern FR rocky coast	26.3	8.0 (17)	4.9 (13)	12.9	49% (30)	611	246	102	7	1	0	0	0	0	967
ES rocky coast	40.5	4.1 (9)	9.0 (26)	13.1	32% (35)	524	11	76	33	0	1	0	0	0	645
Northern Cap de Creus	60.8	6.3 (13)	3.6 (18)	9.9	16% (31)	560	379	151	61	0	0	0	1	0	1152
Southern Cap de Creus	37.3	6.9 (17)	3.8 (17)	10.7	29% (34)	1273	240	416	110	3	1	0	0	1	2044
Total	238.2	33.5 (82)	31.4 (102)	64.9	27.2% (184)	6087	2780	992	281	4	3	1	1	1	10,150

(knowing that sand alone is not the most suitable habitat) (Cheminée et al., 2011; Cuadros et al., 2017; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). See Cuadros et al. (2017) for a pictured illustration of the suitable habitat. Nursery sites were identified and measured on ortho-photographs at a scale of 1:7000. As in Cheminée et al. (2014), a nursery site was identified as a stretch of coastline displaying a continuous portion of suitable habitat (see Sup. Fig. SF1). The length of nursery sites is therefore variable, although another study estimated that the length of nursery sites in 16 different Mediterranean zones was on average $62 \text{ m} \pm 6.8 \text{ m}$ (SE) (Authors unpublished data). Aerial picture analysis was performed using QGIS 2.14 (QGIS Development Team, 2016). These sites can consist of natural or artificial structures as long as they adhere to the aforementioned requirements. A total of 184 nursery sites were located through aerial picture analysis (see Results). Their full cartography (see Sup. Fig. SF1) has been provided to MPA managers of the area (Zawadzki et al., 2015). Of these, we randomly sampled 82 sites spread in 6 sectors along this coast (Fig. 1, Table 1). This field work allowed us to validate the picture analysis criteria and to conduct a visual census of juvenile fish. Afterwards, once ground validation had been done in this subset of sites, the remaining 102 sites were considered as potential nurseries (even though not surveyed). Studied sectors displayed sites with similar habitat type. For example, sites from the sector “sandy coast” were selected to include both some breakwaters as well as rocky natural sites. This allowed us to further discuss density patterns of juveniles between sectors without any bias of habitat type since it is considered constant.

2.2. Study species

We counted every necto-benthic species that we observed in the studied habitat. In study sites, juvenile fish assemblages were described using several descriptors: total abundances (all studied taxa together), assemblage composition (relative abundances of the studied taxa), and taxa-specific abundances. We present data for eleven species that utilized heterogeneous rocky and sandy habitats as nurseries. They were grouped into the following nine taxa (Table 2, Sup. Fig. SF2): white seabream (*Diplodus sargus*, Linnaeus, 1758), sharpnose seabream (*Diplodus puntazzo*, Walbaum 1792), yellowmouth barracuda

(*Sphyræna viridensis*, Cuvier 1829), ornate wrasse (*Thalassoma pavo*, Linnaeus 1758), dusky grouper (*Epinephelus marginatus*, Lowe 1834), zebra seabream (*Diplodus cervinus*, Lowe 1838), red porgy (*Pagrus pagrus*, Linnaeus 1758), common dentex (*Dentex dentex*, Linnaeus 1758) and *Pagellus* spp. (including the axillary seabream (*Pagellus acarne*, Risso 1827), common pandora (*Pagellus erythrinus*, Linnaeus 1758) and the blackspot seabream (*Pagellus bogaraveo*, Brünnich 1768) which are difficult to differentiate at the juvenile stage). *Pagellus* spp. was studied separately and then excluded from the average densities (all taxa together) and assemblage structure analyses because *P. acarne* and *P. bogaraveo* are not found exclusively on rocky habitats and are often found in large schools. Opportunistic species, which have previously been documented as more ubiquitous in term of juvenile habitat choice, were excluded from the presented data. This includes *Sarpa salpa*, *Diplodus vulgaris* and *Oblada melanura* (Cheminée et al., 2011; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola, 1998).

2.3. Fish sampling procedure

In each of the 82 surveyed sites (i.e. replicates), for each studied species, juvenile abundances were monitored once, during the last ten days of July 2015. This allowed us to take into account not only settlers from July but juveniles from a longer period of time as well (from previous September to July) (Crec'hriou et al., 2015; Froese and Pauly, 2011; Garcia-Rubies and Macpherson, 1995; Lejeune, 1985; Raventos and Macpherson, 2001). By doing so, we did not aim to consider the settlement peak of a given species, but rather we performed an estimate of the recruitment level for a variety of species, i.e. quantifying the remaining juveniles after an arbitrary period of time following settlement (sensu Macpherson and Zika (1999)). Juveniles were counted along 1-meter-wide belt-transects parallel to the shoreline, among the previously described habitat. The same divers, previously inter-calibrated, performed underwater visual censuses (UVC) of juvenile fishes as described in previous works (Cheminée et al., 2011; Cuadros, 2015; Cuadros et al., 2017; Macpherson, 1998; Pastor et al., 2013; Vigliola et al., 1998). The diver recorded the abundance and size per taxa of benthic juveniles. The total length (TL) of individuals ($\pm 0.5 \text{ cm}$) was estimated with the help of fish silhouettes of different sizes on a submersible slate. TL estimates were used *a posteriori* in order to study only juvenile individuals (Table 2). Rough sea and poor visibility days were avoided.

For most rocky reef fishes in the Mediterranean, size at settlement is around 10 mm TL (Cheminée et al., 2013; Crec'hriou et al., 2015; Garcia-Rubies and Macpherson, 1995). The smallest specimens of the taxa studied were considered newly settled individuals. Our visual censuses took into account the young of the year (y0 individuals) and size-classes that may correspond to young of the previous year ($y + 1$) (Table 2). At this stage most of the mortality has already occurred so the densities observed are a proxy of what should recruit into the adult population (Macpherson and Zika, 1999). *Thalassoma pavo* is a stenotherm species affiliated to warmer waters from southern parts of the Mediterranean. However, data from the last 20 years suggest a

Table 2

Code and maximum juvenile Total Length (TL) considered for each of the nine surveyed taxa (eleven species in total).

Genus	Species	Code	TL (mm)
<i>Diplodus</i>	<i>sargus</i>	ds	80
<i>Diplodus</i>	<i>puntazzo</i>	dp	90
<i>Sphyræna</i>	<i>viridensis</i>	sv	150
<i>Dentex</i>	<i>dentex</i>	dd	90
<i>Diplodus</i>	<i>cervinus</i>	dc	90
<i>Epinephelus</i>	<i>marginatus</i>	em	200
<i>Pagellus</i>	spp.	pa	90
<i>Pagrus</i>	<i>pagrus</i>	pp	90
<i>Thalassoma</i>	<i>pavo</i>	tp	50

shift in its geographical range concomitant with global change and the warming of the Mediterranean (Guidetti et al., 2002; Milazzo et al., 2016). In the northern Mediterranean coasts, juveniles are still very rare and the detection of adult specimens is important data, as it indicates the shift of its expansion range towards the north. For this reason, we recorded all sizes of this species.

