Les zones portuaires peuvent-elles servir de nourriceries alternatives pour les poissons marins côtiers ? : cas des sars en Méditerranée Nord-occidentale

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THÈSE

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Spécialité : **Océanologie**

Présentée par Marc Bouchoucha

Les zones portuaires peuvent-elles servir de nourriceries alternatives pour les poissons marins côtiers ? Cas des sars en Méditerranée Nord-occidentale.

Soutenue le 13 décembre 2017 devant le jury composé de

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Pierre Cresson, Chercheur, Ifremer, Boulogne/Mer	Examinateur
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Jacques Panfili, Directeur de Recherche, IRD, Ho Chi Minh	Rapporteur
Sandrine Vaz, Chercheur, Ifremer, Sète	Rapportrice

Réussir sa vie

« Rire souvent et sans restriction ; s'attirer le respect des gens intelligents et l'affection des enfants ; tirer profit des critiques de bonne foi et supporter les trahisons des amis supposés ; apprécier la beauté ; voir chez les autres ce qu'ils ont de meilleur ; laisser derrière soi quelque chose de bon, un enfant en bonne santé, un coin de jardin ou une société en progrès ; savoir qu'un être au moins respire mieux parce que vous êtes passé en ce monde ; voilà ce que j'appelle réussir sa vie »

Ralph Waldo Emerson

Avant propos

Ce travail de thèse s'est déroulé dans un contexte très particulier. En effet, diplômé de l’Institut National Agronomique Paris-Grignon en 2004, j’ai été recruté en janvier 2006 au Laboratoire Ifremer Environnement Ressources Provence Azur Corse (LER/PAC), à la station de Bastia, sur un poste d’ingénieur en environnement. Depuis, mes activités concernent essentiellement la coordination de réseaux régionaux et nationaux de surveillance environnementale, la gestion de projet régionaux et la production d'expertises locales.

En 2013, l'Ifremer m'a offert l'opportunité de m'engager dans un travail de thèse qui devait être pour moi l'occasion de développer des compétences sur un sujet nouveau, porteur en Méditerranée. Contrairement à la plupart des thèses professionnelles, il a été décidé que je ne réaliserai pas une synthèse de mes travaux antérieurs mais que, à l'image des doctorants classiques, j'en initierai de nouveaux. Ainsi, rien des échantillonnages, des analyses ou des articles présentés ici n'est issu de mes travaux scientifiques antérieurs. Tout était nouveau pour moi.

Par ailleurs, cette thèse s'est déroulée à temps partiel, en parallèle de mon travail à l'Ifremer. En effet, durant les quatre années de cette thèse, j’ai été chargé de la coordination des activités régaliennes de surveillance du LER/PAC, j’ai eu la responsabilité de sept actions, j’ai assuré la fonction responsable adjoint du laboratoire, j’ai coordonné deux réseaux régionaux de suivi de la contamination chimique dans les organismes vivants (bivalves et poissons), j’ai coordonné la mise en œuvre de la Directive Cadre Eau (DCE) pour l’ensemble de façade méditerranéenne et j’ai piloté l’accord cadre Ifremer / Agence de l’Eau Rhône Méditerranée Corse (AERMC). En outre, j'ai été responsable en 2015 d'une expertise d'ampleur concernant l’impact d’un rejet industriel sur la contamination chimique des produits de la pêche dans le Parc National des Calanques qui m'a mobilisée totalement, m'obligeant à mettre de côté ma thèse pendant 8 mois.

Remerciements

Il est un temps où il faut poser un point final à tout travail. Le moment est difficile, empli de doutes quand tant d'idées restent à préciser et tant de pistes à explorer. C'est à ce moment qu'il est nécessaire de se retourner pour observer le chemin parcouru. Pour le plaisir de contempler, d'abord, et surtout pour réaliser que ce point posé n'est en fait que celui d'une introduction, le commencement d'une longue histoire.

La complexité de l'environnement est telle que la recherche en écologie marine avance souvent en aveugle, par tâtonnement successifs et repose sur la mise en œuvre d'une démarche exploratoire qui contribue par une série d'essais-erreurs à formuler et vérifier des hypothèses. Lorsque je regarde en arrière et me remémore chacune des étapes, parfois difficiles à accepter, qui ont jalonnées ces quatre années de thèse, je ne peux éprouver qu'une certaine satisfaction. Pas tant vis-à-vis du résultat final car j'ai pleine conscience des maladresses que j'ai pu commettre, du temps que j'ai perdu en ignorance ou en précipitation et des limites de mon travail. C'est en réalité des rencontres que cette thèse m'a permis de faire que je tire ma plus grande satisfaction. J'ai aujourd'hui une dette envers des personnes qui m'ont accompagné et parfois guidé tout au long de ces quatre années. Difficile de toutes les citer tant elles sont nombreuses. Je me risquerai néanmoins à en désigner certaines, remerciées ici en quelques mots, bien trop rapidement au regard de ma gratitude.

Parmi mes créanciers, mes deux directeurs de thèse occupent une place toute particulière. Lorsque je les ai rencontrés et que je leur ai présenté mon projet, je n'étais pas un candidat comme les autres. J'étais en poste, dans une autre équipe de recherche et ne pouvait mener ce travail qu'à temps partiel. Pourtant, ils n'ont pas hésité à m'accompagner dans cette aventure et à m'ouvrir sans la moindre retenue les portes de leur science. En ça, je leur serai toujours reconnaissant. Conscient de la chance qu'ils m'ont offerte, je n'ai eu de cesse que d'essayer d'en tirer le meilleur parti. Audrey Darnaude est certainement celle que j'ai le plus exploité tant j'ai sollicité sa disponibilité, son dévouement à son métier et sa rigueur. Avec elle, j'ai forgé mes capacités de raisonnement et surtout d'autocritique… parfois dans la douleur, mais toujours pour mon bien. Malgré un emploi du temps incroyable, Philippe Lenfant, lui, est toujours intervenu avec gentillesse et au moment opportun pour couper court à mes divagations de thésard désinhibé. Son enthousiasme sur le projet a été le phare auquel je me suis raccroché dans les moments de doute. Avec ces deux directeurs, ma thèse ne pouvait que bien se passer.

Je ne peux oublier de citer dans ces remerciements tous ceux qui ont permis à cette thèse de voir le jour. Je pense bien évidemment à Jean-François Cadiou, René Robert et Bruno Andral, mes responsables hiérarchiques en début de thèse, qui m'ont soutenu et qui ont accepté que je dégage du temps sur mes activités pour mener à bien mon projet. Je pense également à Pierre Boissery de l'Agence de l'Eau Rhône Méditerranée-Corse qui a énormément œuvré sur la question de la restauration écologique des zones côtières en Méditerranée. Pierre Boissery est un moteur suffisamment puissant pour m'avoir entraîné sur un sujet que je considérais avec un certain scepticisme la première fois que j'en ai entendu parler. Je ne peux lui en être que reconnaissant.

Je voulais également remercier l'ensemble des personnes qui m'ont aidé dans mes réflexions, notamment Gilles Lecaillon, Amélie Foncuberta, Sébastien Fonbonne, Anaïs Gudefin, Rémy Dubas, Martin Perrot, Matthieu Lapinski, Fabrice Javel. Leur dynamisme et leur passion m'ont toujours fasciné.

D'autres personnes ont très directement contribué à ce travail. Franck Ferraton m'a ouvert les portes de son laboratoire à Montpellier et m'a donné les clés du travail de paillasse. Je ne peux que louer sa gentillesse, sa compétence et sa disponibilité. Aurélie Vion m'a accompagné dans l'eau pendant des heures comptage et de prélèvement. Ni le froid, ni les conditions, ni les bactéries n'auront eu raison de sa persévérance et son enthousiasme. Fabienne Chavanon m'a aidé dans mon travail de laboratoire, parfois avec une certaine résignation face à l'ampleur des tâches à accomplir. D'une humeur constante, j'ai toujours pu compter sur sa présence. A toutes ces personnes, je veux simplement dire merci.

J'ai en ce moment une pensée pour ma famille et en particulier ma femme, Raphaëlle, qui a toujours été présente pour me soutenir. Je pense aussi à mes deux enfants, Alexandre et Adrien, nés respectivement quelques mois avant et pendant cette thèse. Sans eux, ces quatre dernières années de ma vie auraient été beaucoup moins riches… et mes nuits plus longues.

Je profite également de cette page pour remercier chaleureusement les deux rapporteurs, Sandrine Vaz et Jacques Panfili ainsi que les membres du jury Pierre Cresson, Fabien Morat, Pierre Boissery et Rachid Amara d'avoir accepté avec enthousiasme d'évaluer ma thèse. C'est un honneur de voir mon travail critiqué par ces experts dans leur domaine et j'espère que les quelques pages qui suivront sauront préserver leur enthousiasme initial.

Sommaire

Chapitre 1. Introduction générale

I.1. Pourquoi étudier les poissons marins côtiers ?

Les poissons contribuent très largement à la biodiversité mondiale. En effet, ce groupe représente actuellement plus de la moitié des espèces de vertébrés vivants sur Terre (Eschmeyer et al. 2010). De plus, étant présents à de nombreux niveaux des réseaux trophiques, les poissons jouent un rôle régulateur essentiel vis-à-vis des autres espèces, contribuant ainsi indirectement au maintien de la biodiversité totale des milieux aquatiques. Par ailleurs, du fait de leurs capacités migratoires, les poissons contribuent aux flux d'énergie et donc à la connectivité entre les écosystèmes (Carpenter et al. 1992, Holmlund & Hammer 1999). Le rôle de ces espèces dans le fonctionnement des écosystèmes marins est donc primordial.

De tous temps, nos sociétés ont tiré de nombreux bénéfices directs et indirects des poissons (Holmlund & Hammer 1999, Sumaila et al. 2011). Aujourd'hui, ils représentent non seulement 17 % des apports en protéines animales pour la population mondiale (FAO 2012), mais rendent également de nombreux services culturels et récréatifs à forte plus-value économique, notamment ceux associés à la pêche de loisir, à la plongée ou à l'aquariophilie (Holmlund & Hammer 1999).

Malgré cette importance écologique et économique, les poissons marins sont fortement menacés par les activités humaines, en particulier par la surpêche, la pollution et la destruction de leurs habitats (Jackson et al. 2001, Myers & Worm 2003, Jones et al. 2004). En conséquence, 87 % des ressources halieutiques marines mondiales sont aujourd'hui pleinement exploitées ou surexploitées (Pauly et al. 2002), avec un nombre croissant d'espèces menacées d'extinction (IUCN France et al. 2010). La stagnation du nombre de captures (environ 80 millions, figure I.1) malgré l'intensification des efforts de pêche illustre clairement l'épuisement des stocks mondiaux.

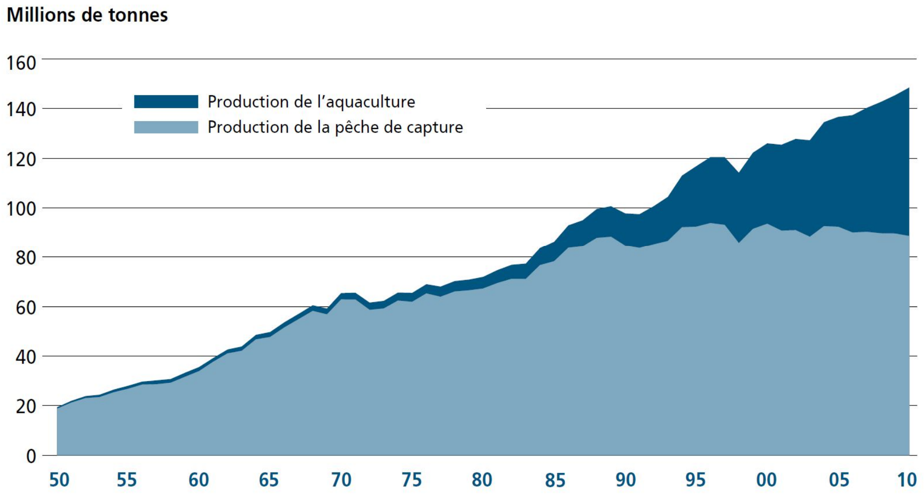

Figure I.1 : Production mondiale de la pêche de capture et de l'aquaculture (source : FAO, 2012).

Plus de 50 % des espèces de poissons recensées au monde sont inféodées aux zones côtières (Mora et al. 2008). Afin de préserver cette biodiversité exceptionnelle ainsi que les bénéfices qui y sont associés, il est indispensable d'identifier les facteurs responsables des variations spatio-temporelles de l'abondance des stocks de poissons marins côtiers.

Les espèces de poissons benthiques (qui vivent sur le fond) et nectobenthiques (qui vivent proche du fond) représentent une part importantes des captures mondiales et sont particulièrement ciblées par les pêcheries artisanales et de subsistance (FAO 2012). Il est donc primordial de comprendre leur cycle de vie.

I.2. Cycle de vie, habitats clés et succès du recrutement chez les poissons marins côtiers

La plupart des poissons marins côtiers benthiques ou nectobenthiques ont un cycle de vie complexe (figure I.2), caractérisé par une phase larvaire planctonique dispersive suivie par une phase juvénile et adulte relativement sédentaire (Öhman et al. 1998, Jones et al. 1999, Armsworth 2002).

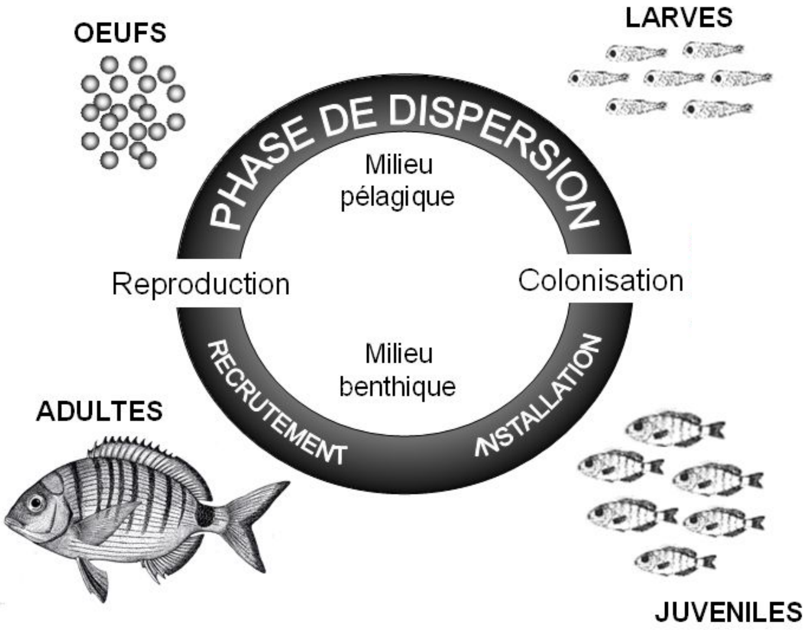

Figure I.2 : Schéma de cycle de vie type des poissons marins côtiers benthiques et nectobenthiques (source : Pastor 2008).

Le cycle biologique d'une espèce ne peut s'accomplir que si ses individus trouvent les conditions nécessaires à leur développement à chacun de leurs stades ontogénétiques[1]. Chez les poissons, ces derniers sont en général caractérisés par des exigences écologiques, physiologiques et biologiques différentes, ce qui peut impliquer une séparation, ou du moins une disjonction, entre les habitats larvaires, juvéniles et adultes (Beck et al. 2001). Ainsi, au cours de leur cycle biologique, les poissons côtiers migrent souvent entre des habitats très différents. Ces migrations ontogénétiques relèvent directement d'un compromis entre le coût énergétique de la migration et celui de rester sur place (compétition et prédation), le tout résultant d'un processus complexe de réponse adaptative à une succession de facteurs biotiques et abiotiques (Gibson et al. 2002).

Après avoir été transportées et dispersées par les courants marins, les larves de poissons côtiers benthiques et nectobenthiques colonisent le plus souvent la zone littorale puis se métamorphosent en quelques heures ou quelques jours en juvéniles (Planes & Lecaillon 2001). Dans ce nouvel environnement complexe, face à de nombreux substrats potentiels et à une diversité de prédateurs et de compétiteurs, les juvéniles de ces espèces vont alors choisir un habitat benthique (Carr & Hixon 1995, Caselle & Warner 1996, Adams & Ebersole 2004) : c'est la phase d'installation benthique, c'est-à-dire la transition immédiate entre le stade larvaire pélagique et le stade juvénile benthique (Andrews & Anderson 2004).

En écologie, le recrutement est défini comme l'entrée de nouveaux individus dans une population adulte (Radtke 1985, McCormick & Kerrigan 1996). Si les variations observées de l'intensité du recrutement ont longtemps été considérées comme le seul résultat des variations de l'apport larvaire (hypothèse du recrutement limitant - Doherty 1991), de nombreuses études ont montré que pour la plupart des poissons côtiers benthiques et nectobenthiques, la qualité des habitats juvéniles a une influence non négligeable sur ce paramètre (Turner & Boesch 1988, Gibson 1994, Jones et al. 2002). En effet, l'absence de corrélation systématique entre l'abondance des stades précoces (œufs et larves) et celle des nouvelles recrues (Bradford 1992, Rooper et al. 2004), l'existence d'une relation directe entre la taille d'un habitat juvénile et le nombre de juvéniles qu'elle produit (Rijnsdorp et al. 1992, Schmitt & Holbrook 2000), la relation entre les variations interannuelles de nourriture dans les habitats juvéniles et l'abondance de poissons qui s'y trouvent (Fujii & Noguchi 1993) et la relation entre la densité et la survie, en lien avec les disponibilités alimentaires et la prédation (Nash & Geffen 2000) montrent toutes que les variations des apports larvaires sont régulés *a posteriori* par la

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[1] L'ontogénie est le processus qui correspond à la différenciation des stades de développement au cours de la vie de l'organisme (Lévêque 2001). Quatre stades ontogénétiques sont généralement décrits chez les poissons marins côtiers : le stade « œufs », le stade larvaire, le stade juvénile et le stade adulte.

capacité d'accueil et la qualité des habitats juvéniles. Par conséquent, le recrutement résulte non seulement des fluctuations de la biomasse féconde du stock adulte et de la survie des stades précoces (œufs et larves) mais dépend également de la surface et de la qualité des habitats où se développent les juvéniles. Ce mécanisme permet de comprendre que la dégradation, la destruction ou la réduction de surface des habitats juvéniles est l'une des principales causes de diminution des stocks ou d'extinction d’espèces chez les poissons marins côtiers (Turner & Boesch 1988, Gibson 1994, Able et al. 1999).

I.3. Le paradoxe des nourriceries côtières : des habitats essentiels souvent menacés

Parmi les habitats juvéniles colonisés par les poissons marins côtiers benthiques et nectobenthiques, les zones de nourriceries ont une fonction écologique[2] particulière qui en fait des habitats clés pour le maintien des populations. Plusieurs définitions ont été proposées pour identifier les zones de nourriceries des poissons (Gibson 1994, Dahlgren et al. 2006, Franco et al. 2006). Celle de Beck et al. (2001) est aujourd’hui communément acceptée : un habitat juvénile est une zone de nourricerie si sa contribution par unité de surface à la production d’individus adultes est supérieure à celles des autres habitats juvéniles. Ainsi, pour les espèces de poissons côtiers benthiques et nectobenthiques, une zone de nourricerie est une zone favorable à l’installation benthique, qui offre aux jeunes poissons un environnement dans lequel ils grandissent plus vite et ont un meilleur taux de survie que dans tous les autres habitats juvéniles, et qui leur permet, à l’issue de ce stade de vie, de rejoindre les habitats adultes. Pour ces espèces, les zones de nourriceries sont donc des habitats juvéniles particuliers qui maximisent la survie et la croissance des juvéniles durant les mois voire les années où ils y résident (Riley 1981, Miller et al. 1984, Diaz et al. 2003).

Du fait de leur rôle clé dans le recrutement de nombreuses espèces, notamment commerciales, l’évaluation de la qualité des habitats juvéniles des poissons et l'identification de leurs zones de nourricerie ont fait l’objet de très nombreuses études. A l’échelle de la planète, plusieurs écosystèmes littoraux ont été identifiés comme zones de nourriceries de poissons côtiers, notamment divers estuaires (e.g. Beck et al. 2001, Vasconcelos et al. 2008, Vinagre et al. 2012), lagunes côtières (e.g. Franco et al. 2006, Abecasis et al. 2009), récifs coralliens (e.g. Doherty 1981, Carassou et al. 2009), mangroves (e.g. Nagelkerken & Faunce 2008), herbiers à phanérogames (e.g.

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[2] La notion de fonction écologique est complexe. Elle est aujourd'hui définie comme le potentiel d'une partie d'écosystème à délivrer un service (De Groot et al. 2010).

Francour 1999, Cheminee et al. 2013, Jones et al. 2013) et petits fonds côtiers (e.g. Harmelin-Vivien et al. 1995, MacPherson 1998, Cheminee et al. 2011). La réduction de la surface ou la dégradation de la qualité de ces zones de nourricerie influence fortement le recrutement et donc le maintien des stocks de poissons qui les fréquentent au stade juvénile (Gibson 1994, Peterson et al. 2000, Jones et al. 2002). Or, ces écosystèmes littoraux, reconnus pour être des écotones riches, productifs et peu étendus (Beck et al. 2001), sont tous fortement exposés aux pressions anthropiques. En effet, situés à l'interface continent-océan, ils sont le lieu de très nombreuses activités anthropiques (pêche, transport, industrie, tourisme, etc.) et le réceptacle de multiples pollutions chroniques ou accidentelles. Leur qualité s'en trouve souvent détériorée par la contamination, l'excès des apports organiques ou encore les hypoxies (Gray et al. 2002) et leur superficie tend à diminuer par les endiguements, les développements portuaires, les chenalisations, les dragages et leurs dépôts (Goeldner-Gianella 2007).

I.4. Les ports : une pression majeure sur les zones littorales

La construction de ports est l'une des principales pressions qui influencent les zones littorales (Rodríguez-Rodríguez et al. 2015). Lors de leur construction, les habitats naturels subtidaux, généralement répartis en une mosaïque hétérogène, sont remplacés par des structures artificielles plus homogènes et moins complexes. Ces structures artificielles supportent souvent moins de biodiversité que les habitats naturels (Moschella et al. 2005, Vaselli et al. 2008, Browne & Chapman 2014). Par ailleurs, de plus en plus d'études montrent que les structures de défense contre les éléments, comme les digues par exemple, peuvent induire un changement dans la composition spécifique (Moschella et al. 2005), dans les abondances (Chapman 2003), dans la structure en taille et les capacités reproductives des populations (Moreira et al. 2006) ainsi que dans les interactions compétitives (Jackson et al. 2008, Iveša et al. 2010). Ainsi, même lorsqu'elles sont colonisées par des espèces, les structures artificielles construites par l'Homme, sans objectif écologique particulier, ne peuvent que très difficilement être considérées comme des substituts aux habitats naturels qu'elles remplacent.

Le manque de complexité (abondance absolue des différentes composantes structurelles) ou d'hétérogénéité (abondance relative des différentes composantes structurelles) de l'habitat a souvent été mis en avant comme cause de diminution de la biodiversité sur les ouvrages portuaires (Chapman & Underwood 2011) car il conduit à une réduction de la survie des organismes (Brokovich et al. 2006), en particulier des juvéniles de poissons (Mellin 2007). Par conséquent, la construction de ports s'accompagne de profondes modifications physiques des zones littorales, pouvant entraîner une augmentation de la mortalité des juvéniles de poissons et donc une perte de capacité et de fonctionnalité des zones de nourricerie affectées.

Par ailleurs, les zones portuaires sont des milieux très particuliers, concentrant de nombreuses activités anthropiques et réceptacles de multiples pollutions microbiologiques et chimiques (Darbra et al. 2004, CETMEF 2010). Ces pollutions impactent les sédiments et la colonne d'eau à l'intérieur et à proximité des ports (Falandysz et al 2002, Neira et al 2011). Ceci peut causer des mortalités importantes chez les juvéniles de poissons, qui accumulent les contaminants à la fois à partir de la colonne d'eau, du sédiment et de leur nourriture (Amiard et al. 1987). Les contaminants chimiques sont bien connus pour affecter négativement la physiologie, la croissance, la santé, le comportement et la survie des poissons, en particulier durant leurs stades de vie les plus précoces (e.g. Laroche et al. 2002, Marchand et al. 2003, Rowe 2003, Kerambrun et al. 2012a). L'exposition à des contaminants chimiques peut également induire une baisse significative de leur fonction d'alimentation (Stephens et al. 2000, Saborido-Rey et al. 2007). Par ailleurs, une des réponses sub-létales des organismes exposés de manière chronique à des contaminants chimiques est une modification dans l'allocation de leur énergie qui est alors préférentiellement utilisée pour résister au stress chimique plutôt qu'au maintien des fonctions basales et à la croissance. Ces deux réponses ont un effet négatif sur la fitness[3] globale des individus (Rowe 2003). Or, les juvéniles de poissons dont la croissance et le stockage d'énergie sont limités ont moins de chance de survivre et donc de recruter dans les stocks adultes (Sogard 1997). Ainsi, même si les contaminants chimiques sont en-deçà des concentrations létales aiguës, l'exposition chronique des juvéniles de poissons à ces derniers peut avoir des conséquences sur leur survie à moyen et long terme. Par ailleurs, cette exposition chronique peut entraîner une baisse de fertilité future des individus avec des conséquences sur le renouvellement des stocks (Rowe 2003). La pollution engendrée par les activités portuaires peut donc avoir des conséquences importantes sur la perte de fonction de nourricerie des habitats littoraux dans et autour des ports construits.

Enfin, la construction d'un port modifie profondément les courants locaux (Martin et al. 2005) et crée un environnement sonore, olfactif et lumineux artificiel. Or, parmi les facteurs permettant aux

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[3] La notion de fitness est l'une des pièces maîtresses de la biologie évolutive du 20e siècle. Elle est évoquée pour qualifier un changement dans la fréquence d'une entité (génotype ou phénotypique), ou pour inscrire l'opération possible de la sélection naturelle dans un formalisme mathématique. La notion intervient dès qu'il est désirable de saisir le succès différentiel des formes vivantes effectivement observées. Ainsi, la fitness est une mesure de la sélection naturelle et peut être définie de nombreuses façons. Plusieurs traductions peuvent être données au mot anglais « fitness ». Si le terme « valeur sélective » semble être le plus consensuel, de vifs débats demeurent sur la traduction. Aussi conserverons-nous le mot anglais « fitness» tout au long de ce manuscrit.

larves de sélectionner leur habitat juvénile, les sons (e.g. Simpson et al. 2005, Mann et al. 2007), les odeurs (e.g. Atema et al. 2002, Gerlach et al. 2007, Paris et al. 2013) ou encore la lumière (e.g. McLeod & Costello 2017) sont les plus fréquemment cités. Il est donc possible que les modifications physiques indirectes engendrées par la construction des ports influencent les flux de larves alimentant les zones littorales concernées.

1.5. Conservation du littoral, urbanisation et maintien des stocks de poissons côtiers

Une des clés du maintien des stocks de poissons côtiers réside dans la préservation et la non-dégradation de leurs zones de nourricerie. Face à l'érosion marquée de la biodiversité marine, au déclin de nombreuses ressources halieutiques et à la dégradation des habitats marins et en particulier des habitats côtiers, les aires marines protégées (AMP) apparaissent de plus en plus comme un instrument privilégié de la gestion intégrée des zones côtières (Lester et al. 2009). Les AMP sont principalement utilisées pour promouvoir la conservation à long terme des habitats et des espèces. En protégeant une zone dans son ensemble, à savoir aussi bien les habitats que les espèces, elles sont destinées à maintenir ou restaurer la biodiversité (Bohnsack & Ault 1996, Dayton et al. 2000), et à protéger des espèces emblématiques et/ou menacées.

La première AMP a été créée en 1935 en Floride (Randall 1969). Depuis, le nombre d'AMP n'a cessé d'augmenter, passant de 430 en 1985 (Silva et al. 1986) à plus de 1 300 en 1995 (Kelleher 1996). A l'heure actuelle, il existe plus de 5 000 AMP dans le monde représentant 0,7 % de la surface des océans. Or, les nouvelles AMP concernent de plus en plus des zones profondes au détriment des petits fonds côtiers où les conflits d'usages sont très importants (Meinesz & Blanfuné 2015). A titre d'exemple, en 2013, la surface protégée entre 0 et 20 m en Méditerranée française était de 962 hectares, soit 0,57 % de la surface totale de cette zone de profondeur (Meinesz & Blanfuné 2015). A la même période, la surface des ports dépassait les 4 000 hectares (MEDAM 2017). Le nombre d'AMP semble donc aujourd'hui insuffisant pour protéger les zones de nourriceries des poissons côtiers. Or leur développement se heurte à de nombreuses difficultés réglementaires et de conflit d'usage (Voyer et al. 2014, Liu et al. 2015, Meinesz & Blanfuné 2015). Par ailleurs, les AMP ne sont souvent pas suffisantes face aux pressions anthropiques. En effet, elles ne protègent pas les écosystèmes de l'ensemble des pressions, en particulier de la pollution côtière ou de l'arrivée d'espèces invasives (Agardy 1994, Halpern 2003).

Contrairement à toutes les autres atteintes au milieu marin, les destructions par recouvrement ou par enclavement, liées à la construction d'un port, sont définitives. Les collectivités peuvent tenter de réduire l'impact chimique des ports (traitement des eaux, limitation des rejets toxiques…) mais il est utopique d'envisager leur destruction pour reconstituer les zones de nourriceries naturelles détruites. En outre, le développement de nos sociétés s'accompagne d'un accroissement des échanges commerciaux, du développement du tourisme nautique et des activités de loisir. De plus en plus de ports seront construits à l'avenir avec des conséquences inévitables sur les zones de nourricerie naturelles et donc sur les populations de poissons qui en dépendent.

Face à ce constat inquiétant, il semble aujourd'hui indispensable d'adopter une approche pragmatique : s'il n'est pas possible de protéger totalement les zones de nourriceries, si l'impact des ports actuels ou futurs sur ces dernières est inévitable et si cette pression va augmenter dans les années à venir, alors, il faut trouver des solutions pour tenter d'atténuer leurs effets négatifs, en particulier sur les nourriceries de poissons côtiers. Pour cela, il est nécessaire dans un premier temps de comprendre le fonctionnement écologique des habitats artificiels créés dans les ports.

Il est frappant de constater que, malgré leur prédominance sur le littoral, l'écologie fonctionnelle des systèmes portuaires n'a été que très peu étudiée à ce jour (Chapman & Blockley 2009, Bulleri & Chapman 2010). Les ports peuvent être qualifiés d'écosystèmes de synthèse (Odum & Barrett 1971) ou encore émergeants (Milton 2003) qui résultent d'actions humaines délibérées et présentent des conditions et des combinaisons d'organismes qui n'existent pas naturellement. Comme l'ont souligné Redford & Richter (1999), ces écosystèmes de synthèse peuvent avoir des fonctions écologiques utiles. Encore faut-il savoir lesquelles et comment les exploiter au mieux.

Jusqu'à présent, peu d'études se sont intéressées aux populations de poissons à l'intérieur des zones portuaires. Or, les digues périphériques des ports sont souvent colonisées sur leur face externe par divers poissons rocheux, notamment au stade juvénile (Ruitton et al. 2000, Pizzolon et al. 2008, Pastor et al. 2013). Par ailleurs, les quelques données publiées semblent indiquer que le nombre d'espèces de poissons et leur abondance à l'intérieur des ports sont souvent comparables à ceux observés en zone naturelle rocheuse (Clynick et al. 2008), notamment en ce qui concerne les poissons juvéniles (Mercader et al. 2017). En outre, certains critères laissent à penser que les zones portuaires, bien abritées et riches d'un point de vue trophique, pourraient, dans certaines conditions, fournir à plusieurs espèces de poissons des zones croissance et de survie juvéniles acceptables (Dufour et al. 2009). Ceci minimiserait d'autant l'impact négatif de la disparition des zones de nourriceries naturelles sur le maintien des stocks. Cependant, encore faut-il que la qualité physique et chimique des habitats portuaires corresponde suffisamment aux besoins des juvéniles de poissons. Il devient alors essentiel d'étudier l'influence des principales pressions anthropiques en zone portuaire (diminution complexité structurale, pollution, etc.) sur le succès de l'installation benthique des juvéniles de poissons, leur survie et leur condition afin de mettre en place des mesures de gestion ou de réhabilitation écologique (encart 1) adéquates dans les ports.

Encart 1 : La réhabilitation écologique.

Les termes de « restauration écologique » et de « réhabilitation écologique » sont souvent confondus. Le premier, souvent mal employé, désigne une activité intentionnelle qui initie ou accélère le rétablissement d'un écosystème avec le respect de sa composition spécifique, sa structure des communautés, ses fonctions écologiques, sa cohérence avec l'environnement physique et sa connectivité avec le paysage alentour (Clewell & Aronson 2013). Envisager des solutions de restauration écologique suppose et nécessite une bonne connaissance de l'écologie fonctionnelle et évolutive des écosystèmes ciblés, de l'histoire de la dégradation anthropique et, enfin, du choix d'un écosystème de référence pour guider la planification, la réalisation, le suivi et l'évaluation du projet de restauration (White & Walker 1997).