2.4. Study design and data analysis

Using sites ($n = 82$) as replication units, we tested the effect of explaining factors (i.e. spatial location, protection level and anthropization level of sites) on the descriptors of juvenile assemblages (i.e. total abundances (all taxa together), assemblage composition (relative abundances of the studied taxa), and taxa-specific abundances). This sampling strategy aimed to test for the variability of juvenile descriptors, at a given time, for a given habitat type, for a given set of species. We did not aim to compare e.g. absolute abundance between species. This would have been irrelevant since different species settle at different time of the year. It is rather the spatial pattern of each descriptor that is discussed and differences between species are only discussed in terms of the relative differences in spatial patterns.

First, the eighty-two surveyed nursery sites (i.e. replicates) were grouped into 6 spatial sectors: sandy coast, northern French (FR) rocky coast, southern French (FR) rocky coast, Spanish (ES) rocky coast, northern Cap de Creus and southern Cap de Creus (Fig. 1, Table 1). Within each sector, sites displayed similar topography, orientation, protection and/or jurisdiction.

Secondly, there exist three Marine Protected Areas (MPAs) along this zone: the Gulf of Lion Natural Marine Park (established 2011, 4019 km²), the Cerbère-Banyuls Natural Marine Reserve (est. 1974, 6.5 km²), and the Cap de Creus Natural Park (est. 1998, 30.7 km²). For a subset of three sectors that contain sites in both levels of protection (southern FR rocky coast, northern Cap de Creus, southern Cap de Creus), sites were classified into two categories according to protection levels: (P1) sites situated outside of heavily regulated or monitored water (including the Gulf of Lion Natural Marine Park) and (P2) sites situated within the partial or reinforced protection of a MPA, i.e. with protection enforced by law.

Finally, two anthropization indices, MedImpact (Mannoni et al., 2014) and Micheli et al. (2013), were used to assess the putative effect of anthropization on juvenile densities. First, we used the MedImpact index. It is derived from intertidal algal community composition along the French rocky coasts. This assessment is based on a methodology for monitoring water quality constructed from the cartography of littoral and upper-sublittoral rocky-shore communities (CARLIT, in short) (Ballesteros et al., 2007). Only the sites located on the FR rocky coast had available MedImpact data. Therefore, we tested the effect of the MedImpact anthropization index only on this spatial subset of juvenile density data. Secondly, we used the index by Micheli et al. (2013). This index aims to map the cumulative human impact on the Mediterranean Sea and Black Sea by taking into account twenty-two different drivers and seventeen different marine ecosystems and calculating the cumulative impact score for each 1 km². It designates ecologically meaningful categories to the cumulative impact scores, i.e. ecosystems that are subject to: very high (>15.52); high (12–15.52); medium high (8.47–12); medium (4.95–8.47); low (1.4–4.95); and very low impact (<1.4). Both indices are available in raster layers compatible with geographic information systems. For each index, each study site was assigned an anthropization value according to the pixel closest to or overlapping the nursery habitat. If the habitat transected several pixels, or lacked values, the average of the transected or closest pixels was calculated.

Accordingly, two factorial models and two correlation models were used to test the influence of the explanatory variables on the spatial variation of descriptors of juvenile assemblages (total abundances, composition, taxa-specific abundances) (Supplementary Table ST1). The first

model tested the influence of the fixed factor “sector” (six levels: sandy coast, northern French (FR) rocky coast, southern French (FR) rocky coast, Spanish (ES) rocky coast, northern Cap de Creus and southern Cap de Creus) on the spatial variability of the total juvenile density, assemblage structure and taxa-specific densities along the Catalan coast from Leucate, France to Roses, Spain. The second model tested the crossed effects of the fixed factor “sector” (three levels: southern FR rocky coast, northern Cap de Creus, southern Cap de Creus) and the fixed factor “protection” (two levels: P1: no regulatory protection, P2: regulatory protection) on the total juvenile density and assemblage structure in the three sectors that contain sites under both levels of protection. The third model tested the correlation between the MedImpact anthropization index (Mannoni et al., 2014) and the total juvenile density found at sites on the northern FR rocky coast and the southern FR rocky coast. The fourth model tested the correlation between the Micheli et al. (2013) anthropization index and the total juvenile density at all 82 sites.

For the factorial models, the effect of the design factors on the total juvenile density and taxa-specific densities (univariate data), was analyzed using permutational univariate ANOVAs (PERANOVAs) with the Euclidean distance. The effect of the design factors on the assemblage structure (multivariate data) was analyzed using permutational multivariate ANOVAs (PERMANOVAs) with a preliminary square root transformation of the data and the Bray-Curtis dissimilarity measure. PERANOVA and PERMANOVA pair-wise comparisons were carried out on all designs obtaining significant results from the global tests. Significant results from the assemblage structure PERMANOVAs were complimented with SIMPER tests to determine the relative contribution of each taxa to the variations in assemblage structure. p-Values were calculated by 999 random permutations of residuals under a reduced model (Anderson, 2001; Anderson and Millar, 2004). Due to the intrinsic variability of ecological data, tests were considered significant for p-values < 0.1. All factorial analyses were performed using the PERMANOVA + package for PRIMER 6 software (Anderson et al., 2008; Clarke and Gorley, 2006). The correlation models were tested using linear regression *t*-tests in R. Data pre-treatment and graphical visualizations were performed in R Environment (R_Development_Core_Team, 2013) using the library ggplot2 (Wickham, 2009).

3. Results

3.1. Nursery habitat availability and protection

We identified 184 sites (i.e. stretches of coastline) on the studied shoreline (238.3 km long) which displayed nursery habitat characteristics. These were therefore considered to be potential nurseries. These sites (including sites surveyed in situ and potential sites not surveyed) represented 64.9 km of coast, or 27% of the studied coast from Leucate to Roses (Table 1, Fig. 1). Of these 64.9 km of nursery habitat, 20.5 km (31%) were under no form of protection, 37.6 km (58%) were under limited protection in the form of natural marine parks, 5.9 km (9%) were within a partial reserve and only 1.3 km (2%) were within an integral reserve.

3.2. Spatial variation of juvenile populations

Among the 82 sampled sites, the overall juvenile abundances were dominated by four taxa (in decreasing order): *D. sargus*, *Pagellus* spp., *S. viridensis* and *D. puntazzo* (Table 1). Fewer than 5 individuals were seen for each of the other five species throughout the entire study area (Table 1).