Tout comme la « restauration écologique », la « réhabilitation écologique » se sert des écosystèmes historiques ou préexistants comme références, mais les buts et stratégies des deux activités diffèrent. La réhabilitation insiste sur la réparation et la récupération des processus, et donc sur la productivité et les services de l'écosystème, tandis que la restauration vise également à rétablir l'intégrité biotique préexistante, en termes de composition spécifique et de structure des communautés. Pour Aronson et al. (1995), la réhabilitation vise à « réparer, aussi rapidement que possible, les fonctions (résilience et productivité), endommagées ou tout simplement bloquées, d'un écosystème en le repositionnant sur une trajectoire favorable (la trajectoire naturelle ou une autre trajectoire à définir) ». Cette approche est la plus pertinente dans les zones portuaires.

I.6. Projets de réhabilitation de la fonction de nourricerie à l’intérieur des zones portuaires

Les principales actions entreprises à ce jour en termes de réhabilitation écologique des zones portuaires se sont basées sur ce que l’on appelle « l'ingénierie écologique ». Ce terme a fait l’objet de nombreux débats et sa définition a évolué dans le temps et selon les auteurs. L’une des plus complète et aboutie est celle dressée par le Manifeste de la recherche pour l’ingénierie écologique rédigé dans le cadre du Programme Interdisciplinaire de Recherche CNRS/Irstea Ingecotech-Ingeco (2007-2011), dans lequel l’ingénierie écologique désigne « les savoirs scientifiques et les pratiques, y compris empiriques, mobilisables pour la gestion de milieux et de ressources, la conception, la réalisation et le suivi d’aménagements ou d’équipements inspirés de, ou basés sur, les mécanismes qui gouvernent les systèmes écologiques. Elle fait appel à la manipulation, le plus souvent *in situ*, parfois en conditions contrôlées, de populations, de communautés ou d’écosystèmes, au pilotage de dynamiques naturelles et à l’évaluation de leurs effets désirables ou indésirables ». L’ingénierie écologique est donc une ingénierie centrée sur le vivant, envisagée comme moyen ou comme objectif de l’action (Rey et al. 2014).

Depuis 2011, plusieurs études pilotes ont été menées, en particulier en Méditerranée, avec l’objectif d'utiliser l'ingénierie écologique pour réhabiliter une fonction de nourricerie à l'intérieur des ports (Lenfant et al. 2015). Le principe des solutions techniques proposées est globalement invariant. Il consiste à pallier la dégradation de l’habitat en fixant des micro-structures artificielles, complexes et tridimensionnelles sur les ouvrages portuaires (figure I.3). Ces travaux supportent donc l’idée que les ouvrages portuaires peuvent être modifiés structurellement pour augmenter leur attractivité et leur qualité pour la survie des juvéniles de poissons, ce qui leur permettrait de contribuer au maintien des populations de poissons tout en assurant leurs fonctions premières. Ces hypothèses se basent sur un socle solide de connaissances sur la biologie et la physiologie des premiers stades de vie chez les poissons.

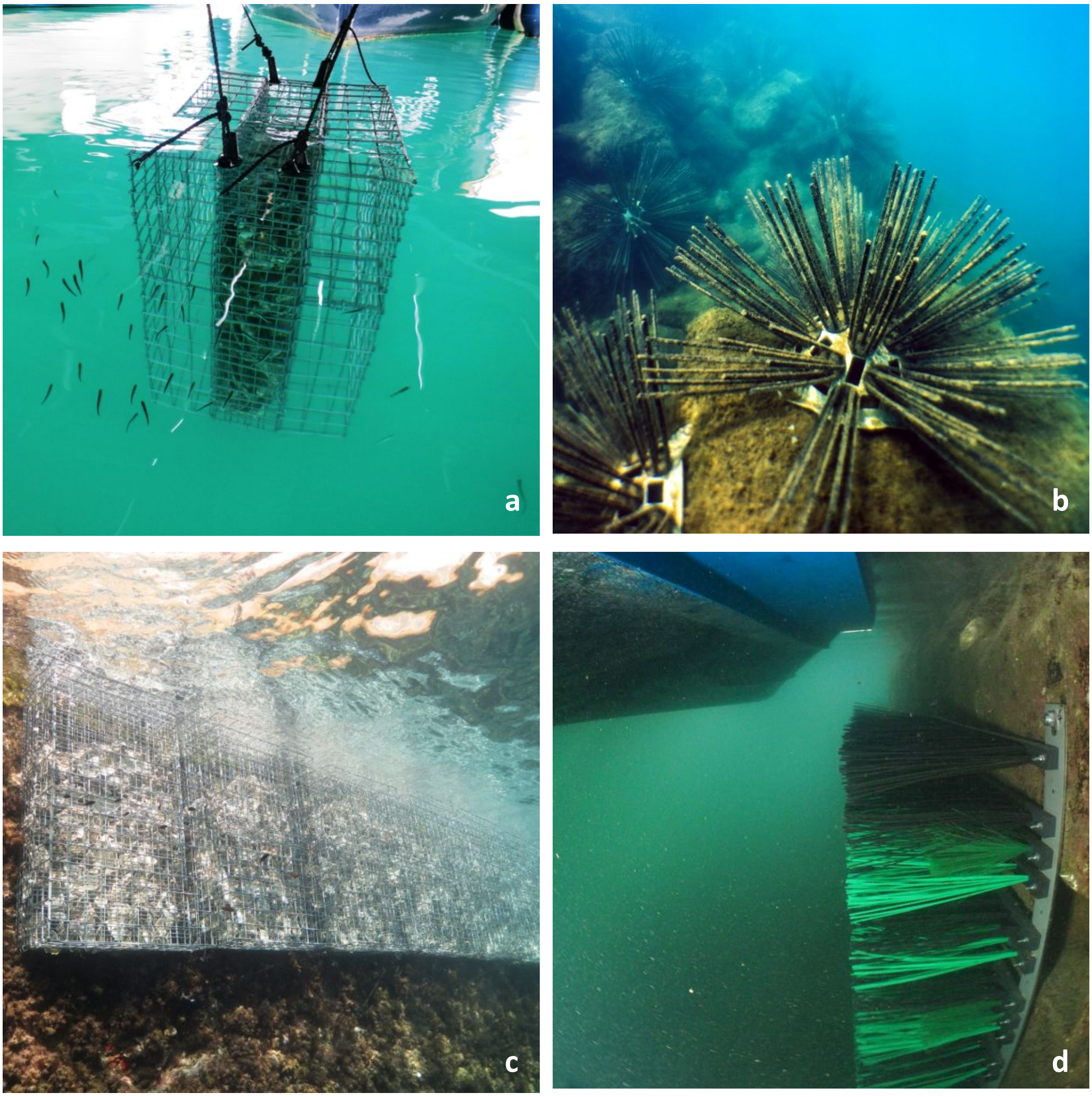


Figure I.3 : Exemples de micro-structures installées sur les ouvrages portuaires en vue d'augmenter leur complexité structurale. a) module Biohut sous ponton – Ecocéan. b) modules oursins fixés sur les digues – Seaboost, EGIS Eau. c) modules Biohut quai – Ecocéan. d) module ReFish – Suez Consulting.

En effet, si d'un point de vue théorique les variations d'abondance des populations de juvéniles après installation benthique ont longtemps été considérées comme le seul résultat des variations des apports larvaires (hypothèse du recrutement limitant - Doherty 1991), de nombreuses études ont montré que pour certaines espèces, la disponibilité des refuges contre les prédateurs dans les habitats juvéniles avait une influence non négligeable sur ce paramètre (hypothèse de l'habitat limitant - Holbrook et al. 2000, Holbrook & Schmitt 2002) en augmentant les taux de survie juvénile

(Forrester 1990, Shima & Osenberg 2003, Lecchini et al. 2007). La quantité de juvéniles issue d'un habitat donné et pouvant rejoindre les populations adultes résulte donc en partie de la disponibilité en refuges contre les prédateurs au moment de l'installation. En ce sens, en offrant des abris aux juvéniles de poissons, la fixation de micro-structures artificielles sur les ouvrages portuaires est susceptible d'augmenter leur taux de survie juvénile et donc leur participation au recrutement.

Les suivis réalisés lors de ces études pilotes ont tous mis en évidence une augmentation des abondances de poissons juvéniles sur les ouvrages portuaires lors de la mise en place des micro-structures artificielles. Ces premiers résultats sont donc pour le moins encourageants. Cependant, ils ne permettent pas de conclure seuls à une véritable amélioration de la fonction de nourricerie dans les zones portuaires car celle-ci dépend également de l'impact des conditions environnementales, en particulier contaminants chimiques, sur la santé et la croissance des juvéniles dans les ports.

I.7. Objectif général de la thèse

Dans ce contexte, l'objectif général de ce travail de thèse était de préciser si les zones portuaires remplissent ou non les conditions pour servir de nourriceries alternatives à certains poissons marins côtiers. Selon Beck et al. (2001), une zone de nourricerie se définit selon quatre critères :

- La présence de fortes abondances de juvéniles,
- Une alimentation locale permettant une croissance élevée,
- Une fréquentation durable permettant une survie élevée,
- Une participation forte des individus fréquentant la nourricerie aux populations adultes.

Parce que l'estimation *in situ* des mortalités est difficile et nécessite un échantillonnage très lourd, plusieurs travaux ont envisagé d'étudier la qualité des nourriceries en utilisant principalement la croissance ou la condition des juvéniles (Scharf 2000, Ross 2003). La forte liaison entre ces paramètres et la mortalité permet en effet d'envisager leur utilisation comme indicateurs synthétiques de la qualité des milieux pour la survie des poissons (Suthers 1998). Une zone de nourricerie peut donc être identifiée sur des critères d'abondance à l'installation, de croissance et de condition des juvéniles et de contribution aux stocks adultes. C'est l'approche choisie ici pour évaluer si les ports peuvent être des nourriceries alternatives pour les poissons côtiers (figure I.4).

Par ailleurs, même si ce paramètre n'entre pas dans la définition de Beck et al. (2001), cette thèse s'est intéressée aux niveaux de contamination des poissons à l'issue de leur vie juvénile pour déterminer l'impact éventuel d'un passage dans les ports sur leur santé et leur fitness.

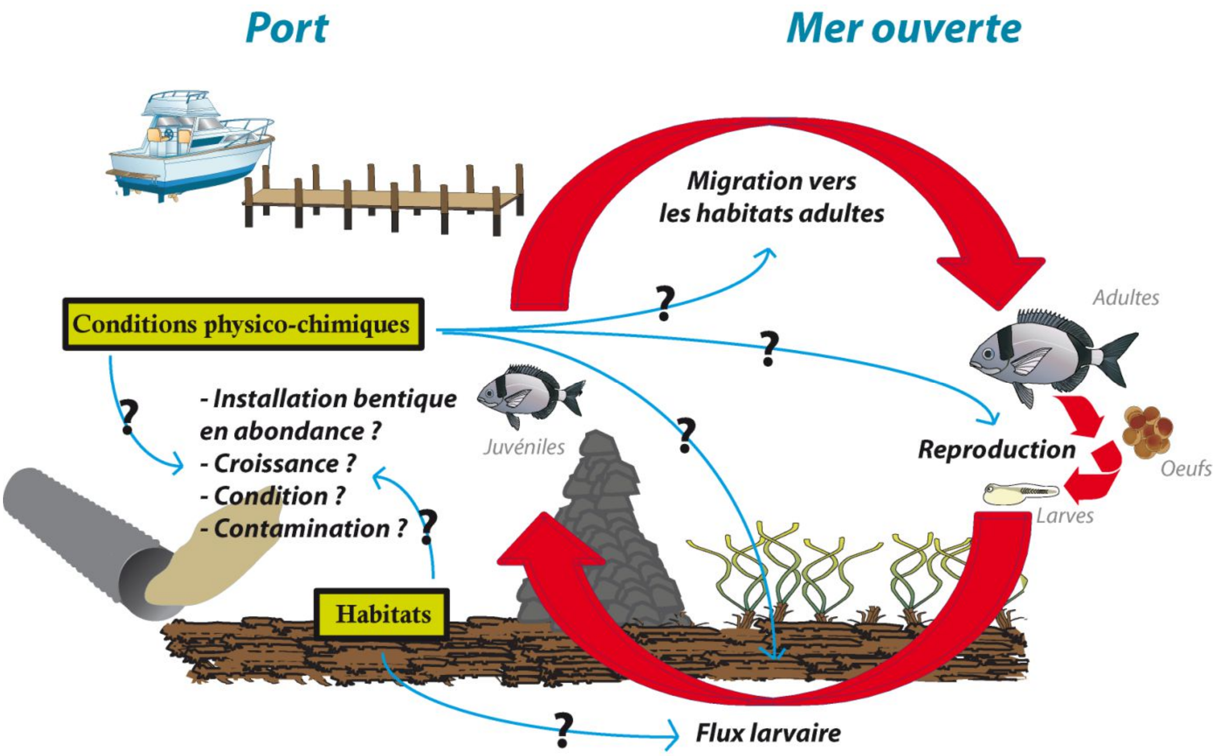


Figure I.4 : Description schématique de la problématique générale de la thèse. Les images proviennent du site http://www. ian.umces.edu.

La qualité d'un habitat juvénile résulte d'interactions complexes et dynamiques entre les organismes y grandissant et différents facteurs environnementaux d'origine naturelle ou anthropique : température, nourriture disponible, présence de prédateurs, pollution, etc. (Gibson 1994, Able et al. 1999). Elle ne peut donc être mesurée directement et doit être évaluée sur la base d'une comparaison inter-sites (Meng et al. 2000, Goldberg et al. 2002, Lloret & Planes 2003). Ainsi, comparer les critères d'évaluation de Beck et al. 2001 entre des zones portuaires et des nourriceries naturelles devrait permettre d'évaluer leur qualité en tant que nourriceries potentielles pour les poissons marins côtiers.

Chapitre 2. Matériels et Méthodes

II.1. La Méditerranée française

La Méditerranée ne représente que 0,8 % de la superficie marine mondiale (Defant 1961). Pourtant, elle accueille presque 18 % de la biodiversité marine connue (Bianchi & Morri 2000, Coll et al. 2010), ce qui fait d'elle un haut lieu de biodiversité (Myers et al. 2000). Or, cette biodiversité n'est pas répartie de façon homogène. Elle est très élevée en zone côtière puis décroît avec la profondeur (Coll et al. 2010), ce qui la rend encore plus vulnérable.

En effet, environ 7 % de la population mondiale vit dans les pays côtiers méditerranéens, soit 460 millions d’habitants auxquels il faut ajouter environ 200 millions de touristes internationaux. La moitié de cette population vit à proximité immédiate des côtes. Le littoral méditerranéen figure ainsi parmi les secteurs les plus densément peuplés et les plus fortement urbanisés de la planète. En outre, selon les projections démographiques à 2025, le pourcentage de la population méditerranéenne vivant sur les côtes devrait croître de 50 % à 88 % avec des conséquences significatives sur l’artificialisation du littoral (PNUE/PAM 2009). Les côtes méditerranéennes et les écosystèmes qu’elles abritent sont donc soumis à des pressions anthropiques parmi les plus importantes de la planète et dont l’intensité devrait encore s’aggraver (Costello et al. 2010).

Par ailleurs, la Méditerranée est aussi un lieu de trafic maritime intense. A titre d'exemple, le nombre de traversées par an par les navires pétroliers est estimé à 200 000, ce qui représente 28 % du trafic pétrolier mondial en mer (Laubier 2003). Ces navires ne se contentent pas de passer en Méditerranée mais viennent alimenter les pays méditerranéens et limitrophes.

Le long du littoral méditerranéen français, la densité démographique n'a cessé de croître durant les 70 dernières années. Elle y est aujourd'hui environ cinq fois supérieure à la moyenne nationale (Béoutis et al. 2004). Cet accroissement de la population s'est accompagné d'un développement urbain rapide et d'une augmentation du taux d'artificialisation du littoral. Aujourd'hui, 11,41 % du linéaire méditerranéen est artificialisé et la majorité des ouvrages construits sont des ports (figure II.1). A ces pressions viennent s'additionner celles liées à la surpêche, à la pollution et aux changements climatiques, avec des conséquences majeures sur le fonctionnement des écosystèmes côtiers (Crain et al. 2008, Darling & Côté 2008, Halpern et al. 2008), notamment en Méditerranée française (MEDAM 2017).

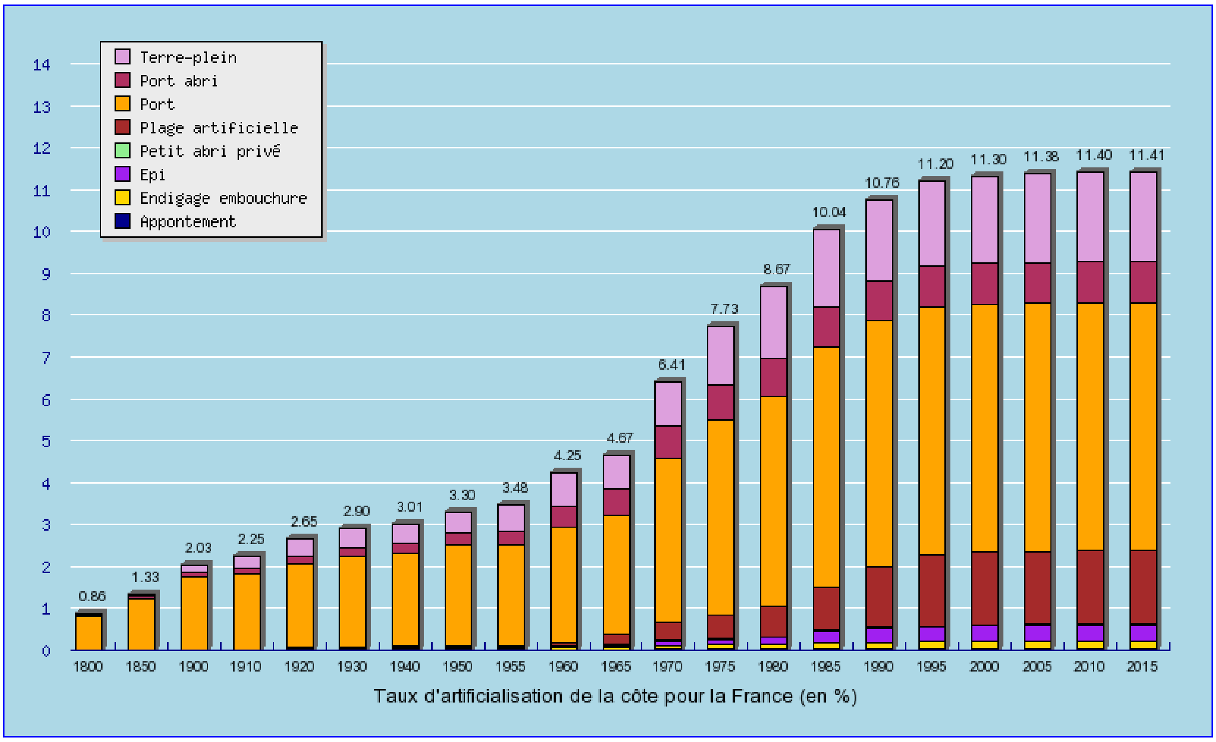


Figure II.1 : Taux d'artificialisation du linéaire côtier en Méditerranée française. Source : www.medam.org, consulté le 30/06/2017.

Ainsi, non seulement la Méditerranée française présente un intérêt écologique majeur mais celui-ci de plus fortement menacé par des pressions anthropiques multiples, dont un nombre important de constructions portuaires.

II.2. La rade de Toulon : un cas d'étude

La rade de Toulon est située au Sud-Est du littoral français sur la façade méditerranéenne, en région Provence-Alpes-Côte d'Azur (PACA), entre les deux grandes métropoles de Marseille et de Nice. Une digue de 1,2 km, construite en 1882, divise la rade en deux parties : la petite rade au Nord-Ouest (9,8 km²) et la grande rade au Sud-Est (42,2 km²) (figure II.2).

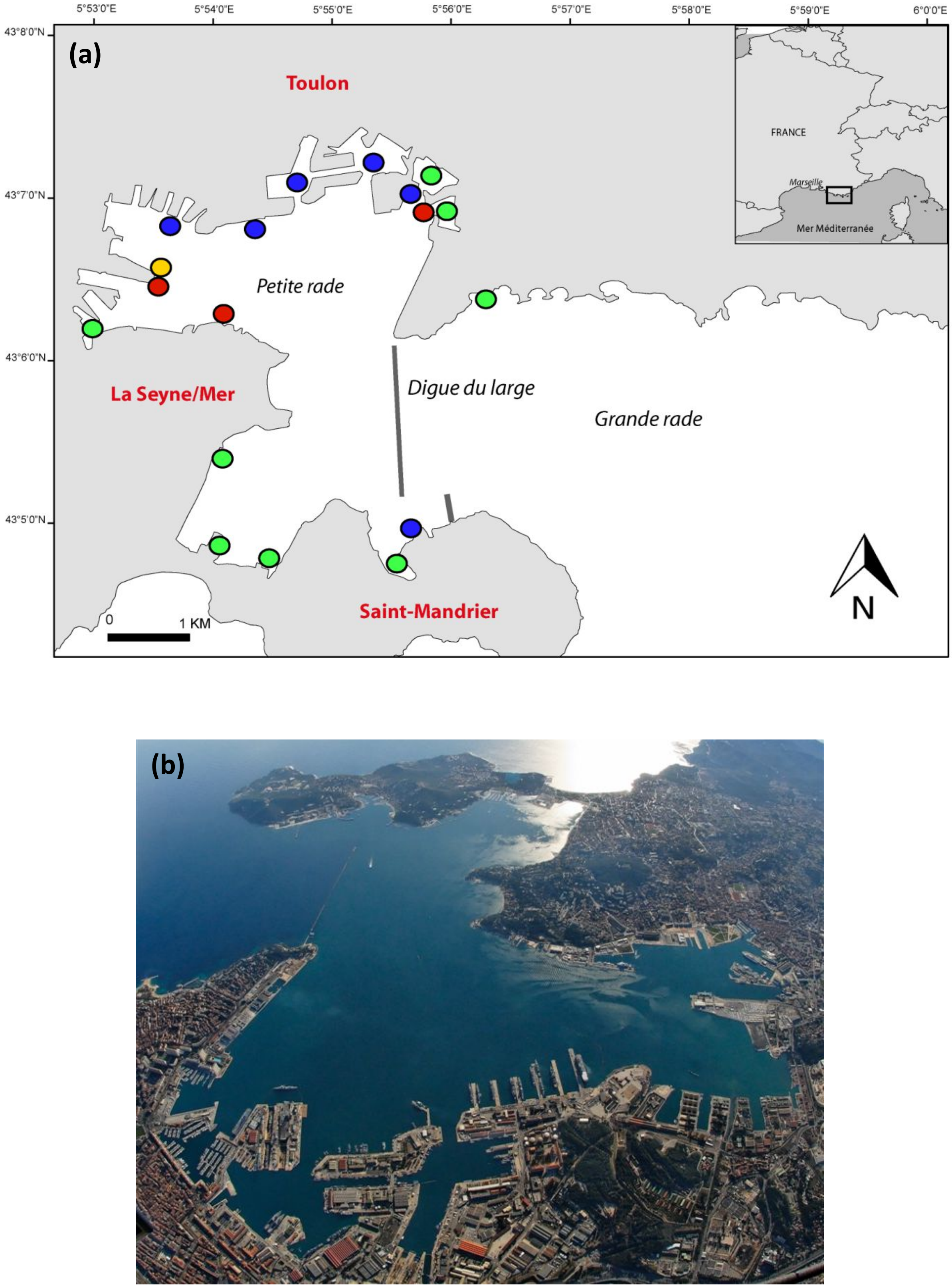


Figure II.2 : Urbanisation dans la rade de Toulon. (a) Carte de la rade. Les cercles correspondent aux zones portuaires : en vert les marinas, en rouge les terminaux de ferry et/ou de bateaux de croisière, en jaune les zones d'accostage des navires de commerce et en bleu les ports militaires. (b) Vue aérienne de la petite rade. Source : http://www.blog.nautal.fr.

La rade de Toulon a une très longue histoire portuaire. Déjà, 2 200 ans avant la colonisation romaine, Toulon était un abri portuaire pour les navires grecs commerçant avec les Ligures et les Celtes. Le site a conservé une vocation portuaire et militaire jusqu'à la chute de Rome. Au Moyen-âge, Toulon a été cédé aux Comtes de Provence qui en ont fait un petit port de pêche. Suite au rattachement de la Provence à la France au XV^{ème} siècle, Toulon est devenu un haut lieu de construction navale abritant les flottes militaires dont les galères françaises à partir de 1610. Durant quatre siècles, l'arsenal s'est développé progressivement au gré des différents événements historiques. En 1942, sous l'occupation de l'armée allemande, la flotte française s'est sabordée, engloutissant ainsi 382 000 tonnes de navires dans la rade. Puis entre novembre 1943 et août 1944, la ville et l'arsenal ont été presque entièrement détruits par les bombardements alliés et les mines allemandes. Cette période a eu des conséquences dramatiques en termes de contamination chimique de la petite rade. En 1956, après des années de reconstruction, l'indépendance de la Tunisie, la guerre d'Algérie et l'expédition de Suez ont redonné à la rade de Toulon son rôle de premier port militaire français et de centre névralgique de la Méditerranée en faisant ainsi le second port militaire de France et le premier de Méditerranée.

Parallèlement à l'activité portuaire militaire, les chantiers navals se sont développés sur la rade de Toulon, en particulier au cours du XIX^{ème} siècle. Ces derniers, largement détruits lors de la Seconde Guerre mondiale, ont été reconstruits et agrandis dès 1949 pour atteindre 25 hectares et un front de mer de 1 400 mètres. En 1973, à la veille du choc pétrolier, ces chantiers navals employaient plus de 5 000 personnes. Puis, après l'échec des fusions avec les chantiers navals de la Ciotat et de Dunkerque en 1983, ils ont connu une baisse conséquente de leur activité jusqu'à leur fermeture définitive en 1989.

Aujourd'hui, le port militaire de Toulon abrite 60 % du tonnage de la Marine Nationale Française (6 sous-marins nucléaires d'attaque, et 37 bâtiments de surface, dont le porte-avion Charles de Gaulle), et emploie plus de 20 000 militaires et 10 000 civils. La navigation de plaisance occupe également une place importante dans la rade puisque les ports de Toulon, de la Seyne-sur-mer et de Saint-Mandrier-sur-Mer totalisent 2 200 places disponibles. Une autre activité économique du port de Toulon est le transport de passagers, essentiellement à destination de la Corse (1 000 rotations de ferries et 1,2 million de passagers par an). Enfin, la rade de Toulon abrite une activité de transport de marchandise et de matières premières.

L'agglomération urbaine qui s'est développée aux abords de la rade de Toulon représente aujourd'hui environ 370 000 personnes. La rade de Toulon est devenue au fil du temps le siège de nombreuses activités industrielles et commerciales qui sont au cœur de l'économie toulonnaise. Il n'existe quasiment plus de zones naturelles dans la petite rade de Toulon qui regroupe l'essentiel des activités militaires (arsenal), industrielles (ex. DCNS), portuaires (transports marchands et touristiques), et aquacoles (pisciculture et conchyliculture) de la baie. En outre, du fait des activités industrielles et militaires actuelles et passées, celle-ci est extrêmement contaminée par les éléments traces métalliques (ETM) dont le plomb, le cuivre, le zinc et le mercure (Tessier et al. 2011, Jean et al. 2012, Pougnet et al. 2014, Dang et al. 2015) (figure II.3). A titre d'exemple, les concentrations en mercure dans les sédiments autour du port militaire et commercial de Toulon sont parmi les plus fortes jamais mesurées dans un système marin (Tessier et al. 2011). Les sites industriels et portuaires de la petite rade présentent donc des niveaux de contamination extrêmes qui les rendent particulièrement bien adaptés à notre étude. Si les conditions environnementales dans les ports de la rade de Toulon sont compatibles avec une fonction de nourricerie, il est probable qu'elles le soient aussi dans d'autres ports moins contaminés.

Contrairement à la petite rade, la grande rade de Toulon est essentiellement destinée aux activités touristiques. Elle abrite plusieurs zones de petits fonds côtiers faiblement impactées par les activités anthropiques et présentant des niveaux de concentrations en ETM proches des bruits de fond géochimiques de la région (Tessier et al. 2011). En outre, les caractéristiques physiques de certaines de ces zones correspondent à celles des nourriceries de plusieurs espèces des poissons marins : des habitats peu profond (0 - 2m), protégés des vents dominants, caractérisés par une faible pente couverte de sable, de cailloutis, de galets ou de roches recouvertes d'algues (Harmelin-Vivien et al. 1995, Cheminee et al. 2011).

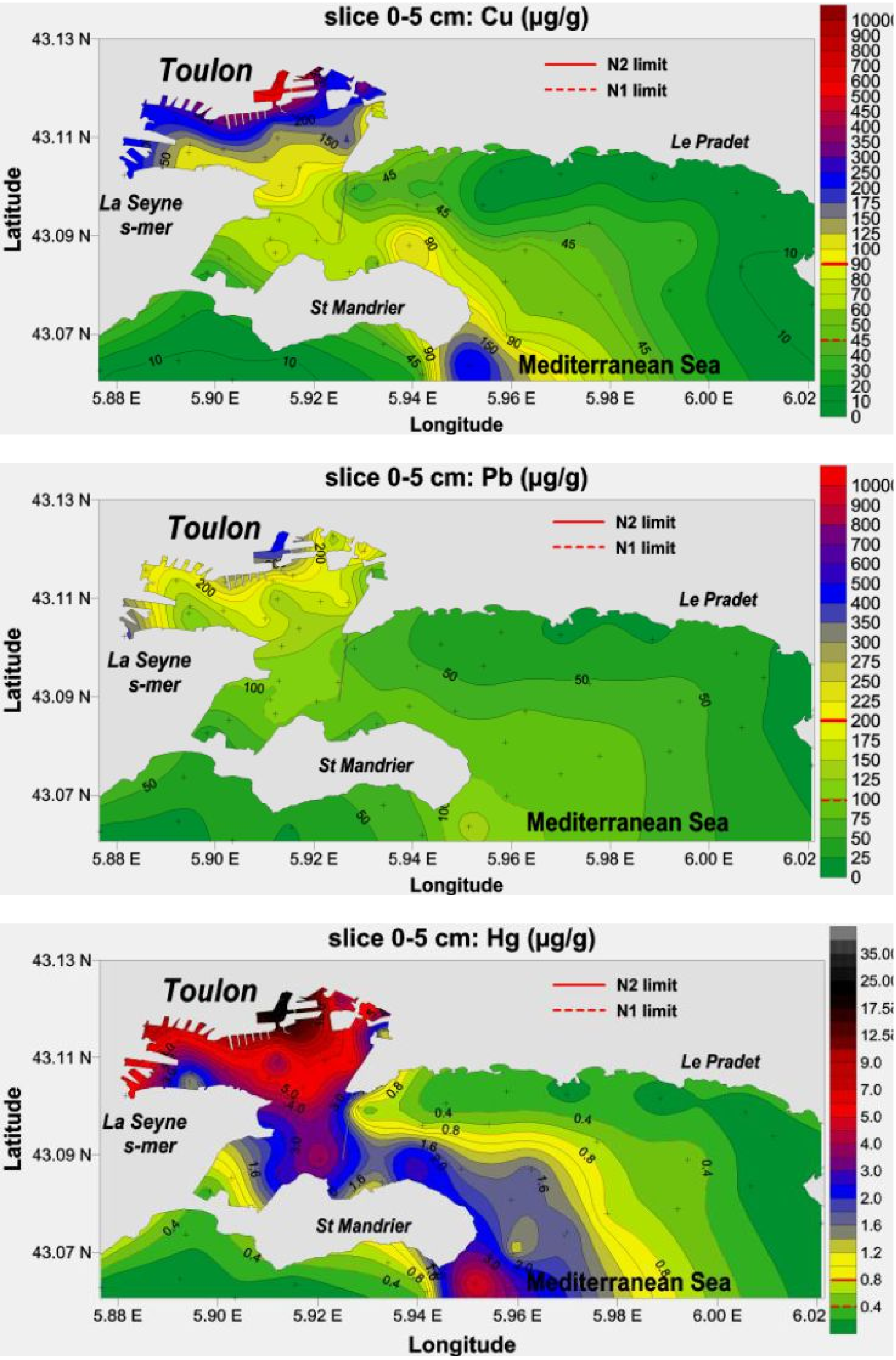


Figure II.3 : Distributions spatiales en Cu, Pb et Hg dans la tranche 0-5 cm des sédiments de la rade de Toulon. Les niveaux N1 et N2 correspondent aux seuils de qualité proposés par le groupe GEODE dans le cadre de la convention OSPAR. En deçà de N1, les valeurs observées sont comparables aux « bruits de fond » environnementaux. Au-delà de N2, les sédiments sont considérés comme contaminés et potentiellement toxiques (Source Tessier 2012).

Ainsi, plusieurs types de ports (commerce, militaire, marinas) sont présents dans la rade de Toulon dont un port majeur, le port de Toulon. Ces ports (et en particulier le port de Toulon) font partie des plus impactés de France par les contaminants chimiques (CETMEF 2010). D'autre part, la rade abrite des zones côtières naturelles, faiblement impactées par les pressions anthropiques qui peuvent fournir des zones de références locales. Elle semble donc particulièrement bien adaptée à notre étude, les résultats obtenus pour les ports de cette zone atelier pouvant très certainement être transposés à d'autres zones portuaires moins denses et moins contaminées.