3.2.1. Total juvenile density

The total juvenile fish densities were unevenly repartitioned among the different sectors (Fig. 2; Table 3; PERANOVA, $F = 11.324$, $p \leq 0.001$) with the sector “sandy coast” containing the highest average density

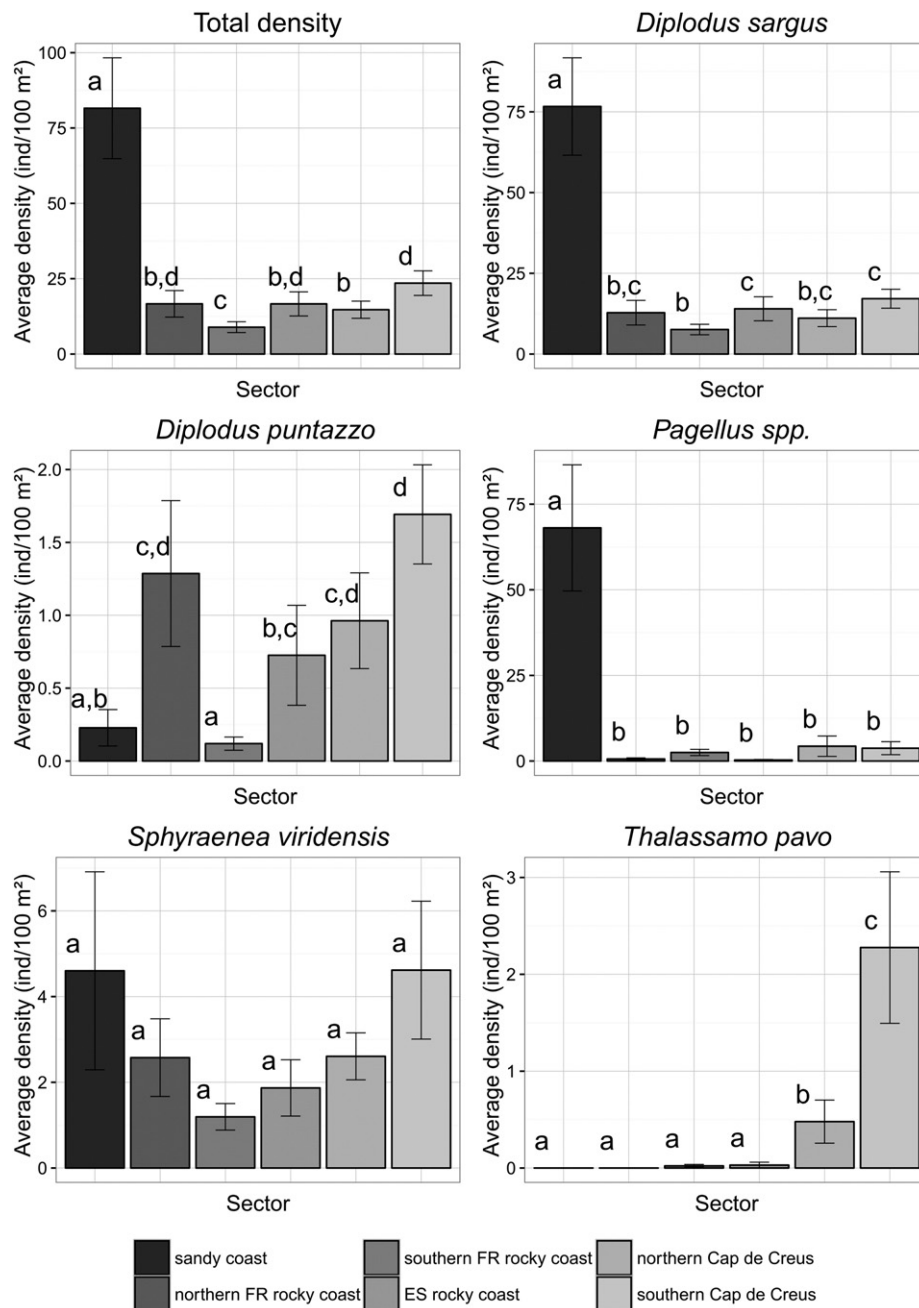


Fig. 2. Barplots of mean juvenile densities by sector. Total juvenile densities (all taxa together) and taxa-specific densities for *Diplodus sargus*, *Pagellus* spp., *Diplodus puntazzo*, *Sphyaena viridensis* and *Thalassoma pavo* (for this taxa densities include adults and juveniles); error bars = standard error. Pairwise results are given by lowercase characters: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs.

(81.6 ind/100 m² ± 16.7 (mean density ± standard error)) and being significantly different from all other sectors. The sector “southern FR rocky coast” had a significantly lower mean density than all of the other sectors (8.9 ind/100 m² ± 1.8). The sectors “northern FR rocky coast” (16.7 ind/100 m² ± 4.4), “ES rocky coast” (16.6 ind/100 m² ± 4.0), “northern Cap de Creus” (14.7 ind/100 m² ± 2.9) and “southern Cap de Creus” (23.5 ind/100 m² ± 4.1) were all situated in-between these two values with varying significant differences (pairwise tests, Fig. 2).

3.2.2. Assemblage structure and taxa-specific density

There was a significant difference in juvenile composition between sectors (Table 3; PERMANOVA, $F = 4.600$, $p \leq 0.001$). The sandy coast was the only sector that was significantly different from all other sectors. All other sectors shared a significant resemblance with at least

two other sectors always including the adjacent sector(s). The northern FR rocky coast was not significantly different from all other rocky coast sectors in terms of species compositions. In all cases *D. sargus* (SIMPER, 45%–75% contribution) is principally responsible for the dissimilarity, followed by *S. viridensis* (18%–31% contribution) and *D. puntazzo* (5%–23% contribution). The combination of these three species always makes up for >90% of the dissimilarity between sectors.

A closer look at the taxa-specific variations shows widely varying spatial patterns depending on the species. *D. sargus* and *Pagellus* spp. showed patterns very similar to that of the total juvenile density. This is not particularly surprising since *D. sargus* represented 83% of the total abundance observed in 2015. In contrast, there was no significant difference in average density of *S. viridensis* between the sectors and *D. puntazzo* had a global north to south increasing gradient but with an elevated average density in the northern French rocky coast sector (Fig. 2).

Table 3
PERANOVA/PERMANOVA table of results: effects of explanatory factors on univariate descriptor of juvenile fish assemblage (total density) and multivariate juvenile assemblage structure.

Source	Df	MS	Pseudo-F	P (perm)
Model 1. Sector				
Response variable: total density				
Secteur (Se)	5	1.1426	11.324	0.001***
Res	76	0.1009		
Total	81			
Response variable: assemblage structure				
Secteur (Se)	5	4419	4.5996	0.001***
Res	76	960.74		
Total	81			
Model 2. Protection				
Response variable: total density				
Secteur (Se)	2	5.29E-02	3.3944	0.052
Protection (Pr)	1	1.14E-02	0.73282	0.365
Sex Pr	2	1.03E-02	0.66405	0.452
Res	41	1.56E-02		
Total	46			
Response variable: assemblage structure				
Secteur (Se)	2	1776.7	2.2123	0.053
Protection (Pr)	1	488.58	0.60834	0.601
Sex Pr	2	726.93	0.90512	0.437
Res	41	803.13		
Total	46			

Significance = $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

A single juvenile of the *T. pavo* species (50 mm TL) was observed, located in one of the most southern sites ("Cadaques" bay, in southern Cap de Creus sector). Taking into account both juveniles (<55 mm TL) and adults a total of 176 individuals of this species were observed (from 50 to 150 mm TL). The southern Cap de Creus had the highest average density ($2.28 \text{ ind}/100 \text{ m}^2 \pm 0.78$) and mean densities showed a strong south to north decreasing gradient (Fig. 2). No individuals were observed on the two northern sectors (the northern FR rocky coast and sandy coast). The mean densities observed on the southern FR rocky coast ($0.02 \text{ ind}/100 \text{ m}^2 \pm 0.02$) and the ES rocky coast ($0.03 \text{ ind}/100 \text{ m}^2 \pm 0.03$), were not significantly different from 0 (Fig. 2).

We observed four juvenile *E. marginatus* in natural habitats: one in the southern FR rocky sector (Paulilles cove, 70 mm TL) and three in the southern Cap de Creus sector, at Peligri cove (120 mm TL), Joncols cove (110 mm TL) and Roses (80 mm TL) (see illustration in Sup. Fig. SF2). In each case they were located at a depth of about 1.5 to 2.0 m, sheltering in crannies between blocks and boulders of the heterogeneous rocky substratum. Finally, we observed three juvenile individuals of *D. dentex* (50, 70 and 70 mm TL), one of *D. cervinus* (50 mm TL) and one of *P. pagrus* (90 mm TL) in the entire study area (Table 1).

3.3. Protection level and anthropization index effect

The level of protection had no significant effect on the total juvenile density (Table 3; PERANOVA, $F = 0.733$, $p = 0.365$) and it had no significant effects on the assemblage structure (Table 3; PERMANOVA, $F = 0.608$, $p = 0.601$).

The MedImpact anthropization index showed a significant interaction with the overall density (Fig. 3; linear regression t -test, $F = 5.184$, $p = 0.032$); the most degraded sites displayed the highest juvenile densities. However the R^2 value of the linear regression was very low ($R^2 = 0.17$, $y = -0.3883x + 0.3415$) meaning that <20% of the variability was described by the linear model. The regression using the Micheli et al. (2013) index was not significant ($p = 0.176$).

4. Discussion

One fourth of the 240 km long coast that was evaluated displayed nursery habitat for the species on which this study focused. However, only a small portion (11%) of this essential fish habitat was under

protection (marine park, natural park or partial reserve), and even a smaller portion (2%) benefited from the highest protection level (integral reserve). Juvenile densities among nurseries varied in space but not as a function of protection level. On the other hand, they were moderately and positively correlated with an anthropization index. Juvenile densities displayed contrasting spatial patterns according to taxa. As regards rare species, it is worthwhile to note that individuals of the protected grouper *E. marginatus*, not reported in the last 20 years in this area, were seen on four occasions during this study in 2015.

4.1. Nursery habitat availability and protection

We highlighted that a small portion of the existing nursery habitat benefited from strict protection (only 2% of the nursery habitat is located in integral reserves). Furthermore, it is important to remember that protection by MPAs does not necessarily protect juvenile fish habitat from transformation or destruction. And yet it has been demonstrated

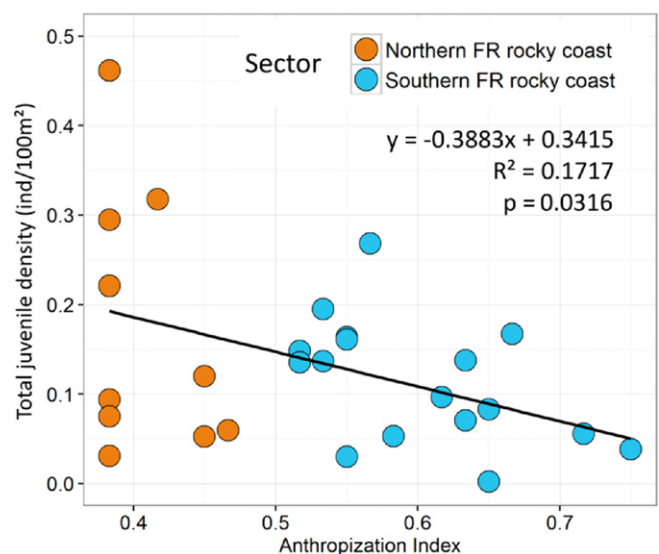


Fig. 3. MedImpact anthropization index in relation to total juvenile density per site. One dot = one site; x-axis: the index varies from 0 (most degraded) to 1.2 (least degraded).

that habitat transformation (e.g. homogenization) is detrimental for its nursery value (sensu Beck et al., 2001; Cheminée et al., 2016). From a socio-economic point of view the implementation of strong regulation in juvenile zones is difficult as they are mainly located on beaches and creeks where touristic activities and coastal developments are concentrated. In the future, managers should focus their efforts on setting up measures to adequately protect this essential habitat, notably in buffer zones or outside of regulated core areas (integral reserve). Co-management (David et al., 2003; Granek and Brown, 2005) could avoid habitat transformations by promoting alternate coastal use and management practices, for example, by avoiding beach nourishment which is a common practice that tends to homogenize habitat and may reduce its nursery value (Cheminée et al., 2014; Cuadros, 2015). For this purpose, our data has been made available to MPA managers through the edition of an atlas displaying the full cartography of nursery sites of the area (Zawadzki et al., 2015). An extract of this atlas is given as an example in Supplementary Fig. SF1.

On the other hand, the results of this study show that the protection level of sites had no significant effects on either total density of juveniles or juvenile assemblage structure. This is not surprising considering that current MPA regulation tends to focus on adult catch limitations. However some indirect effects could be expected since protection may favor potential predators of juveniles and thus influence their survival and abundances (Tupper and Juanes, 1999).

4.2. Spatial variability of juvenile population descriptors: anthropization level impact

Juvenile densities among nurseries were moderately and positively correlated with the MedImpact anthropization index. However, index values were not homogeneously spread among sites with southern sites being the most impacted. Consequently any correlation between juvenile densities and anthropization should be regarded cautiously since it might be linked to a confounding effect of space. The MedImpact anthropization index is calculated on the base of the composition of the photophilic macrophyte assemblages present in the medio-littoral (intertidal) level (Mannoni et al., 2014). The correlation between total juvenile density and the MedImpact anthropization index values, although weak, suggested that sites where composition of macroalgae assemblages, i.e. a proxy of water quality, was the most impacted supported higher densities of juveniles. However, any further correlation between juvenile densities and water quality cannot be conducted since this index may be subject to various biases. For example, this correlation may simply reflect the habitat preferences of the juveniles studied because they are known to prefer heterogeneous rocky and sandy habitats to macroalgae habitats. It would be interesting to find a way to get a direct measure of pollution and of other human pressures. This would allow a closer look at the anthropogenic pressures along this coastline to determine if and how they may have an effect on juvenile populations and habitat nursery value. In contrast with Micheli et al. (2013), others indexes could be developed at a finer spatial scale to better assess pressures such as levels of human site attendance, water and substratum contamination by micro-plastics (de Sá et al., 2015; Šiljić et al., 2015), etc.

4.3. Spatial variability of juvenile population descriptors: other possible drivers

Our results are based on samples from one single year and therefore observed patterns should be interpreted cautiously since juvenile descriptors are known to vary between years. Nonetheless, our data is useful to discuss, at a large spatial scale, for a given year, juvenile density variability and its link with possible drivers.

Our data showed that there was a significant spatial variation in the total juvenile density and assemblage structure of the juvenile assemblages along the Catalan coastline depending on the sector. The “sandy

coast” sector hosted the highest average total density of juvenile fish and a unique assemblage structure, due mainly to a very high density of *D. sargus*. The five other sectors had much lower total juvenile densities and their assemblage structures were never significantly different from those of the adjacent sector(s). These results demonstrate a spatial variation of recruitment level between sites, for a given species in a given juvenile habitat. For a given juvenile habitat, nursery value and its proxy (i.e. recruitment level) are known to vary in space and time (Beck et al., 2001; Cheminée, 2012; Macpherson and Zika, 1999). For scientists and managers, the challenge is to understand what factors drive such variability. The following paragraphs aim to present some possible explanations that should be further investigated.