II.3. Modèles biologiques : les sars (genre *Diplodus*)

Parmi les espèces côtières retrouvées au stade juvénile dans les ports méditerranéens, les sars (espèces du genre *Diplodus*) occupent une place privilégiée en termes d'abondances (Clynick 2006, Mercader et al. 2017). Ces poissons appartiennent à la famille des Sparidae qui regroupe environ 200 espèces réparties en 42 genres et sous genres. En Méditerranée, on recense 23 espèces de sparidae appartenant à 11 genres. Parmi elle, les espèces du genre *Diplodus* sont les plus répandues, avec cinq espèces communément présentes : *Diplodus sargus sargus* (Linnaeus, 1758), dénommé ci-après *D. sargus*, *D. vulgaris* (Geoffroy Saint-Hilaire, 1817), *D. puntazzo* (Walbaum, 1792), *D. annularis* (Linnaeus, 1758) et *D. cervinus* (Lowe, 1938). Les quatre premières espèces sont de loin les plus abondantes et dominent les assemblages de poissons des habitats infralittoraux rocheux méditerranéens (Harmelin 1987). Elles sont en outre très présentes au stade juvénile sur les structures artificielles (digues, récifs, etc.) (Ruitton et al. 2000, Guidetti 2004, Clynick 2006, Pastor et al. 2013), y compris à l'intérieur des ports (Clynick 2008, Bouchoucha et al. 2016, Bosch et al. 2017, Mercader et al. 2017).

Les schémas d'installation benthique des juvéniles *D. sargus*, *D. vulgaris*, *D. puntazzo* et *D. annularis* en zone naturelle ont été largement décrits : *D. annularis*, *D. puntazzo* et *D. sargus* s'installent tous en une vague, respectivement en juin-juillet, en octobre-novembre et en mai-juin alors que *D.vulgaris* s'installe en deux vagues, en novembre-décembre puis en janvier-février, le deuxième pic étant prédominant (García-Rubies & Macpherson 1995, Harmelin et al. 1995, Vigliola et al. 1998). Chez les sars, les caractéristiques physiques de l'habitat (en particulier la nature du substrat, la profondeur, la pente, le degré de protection contre le vent et les vagues, etc.) déterminent fortement le succès de l'installation et les taux de mortalité pré-recrutement (Harmelin-Vivien et al. 1995, Macpherson et al. 1997, Vigliola & Harmelin-Vivien 2001). *Diplodus puntazzo* et *D. sargus* s'installent généralement tous les deux dans des zones très peu profondes (< 1m) caractérisées par une faible pente couverte de sable et cailloutis. *Diplodus vulgaris* semble choisir des profondeurs plus importantes (1-6 m) et peut s'installer sur une variété plus large de substrats (détritique grossier, gravier, cailloutis ou galets). Enfin, l'installation de *D. annularis* a lieu à des profondeurs plus importantes (> 5m) et quasi exclusivement dans l'herbier de posidonies (Harmelin-Vivien et al. 1995, Ventura et al. 2014). S'il est admis que cette dernière espèce demeure fortement liée à l'herbier durant toute sa vie juvénile, une diminution progressive de la spécificité en termes d'habitats au cours de la vie juvénile accompagnée de migrations verticales et horizontales a été démontrée pour *D. puntazzo*, *D. vulgaris* et *D. sargus* (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). Ainsi, la comparaison des résultats obtenus pour ces quatre espèces voisines pourra apporter des renseignements importants sur l'influence des variations saisonnières des facteurs environnementaux sur la qualité des habitats juvéniles.

Par ailleurs, la mortalité des juvéniles de sars dans leurs habitats naturels dépend à la fois de processus denso-indépendants du type "recruitment limitation" et de processus denso-dépendants liés à la à la disponibilité d'abris (Vigliola 1998). Ces espèces sont donc de bonnes candidates pour tester l'effet de la complexification du substrat sur la survie durant la vie juvénile benthique.

Les sars sont donc particulièrement adaptés pour cette étude, étant parmi les espèces de poissons les plus susceptibles d'utiliser les ports comme nourriceries alternatives. Compte tenu des différences dans les dates d'installation benthique et dans les préférences en termes d'habitats juvéniles pour ces espèces, l'étude de leurs abondances et de leurs croissances et leurs conditions respectives dans différents types de zones portuaires devrait permettre d'émettre des conclusions générales sur l'utilisation potentielle des ports comme nourriceries par les poissons marins côtiers.

II.4. Approche retenue dans la thèse

Dans ce contexte, nous avons décidé de commencé l'étude de la capacité des ports à constituer des zones de nourricerie pour les juvéniles de poissons côtiers en Méditerranée française, en prenant les sars comme espèces modèles.

Dans un premier temps (**chapitre 3**), nous avons cherché à vérifier si les juvéniles de sars pouvaient s'installer et grandir sur les principaux ouvrages disponibles à l'intérieur de ports. Pour cela, un suivi des abondances des juvéniles de *D. sargus*, *D. vulgaris*, *D. puntazzo* et *D. annularis* a été réalisé dans cinq ports répartis sur l'ensemble de la façade Méditerranéenne française, pendant deux années consécutives. Afin de tester l'effet de l'augmentation de la complexité structurale des habitats portuaires sur les abondances des juvéniles de poissons, des micro-structures artificielles ont été fixées sur les quais et les pontons des ports étudiés. Les abondances des juvéniles de ces quatre espèces ont été ensuite comparées pendant plusieurs mois consécutifs entre structures nues et structures équipées pour chaque site.

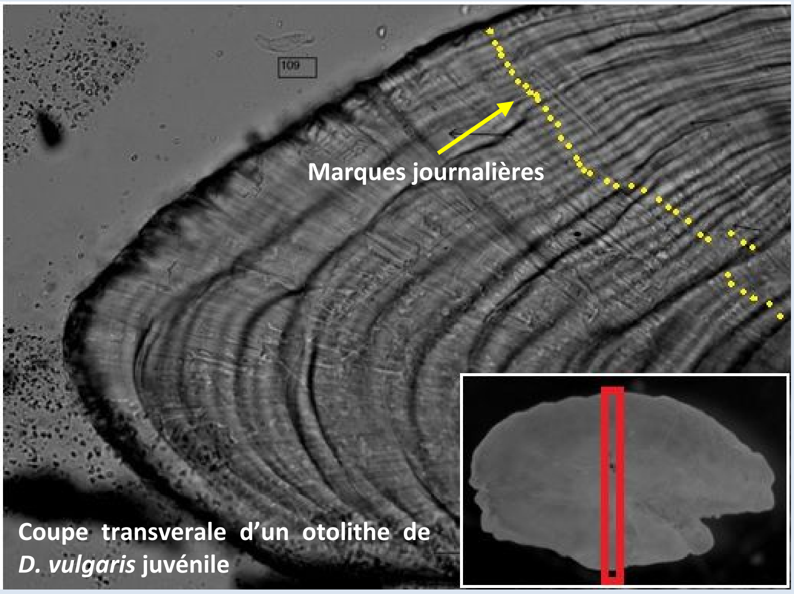
Dans un second temps (**chapitre 4**), nous avons cherché à comparer les taux de croissance et la condition physiologique des juvéniles de sars à l'intérieur et à l'extérieur des ports. Pour cela, les deux espèces de sars les plus abondantes (*D. sargus* et *D. vulgaris*) ont été capturées en fin de vie juvénile dans des zones portuaires contrastées et des zone côtières adjacentes de la rade de Toulon. Les différences de croissance, de condition et de contamination en fonction du type d'habitat juvénile (intérieur ou extérieur des ports) ont été étudiées en lien avec la contamination métallique enregistrée sur chaque site, en partie à l'aide des otolithes (Encart 2) et sur la base d'indices morphométriques.

Enfin, la notion de connectivité entre les stades de vie juvénile et adulte étant essentielle dans la définition des nourriceries, nous avons cherché (**chapitre 5**) à évaluer si la composition chimique des otolithes (Encart 2) peut servir à estimer la contribution relative des ports aux stocks de poissons adultes. Pour cela, nous avons prélevé des juvéniles des deux espèces de sars les plus abondantes (*D. sargus* et D. vulgaris) dans différents ports et dans des zones côtières adjacentes et comparé la composition chimique de leurs otolithes, en lien avec la contamination chimique de chaque site.

Le croisement des résultats obtenus par cette approche comparative à différentes échelles devrait permettre d'améliorer significativement les connaissances sur la qualité des habitats portuaires pour les juvéniles de poissons et de préciser s'ils peuvent être des zones de nourriceries alternatives pour les poissons marins côtier. Elle devrait également permettre de mieux identifier les facteurs anthropiques qui limitent le recrutement des juvéniles issus des ports permettant ainsi d'orienter les projets d'ingénierie écologique en zone portuaire.

Encart 2 : Les otolithes

Les otolithes (de « oto » oreille et « lithos » pierre en grec) sont des concrétions minéralisées de carbonate de calcium ($CaCO_3$) de l'oreille interne des poissons osseux (téléostéens). Ils appartiennent à un système de mécanoréception permettant la détection des changements de position de l'animal ou de pression par la stimulation des cils apicaux des cellules sensorielles directement à leur contact (Popper & Coombs 1980, Popper et al. 2005). Les otolithes se forment durant une période comprise entre la fécondation de l'œuf et son éclosion (Sponaugle 2009) et ils grandissent tout au long de la vie du poisson, par dépôt continu et centrifuge de cristaux de carbonate de calcium sur une matrice organique fibro-protéique (Pannella 1971, Campana & Neilson 1985). Ces incréments journaliers sont visibles au microscope et peuvent être comptés pour estimer l'âge des individus, en particulier chez les juvéniles. Par ailleurs, leur composition chimique reflète en partie celle des masses d'eau environnantes au moment du dépôt (Elsdon & Gillanders 2003).



Coupe transverale d'un otolithe de *D. vulgaris* juvénile

Ainsi, l'étude combinée de la structure et de la composition chimique des otolithes permet d'accéder à l'histoire de vie des poissons, depuis leur naissance jusqu'à leur mort (Campana 1999). A ce jour, elle a permis de décrire les variations de croissance chez de nombreuses espèces (Gilliers et al. 2006, Mercier et al. 2011, Rey et al. 2016) et d'identifier l'origine des poissons adultes en discriminant différents types d'habitats juvéniles côtiers sur la base des signatures chimiques différentes qu'ils induisent dans les otolithes des poissons (e.g. Vasconcelos et al. 2008, Riou et al. 2016, Tournois et al. 2017).

Chapitre 3. Installation benthique dans les ports et influence de la complexité des habitats sur les abondances de juvéniles

« Science sans conscience n'est que ruine de l'âme »

Rabelais

III.1. Introduction

Le premier critère définissant un habitat juvénile de poissons comme une zone de nourricerie est celui de présence durable de fortes abondances de juvéniles (Beck et al. 2001). C'est pourquoi, les bioindicateurs au niveau populationnel, et plus particulièrement les abondances, sont systématiquement utilisés dans les études descriptives des nourriceries ou dans des travaux portant sur la qualité des habitats juvéniles de poissons (e.g. Baltz et al. 1993, Able et al. 1998, Minello 1999, Stunz et al. 2002a). En effet, les abondances reflètent directement deux processus ayant trait à la qualité de l'habitat : la sélection et la mortalité différentielle (Mellin 2007). Ainsi, bien que d'autres critères entrent en ligne de compte (cf. **Introduction**), plusieurs auteurs (e.g. Cheminee et al. 2011, Pastor et al. 2013) n'hésitent pas à utiliser les abondances seules pour identifier les zones de nourriceries parmi les habitats juvéniles. Dans ce cadre, l’objectif premier du **chapitre 3** était de mesurer les abondances de poissons juvéniles au sein de différentes zones portuaires afin de déterminer si elles peuvent ou non se substituer aux nourriceries naturelles au regard de ce critère.

Le deuxième objectif du **chapitre 3** était d'estimer l'influence des différences de nature des habitats juvéniles à l'intérieur des ports sur le succès de l'installation benthique et la survie des espèces. En effet, plusieurs études, menées notamment dans les estuaires, ont montré que les performances biologiques des individus pouvaient varier au sein d’un même site (Rozas & Minello 1998). Ceci a amené certains auteurs à proposer le concept de « partition » de l’habitat juvénile, ou de micro-habitats, avec des zones au sein d’un même secteur utilisées différemment par les poissons et entre lesquelles les performances biologiques, notamment les abondances, sont différentes (Beck et al. 2001). Le terme micro-habitat n’a pas véritablement de définition officielle et doit être considéré en fonction de la taille des organismes étudiés. Il est souvent utilisé pour décrire la plus petite part de l’environnement physique qui supporte les besoins d’un organisme (ou d'une population). C’est donc un « petit habitat » au sein d’un habitat plus large. Plusieurs micro-habitats peuvent être identifiés au sein des ports, chacun d’entre eux possédant des caractéristiques abiotiques et biotiques propres et donc des capacités d’accueil différentes pour les différents stades de développement juvéniles des espèces. Parmi eux, deux sont majoritaires et se retrouvent dans la plupart des ports : les quais et les pontons. Les abondances des juvéniles ont donc été comparées entre ces deux types de micro-habitats.

Par ailleurs, ce chapitre a été l'occasion de tester l'influence de la complexité structurale des substrats portuaires sur les abondances des juvéniles. La complexité structurale du substrat, généralement désignée sous les termes de "complexité de l'habitat", "complexité structurale" ou encore "rugosité", est l’un des facteurs déterminants dans la composition des peuplements de poissons (Randall 1963, Dayton 1971, Ruitton et al. 2000). L’influence de la complexité structurale sur les cinétiques de mortalité des juvéniles de poissons a été démontrée à maintes reprises (Holbrook et al. 2000, Holbrook & Schmitt 2002, Mellin 2007). Dans le milieu marin, la surface fonctionnelle, c’est à dire utilisable par les organismes pour assurer leurs fonction biologiques, dépend de la surface du substrat inorganique et de celle des organismes (algues, phanérogames marines, etc.) qui s’y fixent (Dahl 1973). Même si elles sont généralement colonisées par de nombreux organismes sessiles (Browne & Chapman 2014), les surfaces artificielles verticales des quais et les pontons en zone portuaire sont peu complexes et offrent aux juvéniles de poissons une surface fonctionnelle restreinte avec notamment peu de refuges contre la prédation. Plusieurs travaux ont mis en évidence qu’une complexification du substrat permettait une augmentation de l'abondance des juvéniles de poissons (Gorham & Alevizon 1989, Bulleri & Chapman 2010).

Dans ce contexte, le **chapitre 3** avait donc pour but à répondre spécifiquement aux questions suivantes : les juvéniles de poissons peuvent-ils s'installer et grandir dans les ports ? Les structures portuaires peuvent-elles supporter des abondances de juvéniles compatibles avec la fonction de nourricerie ? L'augmentation de la complexité structurale des ouvrages portuaires améliore-t-elle significativement leur qualité en tant qu'habitats juvéniles ?

Pour répondre aux objectifs du **chapitre 3**, les abondances des juvéniles de quatre espèces de sars (*D. sargus*, *D. vulgaris*, *D. puntazzo* et *D. annularis*) ont été suivies sur les quais et les pontons de cinq ports de la façade méditerranéenne française, tous les 15 jours, entre avril et août, pendant deux années consécutives (2013 et 2014). Ainsi, nous avons choisi d’utiliser une méthode d'échantillonnage visuel en plongée (UVC pour Underwater Visual Census) pour estimer les abondances de juvéniles de poissons. Des micro-structures artificielles ont également été fixées sur chaque type de micro-habitats afin d'évaluer l'effet de la complexité structurale sur ces abondances. Les méthodes permettant d'estimer l'abondance de populations de poissons peuvent être classées en deux catégories : les méthodes dites de "capture", nécessitant de prélever des individus hors de leur environnement, et les méthodes dites "d'observation", qui ne nécessitent pas de prélèvement. Parmi les méthodes de captures, les pièges (Crossland 1976, Miller & Hunte 1987), chaluts, filets (Wallace et al. 1984, Winhold & Kurta 2008), hameçons (Sigler 2000, Zeller et al. 2003), explosifs ou encore d'ichtyocides (Williams & Hatcher 1983, Kulbicki 1990) ont souvent été utilisés. Ces méthodes destructrices ont été écartées pour notre étude car elles sont très difficiles à mettre en œuvre dans une zone portuaire. D'autre part, elles ne permettent pas de suivre l'évolution de la mortalité juvénile des différentes cohortes. Nous avons donc opté pour une méthode d'observation. Les méthodes d'observation permettent en effet d'estimer l'abondance des organismes marins sans perturber la structure des populations (Mallet & Pelletier 2014). Parmi les méthodes d'observation, l'UVC et l'utilisation de la vidéo sous-marine sont les plus répandus (Mallet & Pelletier 2014). Malgré les avancées récentes dans la qualité des capteurs, la vidéo sous-marine demeure à ce jour peu adaptée à l'estimation des abondances des jeunes stades de poissons (Morrison & Carbines 2006).