Both *D. sargus* and *Pagellus* spp. had very high average densities in all sites from the sandy coast sector compared to the five other sectors. In each studied sector (e.g. the sandy coast, the northern FR rocky coast, etc), we selected and studied sites so that, on average, sectors displayed similar habitat type (see **Materials and methods section**). For example, because strictly sandy beaches are not typical nursery habitats, nursery sites from the “sandy coast” sector included both artificial structures and three natural sites at Cap Leucate (a natural rocky outcropping situated in the middle of two long stretches of sandy beach). The artificial structures in the sandy coast sector are comprised of man-made structures placed in shallow zones, primarily in the form of breakwaters and jetties. In the sandy coast sector, high densities of juveniles were observed in both natural sites and artificial structures (see **Results**). Consequently, observed juvenile density patterns are linked with the sector but not with habitat type. During a three year study by Pastor et al. (2013) the breakwaters along the sandy coast sector had higher densities, every year, than sites from the northern and southern FR rocky coast sectors. It could be hypothesized that the juveniles along the sandy coast are simply concentrated in these sites due to the absence of suitable habitat along strictly sandy stretches of the shore. However, when these densities are extrapolated according to the total length of available nursery habitat, and standardized using the total length of each sector, the sandy coast sector truly seemed to be characterized by either a much higher input of juveniles and/or a much better survival rate (see Sup. Table ST2). In comparison, the northern Cap de Creus had an even lower relative percentage of nurseries along its coast but did not boast similar densities of juveniles in its nursery habitats. Thus, for the year 2015, high densities of *D. sargus* and *Pagellus* spp. on the sandy coast may be driven rather by a notably higher initial post-larvae input and/or a better juvenile survival inside nurseries. Initial post-larvae input is mainly driven by (a) adult reproduction location and intensity, (b) the local hydrodynamics, and (c) habitat availability and accessibility. On the other hand, juvenile survival is driven notably by (d) predation pressure and (e) food availability. We discuss these alternatives in the following paragraphs.

The location of *D. sargus* adult reproduction events (a) remains a poorly explored thematic in the Mediterranean. Telemetry research programs studying the movements of adult individuals could shed light on reproduction behavior for *Diplodus sargus* and *E. marginatus* (Koeck et al., 2014; Pastor et al., 2009).

Regional hydrology (b) has a major influence on the initial larval dispersal from breeding sites, the displacement and survival of planktonic larvae, and their input towards settlement sites along the coast (Hindell et al., 2003). In the Catalan region, hydrological data suggests that there is a dominant current coming from the northeast, the “liguro-provençal” current, which could bring with it larval flow (Guizien et al., 2006; Pastor, 2008). If the majority of larvae are grouped in this current, the northern nursery sites (on the sandy coast sector) might capture the post-larvae before they travel farther south (Pastor, 2008). This might explain why between the sandy coast and the rocky coast there is a significant decrease in density. Future research on spawning grounds and Langrangian models of larval transport should be performed and may be able to clarify some of the questions raised by this data.

As regards habitat accessibility (c), most of the sites along the “sandy coast” sector are more “exposed” (i.e. accessible) since more opened towards the sea –*sensu* Cuadros et al. (2017)– than the sites from other sectors. In the area around Cap de Creus, for example, the sites are hidden within the morphology of the coastline. These enclosed coves may provide well-suited habitats for juveniles, but they may also be difficult for post-larvae to access at settlement (Cuadros, 2015; Cuadros et al., 2017). In comparison, the sandy stretches along the southern Gulf of Lion may be adapted for the success of artificial structures as potential juvenile nursery habitat because they provide easily accessible habitat where none exist. Artificial structures may even increase connectivity between natural rocky habitats and help to maintain, if not improve, biodiversity (McCormick and Makey, 1997). However it should not be forgotten that construction of any artificial structure also physically destroys previously present habitats, which may be functionally important for other species. For example, along the sandy coast, ports and jetties were often built in the opening of small estuaries connecting coastal lagoons to the sea. Such soft and flat sandy bottoms are known to be nursery grounds for flat fishes (Le Pape et al., 2003).

We used protection as a proxy of predatory pressure (d), but we could not detect any effect on juveniles (see above). On the other hand, food availability (e) can also play an important role in the quality and nursery value of juvenile habitats (Beck et al., 2001). The sandy coast and the northern FR rocky coast sectors have been subject to strong anthropic pressures resulting from the urbanization of this coastline. Development of a large agricultural industry (viticulture) has led to the input of chemical fertilizers along this coastline (Delay, 2015). Harbors and the protected areas of breakwaters are suitable for zooplankton expansion, which constitutes the staple food of juvenile fishes (Clynick, 2006). The addition of chemical fertilizers to the water around these sites might lead to blooms that could provide adequate food resources to support high densities of *Pagellus* spp. and *D. sargus* along the sandy coast. Other species such as *D. puntazzo* might not be sensitive to this driver; i.e. may not be limited by food, since they do not usually settle in such abundant shoals as usually do *D. sargus* (Cheminée et al., 2011; Vigliola et al., 1998). Further studies would be required to test the effect of food availability.

Furthermore, although high juvenile densities may seem like a positive ecological outcome, it is also true that juvenile growth rates can be density-dependent. Macpherson et al. (1997) found that *D. sargus* was subject to density-dependent mortalities and that this caused the reduction in the variability of year-class strength. Even in nursery habitats with high food availability and low predation risk, an over-population of juveniles can cause diminished growth rates (Dahlgren and Eggleston, 2000) and may be important in limiting the population (Walters and Juanes, 1993). A more detailed study of juvenile TL could help to clarify any potential negative effects that the high densities observed on the sandy coast have on juvenile growth.

In the Mediterranean, recruitment into the adult populations for *D. puntazzo* begins the end of April (Harmelin-Vivien et al., 1995). Therefore we would expect some of the juveniles to have left the nursery habitat by the time of surveying in late July. However, many juveniles remained inside nurseries, with a general north to south increasing gradient. *D. sargus* and *D. puntazzo* occupy spatially different adult habitats and nutrition (Sala and Ballesteros, 1997) but juveniles of both species depend on the same nursery habitats (Vigliola, 1998). However, the temporal repartitioning of their installation within the nursery habitat along this coastline may limit competition for resources (Harmelin-Vivien et al., 1995). A study of *D. puntazzo* juveniles during their settlement peak in the nursery habitat (October/November), along with their size-class distribution, would help to clarify questions regarding their spatial distribution.

Although there appears to be no significant difference in juvenile densities between the sectors for *S. viridensis*, there has been some question as to whether species misidentification may have occurred. It is possible that the European barracuda (*Sphyræna sphyraena*, Linnaeus,

1758) is also present along this coast. These species are difficult to differentiate during their juvenile stage but juveniles of these two species have never been identified in the same juvenile habitat, suggesting habitat segregation between them (Di Blasi et al., 2013). Surveying in subsequent years could aim to clarify this point through the capture and rearing of juveniles for proper identification.