L’ensemble du **chapitre 3** reprend les données recueillies par le CEFREM dans le cadre du projet NAPPEX, financé par l’agence de l’eau Rhône-Méditerranée Corse, le Conseil Général de l’Hérault et la société Ecocéan dans le cadre d’un appel d’offre lancé par le Ministère en charge de l’Environnement en 2011. Une partie des données a été acquise par le CEFREM avant le démarrage de ce travail de thèse.

III. 2. Article 1 (publié dans Marine Ecology Progess Series) : Potential use of marinas as nursery grounds by rocky fishes: insights from four *Diplodus* species in the Mediterranean.

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Potential use of marinas as nursery grounds by rocky fishes: insights from four *Diplodus* species in the Mediterranean

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ABSTRACT: The construction of marinas along the shoreline has caused substantial habitat destruction within the sheltered coastal areas previously used as nursery grounds by many fish species. However, although the negative ecological impacts of these constructions have been reported extensively, their potential roles in the functioning of the coastal zone remain largely unknown. Here, we surveyed the juveniles of 4 *Diplodus* species in 5 marinas located along the French Mediterranean coast to assess whether rocky fishes can successfully settle inside these artificialized coastal areas. Inter-specific differences in the spatiotemporal use of the various artificial habitats provided by marinas were investigated between April and August over 2 consecutive years. We also tested the potential benefit of pegging additional artificial habitats (Biohuts) on docks and pontoons to increase their value as fish nursery grounds. Our results suggest that although variations in marina and artificial habitat preferences exist between species, *Diplodus* juveniles repeatedly colonize marinas. Their average abundances on added Biohut habitats were twice as high as on nearby bare surfaces. This suggests that increasing the complexity of the vertical structures of marinas can considerably enhance their suitability for juvenile rocky fishes, especially at the youngest stages, when mortality is highest. Therefore, as long as marina water quality is well controlled, ecological engineering within these man-made habitats might reduce the ecological consequences of urban development by providing suitable alternative artificial nursery grounds for rocky fishes.

KEY WORDS: Coastal areas · Habitat anthropization · Fish juveniles · Sparids · Habitat preferences · Ecological engineering · Biohut

INTRODUCTION

Until recently, most research in urban ecology has focused on terrestrial habitats (e.g. Clergeau et al. 2006, Hobbs et al. 2006). However, more than 3 billion people currently live within 200 km of the sea, and this number is predicted to double by 2025 (Creel 2003). As a result, the destruction of coastal habitats is one of the main threats to marine ecosystems (Lotze et al. 2006, Airoldi & Beck 2007, Seaman 2007, Halpern et al. 2008), through its combined effects on biodiversity and ecosystem functioning (Beck et al. 2001, Courrat et al. 2009, Verdiell-Cubedo et al. 2013, Seitz et al. 2014, Sundblad et al.

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2014). Although many different types of man-made structures dominate the shoreline, ecological issues relating to the introduction of infrastructures in shallow coastal waters have received little attention so far (Chapman & Blockley 2009, Bulleri & Chapman 2010), and we are just beginning to understand their impact on marine organisms, especially fishes (Duffy-Anderson et al. 2003).

Marinas are among the most common man-made infrastructures found on the shoreline. Their construction not only leads to the direct destruction of natural shallow water habitats but also causes indirect damage through changes to currents and sediment loads, which both have a dramatic impact on the composition of benthic communities (Meinesz et al. 1991, Martin et al. 2005) and fish larval dispersal and recruitment (Roberts 1997). Moreover, the industrial and yachting activities associated with marinas result in chronic biological and chemical pollutions of both the sediment and the water column inside and in the vicinity of marinas, which can have long-term consequences on living organisms (Bech 2002, Falandysz et al. 2002, Neira et al. 2011). All of these factors lead to modifications of the ecological functions of the zones where marinas are built (Airoldi et al. 2007). However, the new shallow water habitats created within marinas might support new ecological functions.

The identification of nursery habitats is particularly important for stock conservation because mortality rates in fish are maximal during the early phases of their life cycle (Macpherson et al. 1997, Jennings & Blanchard 2004). Until now, very few studies have investigated the fish populations associated with marina structures. However, the peripheral breakwaters of marinas are often colonized by marine rocky fishes, at both the juvenile (Ruitton et al. 2000, Pizzolon et al. 2008, Dufour et al. 2009, Pastor et al. 2013) and adult stages (Guidetti 2004, Clynick 2006, Pizzolon et al. 2008, Cenci et al. 2011). Fish species richness on these artificial structures is generally equivalent to that of natural zones, and fish abundances are sometimes higher (Pérez-Ruzafa et al. 2006). The number of fish species and the abundances of the most common rocky species inside marinas also seem to be similar to those found in natural habitats (Clynick 2008). As a result, shallow and protected habitats on the inshore sides of marina breakwaters could provide suitable nursery grounds for some of these fish species (Dufour et al. 2009). In theory, fish nursery grounds are defined according to 4 parameters: they support high abundances of juveniles, sustain faster somatic growth rates, allow higher survival and their populations contribute more to the final adult stock (Beck et al. 2001). At first sight, featureless and steep sloping marina structures, provided, for example, by docks and floating pontoons, seem unlikely to meet these definition criteria. Nevertheless, high abundances of juvenile rocky fishes have been observed on these artificial structures (Clynick 2008). Although not a definitive test, many authors (e.g. Cheminee et al. 2013, Pastor et al. 2013) have used the abundance criterion alone to identify nursery grounds among juvenile habitats. In this context, we decided to investigate the condition for the potential use of marina vertical structures as nursery grounds by rocky fish species, by surveying small-scale spatiotemporal changes in juvenile abundances for 4 sparids of the same genus (*Diplodus* Raffinesque, 1810) within 5 contrasting marinas located along the French Mediterranean coast (northwest Mediterranean). The main aims of this study were: (1) to see whether certain infra-littoral rocky fishes could successfully settle on the artificial vertical structures commonly found inside the marinas, and (2) to investigate how the juveniles of different species make use of the artificial habitats available. However, we also wanted to (3) test the potential benefit of ecological engineering within marinas to increase their value as rocky fish nursery grounds. Indeed, increasing the complexity of vertical structures has been shown to augment biodiversity in artificial aquatic habitats (Browne & Chapman 2014). For rocky fishes, this could also enhance juvenile survival by providing shelter against predators (Bulleri & Chapman 2010). Therefore, increasing the complexity of vertical structures inside marinas could enhance their value as fish nursery grounds, with potentially important consequences in terms of population dynamics.

MATERIALS AND METHODS

Species studied

This study focused on the juveniles of 4 species of the *Diplodus* genus: the annular seabream *D. annularis* (Linnaeus, 1758), the sharp snout seabream *D. puntazzo* (Walbaum, 1792), the white seabream *D. sargus sargus* (Linnaeus, 1758), hereafter *D. sargus*, and the 2-banded seabream *D. vulgaris* (Geoffroy Saint-Hilaire, 1817). These species are common in the Mediterranean and have high ecological and commercial value (Coll et al. 2004, Morales-Nin et al. 2005, Lloret et al. 2008). They are highly abundant in both natural and artificial rocky coastal areas (Tortonese 1965), and their juveniles are present in high abundances inside marinas, at least along the internal side of peripheral breakwaters (Clynick 2006). Natural settlement patterns are fairly well described for all 4 species: *D. annularis*, *D. puntazzo* and *D. sargus* all settle in one pulse, in June–July, October–November and May–June, respectively, whereas *D. vulgaris* settles in 2 pulses, in November–December and in January–February, the first pulse being the more predominant (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995, Vigliola et al. 1998, Cheminee et al. 2011, Ventura et al. 2014). In *Diplodus* species, physical habitat characteristics (substrate, depth, level of protection from the prevailing winds, etc.) strongly determine both settlement success and pre-recruitment mortality (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Cheminee et al. 2011, Ventura et al. 2014). *D. puntazzo* and *D. sargus* both usually settle in very shallow parts (<1 m) of small crannies characterized by gentle slopes covered with pebbles or sand. *D. vulgaris* seems to prefer deeper waters (1–6 m) and can settle on a wider range of substrates (coarse sand, gravel, pebbles or boulders). Finally, settlement in *D. annularis* occurs at even greater depths (>5 m) but almost exclusively on seagrass beds (Harmelin-Vivien et al. 1995, Ventura et al. 2014). The species is thought to remain sedentary on the same seagrass bed for the entire duration of its juvenile life, whereas in *D. puntazzo*, *D. vulgaris* and *D. sargus*, substrate specificity disappears progressively during juvenile life, resulting in horizontal and then vertical migrations (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). Given the differences in settlement dates and natural habitat preferences between these 4 species, the investigation of the variation in their respective abundances and habitat preferences between different types of marina should allow us to reach global conclusions on the conditions of use of these man-made habitats by juvenile rocky fishes.

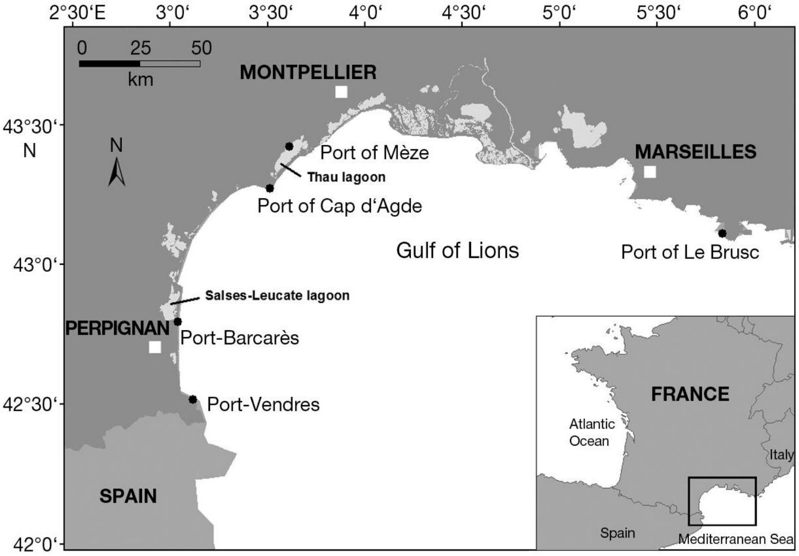

Fig. 1. Location of the 5 marinas (●) studied along the French Mediterranean coast

Study area

One hundred and fifty-five marinas are listed along the French Mediterranean coast (Pinar Genc & Guler 2012). Our study was carried out within 5 of them, located at distances ranging from 20 to 180 km along the coasts of the Gulf of Lions and the French Riviera, in the towns of Port-Vendres, Port-Barcarès, Cap d'Adge, Mèze and Le Brusc (Fig. 1). These 5 marinas have all been in operation for over 40 yr and each harbors more than 200 pleasure craft; however, they have different surface areas, depths and surrounding environmental characteristics (Table 1).

Table 1. Characteristics of the 5 marinas studied in this work. PV: Port-Vendres; BA: Port-Barcarès; CA: Cap d'Agde; ME: Mèze; BR: Le Brusc (MEDAM 2015)

Marina	Construction date	Surface area (ha)	Number of rings	Average depth (m)	Connection(s)	Coast type
PV	1853	33	253	8	Sea	Rocky
BA	1963	81	950	2	Sea and Salses-Leucate lagoon	Sandy
CA	1969	53	3100	3	Sea	Rocky
ME	6th century	18	200	2	Thau lagoon	Sandy
BR	1960	8	796	4	Sea	Rocky

Port-Vendres marina is the deepest (8 m on average). Surrounded by a rocky coast, it covers a surface of 33 ha. The Cap d'Agde marina was also built on a rocky peninsula, but it can harbor up to 3100 boats (on 53 ha), so it is the most artificialized of the 5 marinas. Le Brusc marina is the smallest (8 ha), but also the closest to natural conditions. It was constructed on a rocky shore, near one of the last 4 *Posidonia oceanica* barrier reefs remaining in the French Mediterranean (Boudouresque et al. 1985). With a surface area of 81 ha, Port-Barcarès marina is very shallow (2 m on average). It was constructed in the channel connecting the Salses-Leucate lagoon to the sea and therefore communicates easily with the 2 habitats. The Mèze marina is also linked to a lagoon (Thau) but has no direct link with the sea (although it ultimately communicates with it through the 3 exits of the lagoon). Because these 5 marinas all have very different topographies and levels of human impact, the study of their respective use by fish juveniles should allow generalization of our results.

Surveys

Juvenile fish abundances and sizes were monitored along with water temperature (°C) in all 5 marinas, every 2 wk for 5 consecutive months (April–August) in 2013 and in 2014. Due to logistic constraints, this timespan could not be extended to include the settlement dates for *D. puntazzo* (October–November) and *D. vulgaris* (November–December) (Harmelin-Vivien et al. 1995, Vigliola et al. 1998). However, it corresponds to the main period when the juveniles of all 4 species are found in natural coastal areas (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola et al. 1998). Therefore, we expected it to also cover most of the period for their joint presence in the marinas.

Two different artificial vertical structures frequently found in marinas were compared in our work: vertical docks and floating pontoons. For each of them, 2 types of conditions were investigated: the structure (i.e. docks or pontoons) left bare (for control) or equipped by patented multifaceted devices specially designed to increase substrate complexity and facilitate fish post-larval settlement in man-made coastal habitats (Biohuts®). The latter were consistently positioned under the surface of the water on both structures and immersed for at least 1 mo before the start of the annual surveys to harmonize benthic fauna densities between biohuts and controls. For each marina, 3 distinct zones containing only docks and 3 distinct zones containing only pontoons were used as replicates. They were consistently separated by at least 20 m and positioned to encompass most of the local variability in physicochemical conditions.

The sizes and locations of the surface areas of docks and pontoons dedicated, respectively, to Biohut positioning and control surveys in each zone were chosen to harmonize Biohut surfaces between artificial structures and were based on the minimum dimensions of the docks and the pontoons across all marinas. As a result, the Dock Biohut (DB) consisted of 8 pegged cages measuring 0.5 × 0.8 × 0.25 m grouped along a 5 m long dock section and covering a total vertical surface of 4 m^2. Each DB cage was composed of 2 inseparable parts: an empty part and a part filled with oyster shells to maximize the surface for benthic fauna development (Fig. 2A,C). The Pontoon Biohut (PB) consisted of 3 cages measuring 0.5 × 0.8 × 0.34 m suspended under the pontoons by polyurethane ropes to provide a total vertical surface of ca. 4 m^2. Each PB cage was composed of 3 inseparable parts: one part filled with oyster shells surrounded by 2 empty parts (Fig. 2B,D). Each replicate dock zone contained one DB and one control, the latter consisting of a 5 × 0.8 m (4 m^2) vertical surface of bare dock (hereafter DC for Dock Control). Similarly, each replicate pontoon zone contained one PB and one control, the latter consisting of a vertical surface of 4 m^2 positioned on the upper part of a pile used to anchor the pontoon (hereafter PC for Pontoon Control). In all replicate zones (dock or pontoon), the distance between the biohut and the control was always at least 10 m.

For each replicate dock and pontoon zone, a submersible data logger (IbCod 22L) was positioned to record water temperature (°C) hourly during the 5 mo of the study (April–August), and surveys of juvenile fish abundances and sizes were scheduled every 2 wk on all 4 artificial habitat types (AH, referring to DB, DC, PB and PC).

Abundances for all species were estimated by underwater visual census using stationary point counts, as they are particularly appropriate in restricted areas with homogeneous habitats (Bohnsack & Bannerot 1986, Clynick 2008, La Mesa et al. 2011). To do this, individual fish were always counted for 3 min. The surveys were carried out between 10:00 and 16:00 h, and poor visibility and evident chemical or bacterial pollution conditions were consistently avoided. For each replicate zone, the survey of the docks was designed to include 4 successive stationary point counts per AH (one per pair of cages

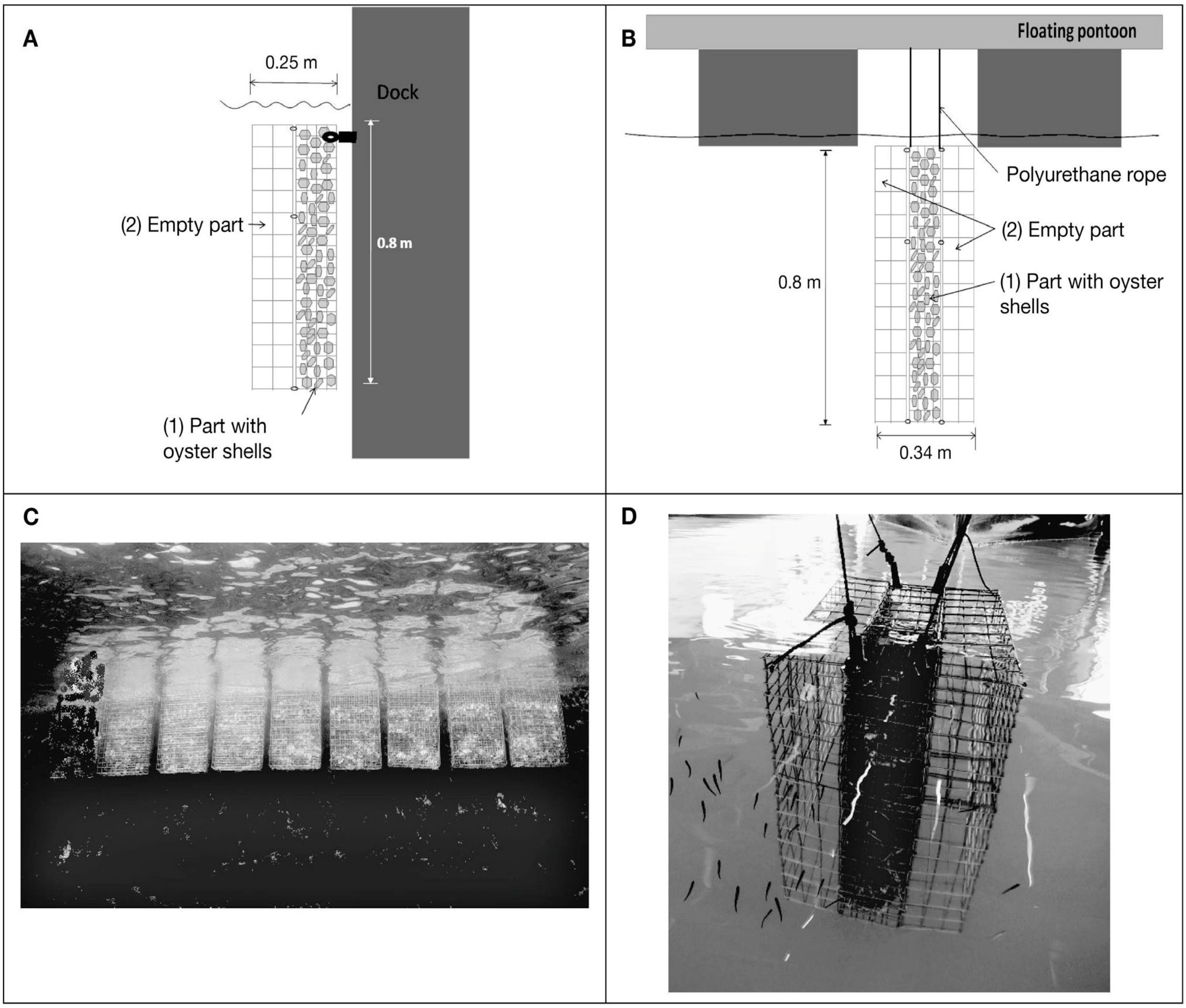

Fig 2. (A) Dock Biohut steel cage including: (1) a part filled with oyster shells (0.5 × 0.8 m, 2.5 cm mesh size) and (2) an empty part (0.5 × 0.8 m, 5 cm mesh size). (B) Pontoon Biohut steel cage including: (1) a part filled with oyster shells (0.5 × 0.8 m, 2.5 cm mesh size) and (2) 2 empty parts (0.5 × 0.8 m, 5 cm mesh size). (C) Dock Biohut sampling unit consisting of 8 adjacent cages pegged on 5 m of dock. (D) Pontoon Biohut cage fixed under a floating pontoon with polyurethane ropes

for DB and one per square meter of bare dock surface for DC), so both DB and DC were each surveyed for 12 min. Moreover, for each replicate zone, the survey of the pontoons consisted of 3 successive point counts per AH (one point count per cage for PB and one per 1.33 m^2 of pile for PC), so their survey took 9 min each. As a result, fish counts took 24 min in a dock zone, 18 min in a pontoon zone, and underwater visual censuses of 126 min were needed for the complete survey of each marina.

During the visual censuses, the juveniles of the 4 species were discriminated according to the morphological and size criteria given in FishBase (Froese & Pauly 2014). All the juveniles identified were counted and their sizes (total length, TL) were estimated to the nearest 5 mm. To minimize bias in this estimation, fish silhouettes of different sizes were printed on plastic slates and used *in situ* by the divers (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995). When *in situ* identification was difficult, pictures and videos of individuals were taken and interpreted once back at the laboratory, with the assistance of expert underwater visual census divers. The same 2 divers worked throughout the sampling period.

To investigate changes in habitat use within the marinas, the juveniles of all species were also classified *a posteriori* into 3 successive development stages, according to the size ranges provided by Vigliola & Harmelin-Vivien (2001) for *D. sargus*, *D. vulgaris* and *D. puntazzo*, and by Ventura et al. (2014) for *D. annularis* (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m547p193_supp.pdf). Irrespective of species, the 'post-settlement' stage refers to the smallest individuals found during the short time period that immediately follows benthic settlement (Vigliola & Harmelin-Vivien 2001). The 'intermediate' stage is longer and includes juveniles of medium sizes that usually colonize all suitable habitats within the nursery ground. Finally, the 'pre-dispersal' stage refers to the largest individuals that have acquired adult-like morphology and are ready to leave the nursery ground.

Statistical analysis

All calculations and statistical analyses were performed using PRIMER 6 software with the PERMANOVA add-on (Clarke & Warwick 2001) or using R software (R Core Team 2014) and the indicspecies package. The significance level for the tests was consistently set at $\alpha = 0.05$.

Preliminary data analyses showed that sampling year did not have a significant effect on juvenile *Diplodus* abundances and produced negative variance component estimates in all models but one (that for *D. sargus*). Therefore, following Fletcher & Underwood (2002), the data for the 2 consecutive years sampled in this work were consistently analyzed pooled, to reduce the effect of random variability in fish abundances among fish counts for certain AH and species, and thereby give a more robust image of the overall patterns of marina use by juvenile rocky fishes.

As the corresponding data were not normally distributed, spatial differences in water temperatures during the period studied (April–August) were investigated using a non-parametric Kruskal-Wallis test followed by Steel-Dwass-Critchlow-Fligner bilateral pairwise tests. Spatiotemporal variations in fish abundances (in numbers of individuals per count, hereafter ind. count^{-1}) were analyzed for all 4 species, separately or grouped, according to month, marina and AH. For this, we performed 3-way univariate PERMANOVAs because this method allows the handling of complex, unbalanced and multiple-factor designs, considers interaction among factors and does not assume a normal distribution of errors (Anderson 2001). Fish abundances were $\log(x + 1)$ transformed prior to the generation of Euclidean distance similarity matrixes, and the factors month (with 5 levels: April–August) and AH (with 4 levels: DB, DC, PB and PC) were treated as fixed, whereas the marina factor (with 5 levels: Port-Vendres, Port-Barcarès, Cap d'Agde, Mèze and Le Brusc) was treated as random. In addition to the main PERMANOVA test, contrasts were used to compare fish abundances between DB and DC and between PB and PC (Glasby 1997). The *p*-values were calculated by 9999 random permutations of residuals under a reduced model and Type III sum of squares (Anderson 2001).

For each species, ontogenetic changes in habitat use during juvenile life in marinas were also investigated, by identifying the type(s) of AH(s) preferred at each development stage using the indicator value (IndVal) index (Dufrêne & Legendre 1997). This composite index was originally developed to compare populations between sites and link species to communities based on habitat conditions (De Cáceres & Legendre 2009). It combines 2 estimates of habitat use for each species: specificity (S) and fidelity (F), based on the species' relative abundance and its relative frequency of occurrence among sites or habitat types, respectively. Therefore, it gives precise and accurate information on species habitat preferences (Legendre & Legendre 1998). In the present study, we applied it to explore differences in AH preferences within the marinas between all the development stages of the 4 species. Therefore, development stages (post-settlement, intermediate and pre-dispersal) by species were used instead of species in IndVal calculations per AH, following the formula:

$$\mathrm{IndVal}_{ijk} = 100 \times S_{ijk} \times F_{ijk} \tag{1}$$

with specificity S_{ijk} defined by:

$$S_{ijk} = A_{ijk}/A_{ij} \tag{2}$$

where A_{ijk} is the mean abundance per count of development stage i of species j in the AH k, and A_{ij} is the sum of the mean abundances per count of the same stage i of the same species j over all AH. Fidelity F_{jk} is defined by:

$$F_{jk} = N_{ijk}/N_{...k} \tag{3}$$

where N_{ijk} is the number of the survey with at least one individual of the development stage i of the species j in the AH k, and $N_{..k}$ is the total number of surveys for this AH during the entire study.

To generalize our results, IndVal was also calculated per development stage for all 4 species grouped. Differences in IndVal values between AH were tested by 9999 random permutations among groups (De Cáceres & Legendre 2009).

RESULTS

Due to unexpected adverse environmental conditions in the marinas (e.g. occasional days with poor underwater visibility, pollution events) or logistic constraints on some of the sampling dates scheduled during the 2 years of the study, only 896 surveys were performed of the 1200 initially planned. However, this did not prevent accurate investigation of fish AH use in the 5 marinas, as all of the sites were fully surveyed at least twice per month over the whole duration of the study when considering the 2 years pooled. However, pooling data from the 2 years can bias estimates of variance in some analyses, and caution should be taken when interpreting the results. Similarly, logistic constraints in 2013 allowed us to perform only one stationary count per replicate zone for the controls, so the vertical surfaces investigated for DC and PC in this year covered only 4 m^2 per marina, instead of 12 m^2 as in 2014. However, this should not affect our conclusions because fish abundances on controls for 2014 were similar (premutational multivariate analysis of variance [PERMANOVA], $p > 0.5484$) when using one or all stationary counts, irrespective of species or marina.

Water temperatures in April–August differed significantly according to survey site ($p < 0.0001$; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m547p193_supp.pdf), with higher and lower averages in Mèze (22.37 ± 3.77°C) and in Port-Vendres (19.39 ± 3.29°C), respectively, than in the 3 other marinas (19.76 ± 3.40°C in Port-Barcarès, 20.49 ± 3.16°C in Cap d'Agde and 20.56 ± 3.21°C in Le Brusc).

Juvenile fish abundances in the marinas

Over the time period surveyed, the maximum number of *Diplodus* juveniles observed throughout one point count was 60 individuals (on 15 April 2013 on a DB habitat in the Cap d'Agde marina). However, single counts with no observations were very frequent (83%) and occurred irrespective of month or location. Finally, a total of 1766 observations of *Diplodus* juveniles were made within the 5 marinas. However, most of the juveniles counted were *D. vulgaris* (N = 653) or *D. annularis* (N = 520), whereas observations of *D. sargus* (N = 388) and *D. puntazzo* (N = 205) were less frequent. Spatiotemporal patterns of marina use varied greatly between species (Table 2, Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m547p193_supp.pdf). Significant interactions between the month and marina factors in the PERMANOVAs for all 4 species, whether grouped or not (Table 2), also indicated that the temporal variations in juvenile abundances were not consistent across locations. Despite this complicated data interpretation, some general temporal and spatial trends could still be discerned.

Temporal variations in juvenile abundances were significant only for *D. annularis* and *D. sargus* (Table 2), with the highest abundances for these species being reached in August (mean: 0.73 ± 0.14 ind. count^{-1}) and July (mean: 0.48 ± 0.14 ind. count^{-1}), respectively. Temporal trends in the abundances of the post-settlement juveniles of the 2 species allowed us to identify their respective periods of settlement in the marinas, in June–July for *D. sargus* and in July–August for *D. annularis* (Fig. 3). Similarly, a detailed analysis of the temporal variations in abundance for the post-settlement and pre-dispersal development stages of *D. puntazzo* and *D. vulgaris* suggested that settlement in the marinas probably occurred before the sampling period (April–August) for both species and suggested that their departure from the marinas started from July at certain locations (in particular Port-Vendres; Fig. S2 in the Supplement). It is probable that sampling was stopped well before *D. annularis* dispersal because very few pre-dispersal individuals were observed for this species, and most juveniles were still at the intermediate stage in August (Fig. 3).

Regarding general spatial trends, the number of observations of *Diplodus* juveniles varied considerably between marinas, with a total of 646 individuals being counted in Cap d'Agde, 393 in Le Brusc, 387 in Port-Vendres, 337 in Port-Barcarès, and only 3 in Mèze. Accordingly, juvenile abundance differed significantly between locations ($p < 0.001$; Table 2), with a maximum (1.08 ± 0.18 ind. count^{-1}) in Cap d'Agde and a minimum (0.04 ± 0.003 ind. count^{-1}) in the marinas of Mèze and Port-Barcarès, whereas similar intermediate values were obtained for Le Brusc and Port-Vendres (respectively of 0.85 ± 0.24, 0.96 ± 0.15 and 0.98 ± 0.14 ind. count^{-1}, respectively).

Species composition also depended on location, with spatial variations in juvenile abundance for all 4 species (Table 2), but the nature of the variation differed (Fig. S2 in the Supplement). Indeed, juveniles from all 4 species were observed in Port-Vendres, Port-Barcarès, Cap d'Agde and Le Brusc, while only 3 individuals of *D. vulgaris* were seen in Mèze (one post-settler in April and 2 pre-dispersal juveniles in June, observed on a DC and on a DB, respectively). Over the April–August period, the global average

Table 2. Results of the univariate 3-way PERMANOVAs performed to compare juvenile fish abundances (ind. count^{-1}) between months (April–August), marinas (Port-Vendres, Port-Barcarès, Cap d'Agde, Mèze and Le Brusc) and artificial habitat type (Dock Biohut [DB], Dock Control [DC], Pontoon Biohut [PB] and Pontoon Control [PC]). Contrasts were used to compare juvenile fish abundances between DB vs. DC and PB vs. PC. Significant p-values (<0.05) are indicated in bold. Asterisks indicate that data are the results of contrast tests

Source	df	MS	Pseudo-*F*	p (perm)
***Diplodus* spp.**				
Month (Mo)	4	1.3285	1.8282	0.1718
Marina (Ma)	4	6.2927	23.643	**0.0001**
Artificial habitat (AH)	3	3.4027	4.0546	**0.0309**
*DB v DC	1	2.6958	2.8197	0.1742
*PB v PC	1	7.3272	7.4131	0.0619
Mo × Ma	16	0.737	2.769	**0.0005**
Mo × AH	12	0.6153	1.7594	0.0881
*Mo × DB v DC	4	0.74754	6.2743	**0.0036**
*Mo × PB v PC	4	0.27934	0.88306	0.4933
Ma × AH	12	0.84719	3.183	**0.0004**
*Ma × DB v DC	4	0.96961	3.2608	**0.0117**
*Ma × PB v PC	4	0.99439	4.2266	**0.0022**
Mo × Ma × AH	48	0.3522	1.3233	0.0771
*Mo × Ma × DB v DC	16	0.11284	0.37948	0.9883
*Mo × Ma × PB v PC	16	0.31847	1.3536	0.1618
Residuals	796	0.26616		
Total	895			
D. annularis				
Month (Mo)	4	2.9147	5.4272	**0.0052**
Marina (Ma)	4	1.2478	20.884	**0.0001**
Artificial habitat (AH)	3	1.0537	3.4146	0.0506
*DB v DC	1	1.5682	6.1272	0.0778
*PB v PC	1	1.5927	2.7135	0.1796
Mo × Ma	16	0.54779	9.1682	**0.0001**
Mo × AH	12	0.5233	3.3548	**0.0011**
*Mo × DB v DC	4	0.79985	5.4357	**0.0053**
*Mo × PB v PC	4	0.76441	3.4679	**0.0286**
Ma × AH	12	0.31205	5.2228	**0.0001**
*Ma × DB v DC	4	0.26008	4.7304	**0.0011**
*Ma × PB v PC	4	0.59113	9.1692	**0.0001**
Mo × Ma × AH	48	0.15884	2.6584	**0.0002**
*Mo × Ma × DB v DC	16	0.15041	2.7356	**0.001**
*Mo × Ma × PB v PC	16	0.22453	3.4827	**0.0004**
Residuals	796	5.9749×10^{-2}		
Total	895			
D. puntazzo				
Month (Mo)	4	0.11838	1.7037	0.185
Marina (Ma)	4	0.58042	17.379	**0.0001**
Artificial habitat (AH)	3	0.40819	2.1155	0.1367
*DB v DC	1	0.13055	5.1787	0.0947
*PB v PC	1	0.80851	1.9883	0.2246
Mo × Ma	16	7.0293×10^{-2}	2.1048	**0.0084**
Mo × AH	12	5.5525×10^{-2}	2.0167	**0.0413**
*Mo × DB v DC	4	2.2988×10^{-2}	2.6866	0.0726
*Mo × PB v PC	4	0.12138	2.6845	0.0708
Ma × AH	12	0.19517	5.8438	**0.0001**
*Ma × DB v DC	4	2.5248×10^{-2}	1.0828	0.3637
*Ma × PB v PC	4	0.40952	9.4409	**0.0001**
Mo × Ma × AH	48	2.7359×10^{-2}	0.8192	0.7967
*Mo × Ma × DB v DC	16	8.0345×10^{-3}	0.34458	0.99
*Mo × Ma × PB v PC	16	4.5265×10^{-2}	1.0435	0.4057
Residuals	796	3.3397×10^{-2}		
Total	895			