4.4. Scarce species: even punctual observations have meaningful implications

Only one juvenile of the species *T. pavo* was observed in 2015, in the southern-most sector. Our results also show that adults in 2015 were present in the four southern-most sectors, with increasing densities towards the South. This stenotherm species is usually found on the southern Mediterranean coasts, in warmer waters. According to the maps presented in Guidetti et al. (2002) and Milazzo et al. (2016), the Gulf of Lion remain one of the last areas of the Mediterranean not populated by *T. pavo*. Generally *T. pavo* adults are the first to be observed colonizing a new area, followed by the juveniles (Figueiredo et al., 2005). Recent works highlighted the warming-related shifts of this species' distribution towards the north-western parts of the Mediterranean (Milazzo et al., 2016). Therefore the presence of a juvenile in this sector, along with the higher abundances of adults observed in the south part of the study area, may be strong indicators of this distribution shift. A yearly survey of this species would help to analyze and determine the extent and rapidity of this process.

We observed four juvenile *E. marginatus* in natural habitats in 2015, one in the southern FR rocky sector and three in the southern Cap de Creus sector. The southern FR rocky sector has been monitored during the past 20 years using a comparable method and absolutely no young-of-the-year groupers (<10 cm TL) had been reported there (Bodilis et al., 2003a, 2003b). Once highly hunted by spearfishers, this species suffered an alarming decrease in abundance in the north-western Mediterranean (Coll et al., 2004). Since its strict protection in France in the 90's it has been slowly recolonizing the area. However, along French coasts of the entire Gulf of Lion, only one young-of-the-year had been observed in natural habitats over the last twenty-five years (Bodilis et al., 2003a). Accordingly, our observation of four juvenile groupers over a short stretch of shoreline in the same year is exceptional. Moreover, another observation of a juvenile *E. marginatus* was documented in an artificial habitat in the same study area (Northern FR rocky coast, Port Vendres harbor) in 2015 and in two other artificial habitats placed in harbors in the northern Gulf of Lion in 2013 and 2014 (Mercader et al., 2016). As juveniles, dusky groupers tend to be easily frightened so their absence in previous years might not mean they were not present. However, the density of juveniles seems to have reached a threshold at which observations are more likely. This is a major observation in the context of the conservation and stock replenishment of this emblematic and protected species.

Only one individual of *D. cervinus* was observed during the surveys and it was located on the sandy coast. The low abundance of adults of this species in the NW Mediterranean, even inside MPAs (Derbal and Kara, 2006), is probably preventing strong reproduction and settlement events. Moreover, *D. cervinus* shows large inter-annual variations, peaking approximately every ten years (Authors unpublished data). Peaks in *D. cervinus* settlement typically coincide with peaks in *D. sargus* settlement but at much lower densities (Garcia-Rubies and Macpherson, 1995). It is known that if the appropriate meteorological conditions do not occur during the limited settlement period, larvae will be subject to massive mortality due to famine and predation, resulting in low juvenile populations. The random nature of these events explains why the settlement process of most organisms is unpredictable and why settlement intensity is highly variable through space and time (Vigliola et al., 1998).

The very low densities of other species that were observed (*D. dentex*, *P. pagrus*) put into question our knowledge of their juvenile habitat preferences. Some previous studies (Cheminée, 2012; Thiriet et al., 2014) pointed out that these taxa may rather use transitional zones between different habitats, an illustration of the “edge-effect” (Smith et al., 2011).

4.5. Perspectives at the Mediterranean scale

In this study, we provide useful information regarding the ecology and management of some important species. However, due to the temporal variability of settlement events, further studies repeated in other years are needed to confirm or contrast trends observed in 2015. Furthermore, future objectives for the fundamental understanding of species life cycles and for management practices must be seen in the context of the complex seascape mosaic of coastal environments. First, the nursery value of other habitats, for other species, must be studied since the replenishment of coastal biodiversity relies not only on a few habitat types but on the complementarity of the seascape mosaic (Colloca et al., 2015). Secondly, pre-settlement and post-settlement factors and processes driving nursery value variability (between habitats, between sites for a given habitat) must be understood (Cuadros et al., 2017). For example, before settlement, these include, among others things, successful reproduction and egg and larval dynamics. After settlement, they include the effect of anthropogenic drivers (e.g. pollution, invasive species, habitat degradation as well as habitat restoration, etc.) on juvenile growth and survival. Thirdly, for the coastal management of a given area, protecting essential habitat from degradation is a multivariate task, since it must include not only the various nursery habitats corresponding to various species, but other functionally important habitats as well (breeding and feeding grounds for example) (Cheminée et al., 2014). Furthermore it must take into account the possible failure of a given site a given year, which means acting among a network of connected managed areas. In this sense, both fundamental research and management require further studies of population connectivity at various life stages.

5. Conclusions

Regarding the ecological dynamics of the studied species, our results from 82 sites in 2015 underline that although the suitable habitat for juvenile fish was present, strong spatial differences in the final recruitment level exist between sites spread over a 240 km long coastline. Furthermore, only a small portion of these essential habitats was under efficient protection. This data stresses the need, first, to promote nursery habitat protection as a complement to adult stock management, and second, to implement protection in a variety of sites in order to prevent local failure of recruitment. Our results provide some insights into factors shaping recruitment level: it was not explained by protection level, but it was moderately and positively correlated with an anthropization index. Further studies of these driving factors, including over several years, will be required. By considering an even larger spatial scale, e.g. the entire Mediterranean, future work could allow a better comprehension of possible forcing factors, such as global warming, pollution or invasive species. Juvenile densities displayed contrasted spatial patterns according to taxa. As regards rare species, it is worth noting that individuals of the protected grouper *E. marginatus*, unseen in the last 20 years in this area, were seen on four occasions during this 2015 study. Additionally, our data will be useful for monitoring further the expansion of a stenotherm species, *T. pavo*, in response to global warming. In this way, our results underline the importance of setting up and maintaining long term monitoring.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marpolbul.2017.03.051>.

Acknowledgements

This work was performed in the frame of eCATE program [2014–2016]. This program was supported by the Total Foundation, the Fondation de France and the Conseil Départemental 66. The authors sincerely thank the MPA managers who greatly facilitated access to the field and helped to interpret the data: Jérôme Payrot and the team of the RNMCB, Bruno Ferrari and the team of PNMGL, Victoria Riera and Josep Lloret at the PNCC. The authors also wish to thank Mas Caials park rangers for hosting the team during field work as well as the Xiringuito de la Mei and Youyou's team for essential logistical support. The authors sincerely thank the editor and two anonymous referees for their constructive comments on an earlier version of the manuscript.

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Biohut® Quai

- fixation béton par perforation -

1 Description du produit

Fonctions écosystémiques :

- nurserie pour jeunes recrues de poissons.
- support faune flore fixées.
- habitat faune vagile.

Composition : caisson grillagé vide (protection) accolé à un caisson grillagé contenant des coquilles (fixation nourriture), le tout fixé au quai.

Hauteur d'immersion : subsurface

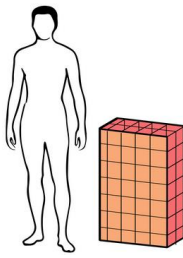
Prix : devis sur demande

Efficacité écologique : démontrée (publications)

Production : industrielle

Existence d'un protocole de suivi biologique éprouvé : oui

Dimensionné pour l'export : oui, les Biohut® non assemblés sont propres au gerbage.



Volume (h*L*e):
 $0,8*0,5*0,24 = 0,1m^3$

Maille grille protection:
5cm*5cm

Maille grille substrat:
2,5cm*2,5cm

Matériau :
acier + coquilles d'huîtres désinfectées

Poids: 20kg

2 Installation des Biohut®

Description des opérations : perforation quai, fixation du treillis, fixation et amarrage du Biohut®.

Remarque : utilisation du treillis réservé aux eaux calmes, sinon les Biohut® sont fixés individuellement.

Impact sur les infrastructures : perçage superficiel du quai (profondeur 7cm, diamètre 13mm).

Moyens Humains : 3 personnes dont un plongeur classe 1B en apnée entre 0 et 1m.

Durée de l'opération : ~ 20 Biohut® installés par jour.

3 Maintenance des Biohut®

Description de l'opération : démontage de la grille externe, nettoyage à haute pression.

Fréquence : 1 ou 2 fois par an selon biofouling.

Moyens Humains : 2 personnes dont un plongeur classe 1B.

Durée de l'opération : ~ 60 Biohut® par jour.

4 Dimensionnement projet

Nombre de modules: en fonction du nombre d'anneaux/linéaire de quai : entre 50 et 150 modules.

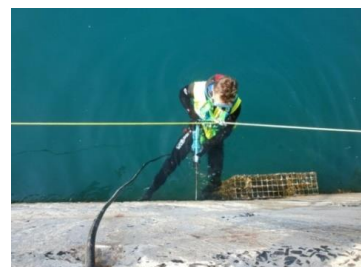
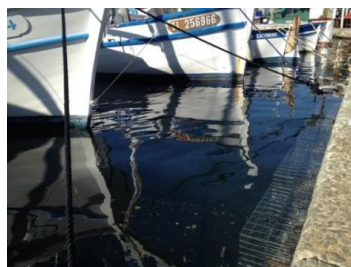
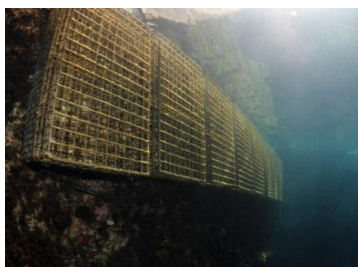
Chronogramme : Janvier à Mars: installation Biohut® / Avril à Septembre: recrutement post-larves / Octobre à Mars: maintenance Biohut®.

Modes de prestation :

- Location OU vente des Biohut®
- Maintenance : service clé en main OU prestation et formation la première année.

Subventionnements possibles :

- Régions PACA, LR, Corse : procédé soutenu par Agence de l'Eau RMC. Taux de subvention variable.
- Région PACA : aide supplémentaire pour signataires de la charte Ports Propres.



Biohut® Quai

- fixation magnétique sur palplanches -

1 Description du produit

Fonctions écosystémiques :

- nurserie pour jeunes recrues de poissons.
- support faune flore fixées.
- habitat faune vagile.

Composition : caisson grillagé vide (protection) accolé à un caisson grillagé contenant des coquilles (fixation nourriture) fixé au quai par 3 aimants.

Hauteur d'immersion : entre 0,5 et 2m

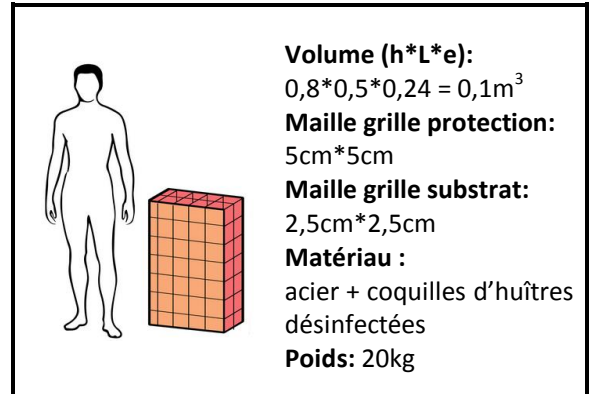
Prix : devis sur demande

Efficacité écologique : démontrée (publications)

Production : industrielle

Existence d'un protocole de suivi biologique éprouvé : oui

Dimensionné pour l'export : oui, les Biohut® non assemblés sont propres au gerbage.



2 Installation des Biohut®

Description des opérations : positionnement puis fixation du Biohut® par des aimants étanches et isolés.

Remarque : les palplanches doivent être récentes et peu biofoulées pour une fixation optimale.

Impact sur les infrastructures : aucun.

Moyens Humains : 2 personnes dont un plongeur classe 1B en apnée entre 0 et 1m.

Durée de l'opération : ~ 50 Biohut® installés par jour.

3 Maintenance des Biohut®

Description de l'opération : démontage de la grille externe, nettoyage à haute pression.

Fréquence : 1 ou 2 fois par an selon biofouling.

Moyens Humains : 2 personnes dont un plongeur classe 1B.

Durée de l'opération : ~ 60 Biohut® par jour.

4 Dimensionnement projet

Nombre de modules: en fonction du nombre d'anneaux/linéaire de quai : entre 50 et 150 modules.

Chronogramme : Janvier à Mars: installation Biohut® / Avril à Septembre: recrutement post-larves / Octobre à Mars: maintenance Biohut®.

Modes de prestation :

- Location OU vente des Biohut®
- Maintenance : service clé en main OU prestation et formation la première année.

Subventionnements possibles :

- Régions PACA, LR, Corse : procédé soutenu par Agence de l'Eau RMC. Taux de subvention variable.
- Région PACA : aide supplémentaire pour signataires de la charte Ports Propres.



Biohut® Ponton

1 Description du produit

Fonctions écosystémiques :

- nurserie pour jeunes recrues de poissons.
- support faune flore fixées.
- habitat faune vagile.

Composition : deux caissons grillagés vides (protection) de part et d'autre d'un caisson grillagé contenant les coquilles (fixation nourriture).

Hauteur d'immersion : subsurface

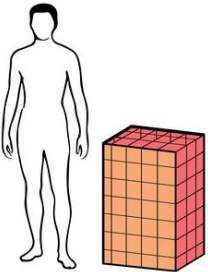
Prix : devis sur demande

Efficacité écologique : démontrée (publications)

Production : industrielle

Existence d'un protocole de suivi biologique éprouvé : oui

Dimensionné pour l'export : oui, les Biohut® non assemblés sont propres au gerbage.



Volume (h*L*e):
 $0,8*0,5*0,36 = 0,14m^3$

Maille grille protection:
 5cm*5cm

Maille grille substrat:
 2,5cm*2,5cm

Matériaux :
 acier + coquilles d'huîtres désinfectées

Poids: 22kg

2 Installation des Biohut®

Description des opérations : suspension du Biohut® via 4 points d'attache sous les pontons.

Impact sur les infrastructures : aucun.

Moyens Humains : 2 personnes dont un plongeur classe 1B en apnée entre 0 et 1m.

Durée de l'opération : ~ 45 Biohut® installés par jour.

3 Maintenance des Biohut®

Description de l'opération : démontage des grilles externes, nettoyage à haute pression.

Fréquence : 1 ou 2 fois par an selon biofouling.

Moyens Humains : 2 personnes dont un plongeur classe 1B.

Durée de l'opération : ~ 40 Biohut® par jour.

4 Dimensionnement projet

Nombre de modules: en fonction du linéaire de pontons flottants : entre 50 et 200 modules.

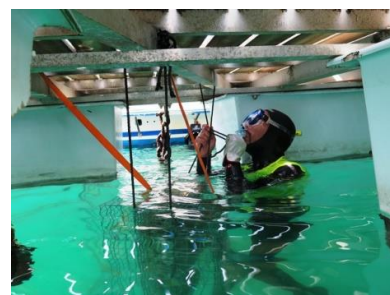
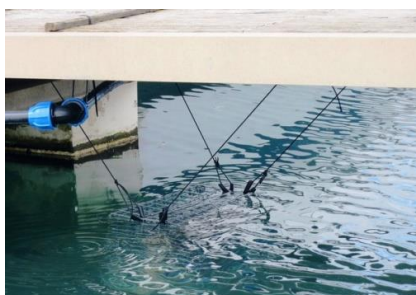
Chronogramme : Janvier à Mars: installation Biohut® / Avril à Septembre: recrutement post-larves / Octobre à Mars: maintenance Biohut®.

Modes de prestation :

- Location ou vente des Biohut®.
- Maintenance : service clé en main OU prestation et formation la première année.

Subventionnements possibles :

- Régions PACA, LR, Corse : procédé soutenu par Agence de l'Eau RMC. Taux de subvention variable.
- Région PACA : aide supplémentaire pour signataires de la charte Ports Propres.



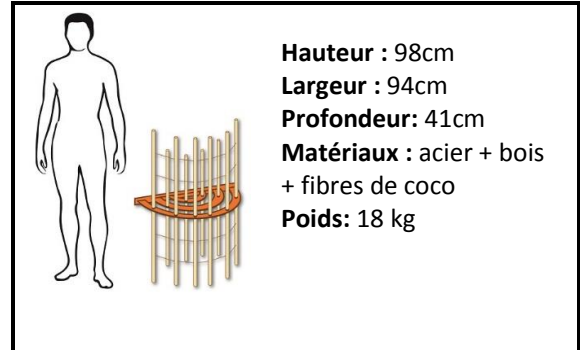
1 Description du produit

Fonctions écosystémiques :

- Nurserie pour poissons côtiers
- Habitat corridor
- Support faune flore fixées.

Composition :

- Protection: tiges en bois de longueur variable, emboîtées à hauteur variable sur une platine métallique perforée de taille modulable (demi-cercle grand modèle et petit modèle).
- Fixation nourriture : brins de fibre de coco tendus entre les tiges de bois.



Hauteur d'immersion : entre 0 et 5 m de façon à fournir un habitat plus profond aux juvéniles de l'année.

Maintenance : visite de contrôle tous les deux ans.

Prix : devis sur demande.

Efficacité écologique : démontrée.

Niveau de maturité technologique : TRL = 8.

Production : industrielle.

Existence d'un protocole de suivi biologique éprouvé : non

Dimensionné pour l'export : oui, les Biohut® non assemblés sont propres au gerbage.

2 Installation des Biohut®

Description des opérations : perçage, mise en place Biohut®

Impact sur les infrastructures : perçage superficiel du quai (profondeur 7cm, diamètre 13mm).

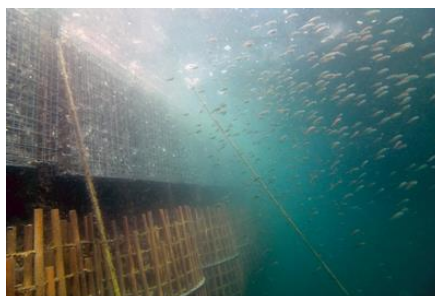
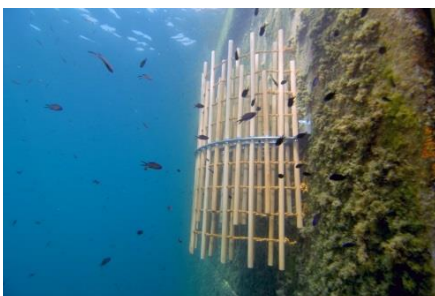
Moyens Humains : 1 plongeur classe 1A à l'eau + 1 plongeur classe 1A pour assistance et sécurité

Durée de l'opération : ~ 40 Biohut® installés par jour

3 Dimensionnement projet

Nombre de modules: ~ 1 Biohut® par m² de quai

Chronogramme : installation de mars à octobre, pas de dépose.



Résumé

La perte d'habitat engendrée par l'artificialisation des côtes a de graves conséquences sur la biodiversité marine. Aussi, dans une optique de maintien de la biodiversité et des stocks de poissons, il peut s'avérer intéressant de restaurer certaines fonctions écologiques dans les zones anthropisées. Cette thèse avait pour objectif d'estimer le rôle potentiel des ports en tant qu'habitat pour les juvéniles de poissons côtiers et d'évaluer dans quelle mesure ce rôle peut être amélioré par le biais d'actions de restauration. Des expérimentations en aquarium ont permis d'estimer que le taux de survie des juvéniles sur des habitats artificiels utilisés à des fins de restauration était comparable à celui observé sur des roches. Une étude de la distribution spatiale des juvéniles à l'échelle d'un paysage sous-marin a ensuite montré que les ports pouvaient abriter des densités en juvéniles représentant de 50 à 90 % de celles retrouvées en milieu naturel. Les densités à l'intérieur des ports étaient cependant tributaires du type d'habitat considéré; les quais sans complexité structurale abritant les densités les plus faibles. Enfin, l'étude de cas concrets, a montré que la réhabilitation des ports pouvait significativement augmenter les densités de juvéniles à l'échelle de l'habitat, celles-ci pouvant atteindre des niveaux comparables au milieu naturel. Toutefois, ces bénéfices restaient faibles à l'échelle d'un port dans sa globalité. Ces travaux suggèrent un réel potentiel des infrastructures portuaires en tant qu'habitat juvénile alternatif, en particulier si des actions de restauration y sont entreprises. Cependant, pour plus d'efficacité, les projets de restauration devraient être menés à large échelle et utiliser une diversité d'habitats artificiels. La restauration écologique des ports peut ainsi être employée comme un outil complémentaire aux mesures de protection dans le cadre d'une gestion intégrée des zones côtières à l'échelle du paysage.

Mots-clés : juvénile, téléostéens, restauration écologique, nurserie, Méditerranée, destruction d'habitat

Abstract

Habitat loss caused by urban sprawl has harmful consequences on marine biodiversity. With a view to maintaining biodiversity and fish stocks, it may be worthwhile to restore some ecological features in anthropized areas. The aim of this thesis was to estimate the potential role of ports as habitat for juvenile coastal fish and to evaluate how this role can be improved through restoration actions. Tank experiments revealed that juvenile survival rate on artificial habitats used for restoration purpose could be equivalent to that observed on natural habitat. The assessment of the spatial distribution of juvenile at the scale of a seascape permitted to estimate that harbors could host densities of juvenile that were between 50 to 90% of those observed in natural sites. Within harbors densities were highly dependent on the type of habitat, featureless dock hosting the lowest densities. Subsequently, based on case studies, this work demonstrated that harbors rehabilitation could significantly enhance juvenile densities at the habitat scale. Densities on restored habitat might reach those observed in natural habitats. However, at the scale of the whole harbor benefits were low. This work suggests that harbors have a real potential as an alternative juvenile habitat, especially if restoration actions are undergone. However, for more efficiency, restoration projects should be led at the scale of the whole site and include a diversity of artificial habitats. Thereby, restoration approaches should be considered as a complementary tool to protection measures in a seascape integrated management approach of coastal areas.

Key-words: juvenile, teleostean, restoration ecology, nursery, Mediterranean, habitat loss