Source	df	MS	Pseudo-*F*	p (perm)
D. sargus				
Month (Mo)	4	1.3037	4.225	**0.0156**
Marina (Ma)	4	0.7363	9.4466	**0.0001**
Artificial habitat (AH)	3	0.69136	1.5925	0.2432
*DB v DC	1	6.022×10^{-2}	4.8709	0.0998
*PB v PC	1	0.29581	0.60032	0.4789
Mo × Ma	16	0.31376	4.0256	**0.0002**
Mo × AH	12	0.17219	1.1333	0.354
*Mo × DB v DC	4	1.056×10^{-2}	0.33165	0.8579
*Mo × PB v PC	4	0.14321	1.0896	0.3924
Ma × AH	12	0.4391	5.6336	**0.0001**
*Ma × DB v DC	4	1.2007×10^{-2}	0.40495	0.8068
*Ma × PB v PC	4	0.49567	3.9417	**0.0042**
Mo × Ma × AH	48	0.15413	1.9775	**0.0007**
*Mo × Ma × DB v DC	16	3.1919×10^{-2}	1.0765	0.3708
*Mo × Ma × PB v PC	16	0.13158	1.0463	0.4124
Residuals	796	7.7943×10^{-2}		
Total	895			
D. vulgaris				
Month (Mo)	4	0.56464	1.9424	0.1555
Marina (Ma)	4	1.4537	12.35	**0.0001**
Artificial habitat (AH)	3	1.9162	3.709	0.0433
*DB v DC	1	1.5172×10^{-3}	3.0143×10^{-3}	0.9144
*PB v PC	1	1.3173×10^{-3}	0.0069712	0.9741
Mo × Ma	16	0.29459	2.5029	**0.0017**
Mo × AH	12	0.26063	1.4489	0.1845
*Mo × DB v DC	4	8.1717×10^{-2}	0.78894	0.5441
*Mo × PB v PC	4	6.4966×10^{-2}	1.2575	0.3328
Ma × AH	12	0.5222	4.4367	**0.0001**
*Ma × DB v DC	4	0.50927	2.3585	0.0509
*Ma × PB v PC	4	0.1903	9.3036	**0.0001**
Mo × Ma × AH	48	0.18172	1.5439	0.0149
*Mo × Ma × DB v DC	16	9.9605×10^{-2}	0.46128	0.9627
*Mo × Ma × PB v PC	16	5.2481×10^{-2}	2.5657	**0.0028**
Residuals	796	0.1177		
Total	895			

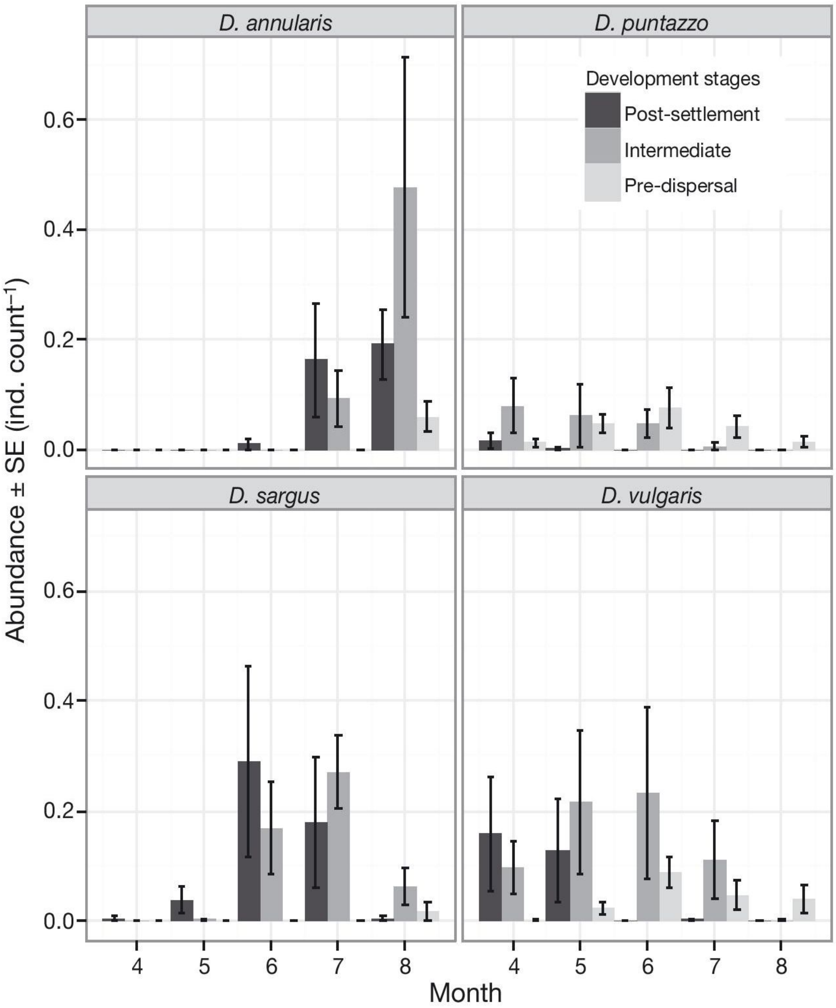

Fig. 3. Mean monthly abundances of juveniles (expressed in ind. count^{-1}) at the post-settlement, intermediate and pre-dispersal stages observed for the 4 *Diplodus* species investigated. Results for all locations, artificial structures and artificial habitats are pooled. Error bars represent standard errors around the means

abundance of juveniles per count was highest in Le Brusc for *D. annularis* (0.53 ± 0.14 ind. count^{-1}), in Port-Vendres for *D. puntazzo* (0.24 ± 0.05 ind. count^{-1}), in Port-Barcarès for *D. sargus* (0.67 ± 0.23 ind. count^{-1}) and in Cap d'Agde for *D. vulgaris* (0.55 ± 0.16 ind. count^{-1}). This may suggest differences in habitat suitability for *Diplodus* juveniles between the 5 marinas investigated, with further variation between the marinas according to species.

With regards effects of the artificial habitat type, abundances for the 4 species grouped were on average 2 times higher on the Biohut (mean: 1.02 ± 0.12 ind. count^{-1}) than on the nearby bare vertical surfaces used as controls (mean: 0.52 ± 0.12 ind. count^{-1}). The significance of the interactions Ma × DB vs. DC ($p = 0.012$) and Ma × PB vs. DC ($p = 0.002$) suggested that *Diplodus* abundances were higher on the biohut than on controls irrespective of the artificial structure considered (dock or pontoon), but also revealed that this effect was strongly dependent on location. Considering species separately revealed that on the pontoons, this pattern held for all 4 species (Ma × PB vs. PC, $p < 0.004$). However, on the docks, the interaction was significant for *D. annularis* (Ma × DB vs. DC, $p = 0.001$), approached statistical significance for *D. vulgaris* ($p = 0.050$), but was not significant for *D. puntazzo* ($p = 0.364$) or *D. sargus* ($p = 0.807$). As a result, for docks, month also had a significant effect on the global difference in *Diplodus* spp. abundances between biohut and controls (Mo × DB vs. DC, $p = 0.004$).

Changes in habitat use during juvenile life

Our results revealed a generalized loss of habitat specificity during juvenile life in marinas in the 4 fish species investigated (Fig. 4). Indeed, when considering all *Diplodus* spp. grouped, IndVal values at the post-settlement stage were significantly higher ($p < 0.036$) for DB and PB than for DC and PC, reflecting a preference for biohut habitats than for bare structures. At the intermediate stage, although IndVal values were still significantly higher ($p < 0.0001$) for DB and PB than for PC, the values for DB and DC were no longer statistically different ($p = 0.067$). Finally, at the pre-dispersal stage, IndVal did not differ significantly between any habitat pair ($p > 0.057$), so no AH preference could be detected. This general trend was, however, slightly complicated by differences in AH preference between species, especially at the post-settlement and intermediate stages (Fig. 4). In *D. annularis*, IndVal values for DB and PB were similar ($p > 0.611$), irrespective of the development stage, and consistently higher ($p < 0.023$) than those of DC and PC. This indicated a preference for the biohut habitats (on both docks and pontoons) in this species throughout its juvenile life within marinas. For the 3 other species investigated, ontogenetic shifts in habitat use were observed, all resulting in an

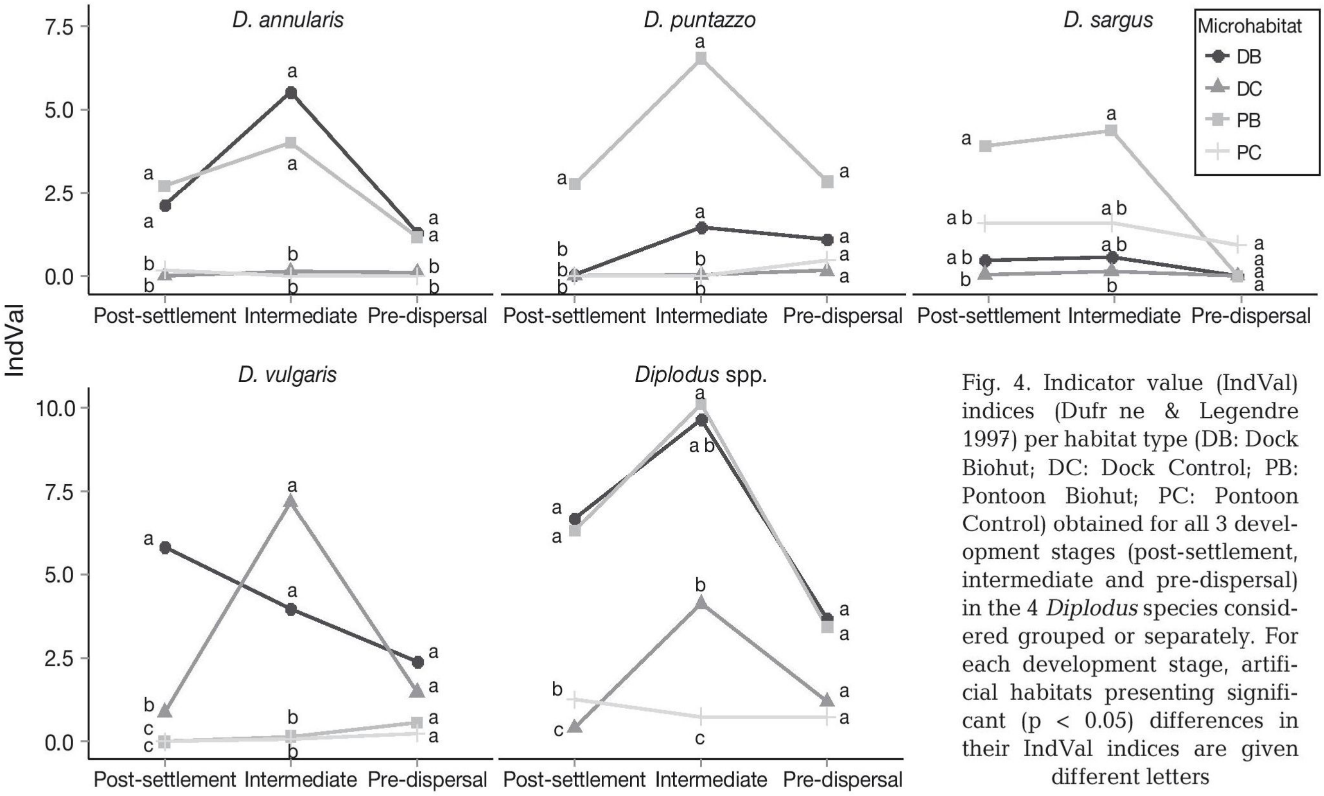

Fig. 4. Indicator value (IndVal) indices (Dufrêne & Legendre 1997) per habitat type (DB: Dock Biohut; DC: Dock Control; PB: Pontoon Biohut; PC: Pontoon Control) obtained for all 3 development stages (post-settlement, intermediate and pre-dispersal) in the 4 *Diplodus* species considered grouped or separately. For each development stage, artificial habitats presenting significant ($p < 0.05$) differences in their IndVal indices are given different letters

absence of AH preference at the pre-dispersal stage ($p > 0.073$). *D. vulgaris* settled essentially on DB, as indicated by the significantly higher ($p = 0.0001$) IndVal value found for this AH at the post-settlement stage. At the intermediate stage, it enlarged its habitat use to all dock habitats, which resulted in similar IndVal values for DB and DC ($p = 0.55$), both significantly higher ($p < 0.0003$) than those of PB and PC. In *D. puntazzo*, juveniles showed a preference for PB ($p < 0.032$) at the post-settlement stage and then gathered preferentially around either of the 2 types of biohut provided in the marinas. Thus, at the intermediate stage, the IndVal indices for DB and PB in this species were significantly higher than those for DC and PC ($p < 0.014$) but did not differ significantly from each other ($p = 0.059$). Finally, post-settlement and intermediate juveniles of *D. sargus* had similar AH preferences. Their IndVal index for PB was significantly higher than that for DC ($p < 0.002$) but did not differ significantly from those of PC and DB ($p > 0.162$).

DISCUSSION

To our knowledge, this is the first time that the use of man-made structures inside marinas, such as docks and pontoons found all around the world, by juvenile rocky fishes has been investigated this thoroughly. Juvenile fishes of the *Diplodus* genus were present on docks and pontoons in several of the marinas we investigated along the French Mediterranean coast. All 4 species were observed inside the marinas and at all development stages (i.e. from post-settlement to pre-dispersal). However, even within these highly artificialized ecosystems, inter-specific variations in habitat preference (mostly associated with the complexity of the vertical substrate available) were evidenced, especially at the youngest stages, when mortality is highest (Macpherson et al. 1997). These findings have strong implications for the evaluation of the potential suitability of marinas as fish nursery grounds.

Conditions for the use of marinas as juvenile fish habitats

Juveniles of *Diplodus* spp. have already been reported in high numbers in the peripheral breakwaters of certain Mediterranean marinas (Ruitton 1999, Clynick 2006), but up to now no study has investigated their abundances on the AH present inside these marinas. Our work shows that these species are also present at all development stages on both the docks and the pontoons available inside the marinas. This suggests that docks and pontoons (or at least parts of them) have the potential to meet the habitat requirements for the successful settlement and juvenile growth of various *Diplodus* species in the Mediterranean.

This result was relatively unexpected, in particular for *D. annularis*, for which juveniles were previously thought to be strongly associated with *Posidonia oceanica* beds in the Mediterranean (Gordoa & Moli 1997, García-Charton et al. 2004, Ventura et al. 2014). During the 2 summer months considered in the present study, 520 juveniles of *D. annularis* were observed in the 5 marinas tested, with high inter-location variability (see Fig. S2 in the Supplement); 54 and 42 % of these observations were made on DB and PB, respectively. Because different protocols were used for the juvenile counts, the abundances measured in this study cannot be compared directly with those observed in natural areas. However, this result suggests that certain parts of marina ecosystems can allow the settlement of *D. annularis* juveniles. Pelagic fish larvae are known to often settle in the first suitable habitat they encounter (Shapiro 1987). Therefore, high abundances of *D. annularis* juveniles in certain marinas could partially result from an absence of suitable natural habitat in their immediate vicinity. This could be the case in Port-Barcarès, since this marina is located on a sandy coast, far from any *P. oceanica* bed. However, this explanation is not valid for the 2 marinas where the species was the most abundant (Le Brusc and Cap d'Agde), as they are both located in the neighborhood of one of the largest meadows of *P. oceanica* remaining along the Mediterranean coast (Boudouresque et al. 1985, Descamp et al. 2011). Therefore, our results suggest that plasticity in juvenile habitat requirements is probably higher than previously thought in *D. annularis* and may be close to that already pointed out in the 3 other *Diplodus* species investigated (Guidetti 2004, Martin et al. 2005, Clynick 2006, Pastor et al. 2013). Further research should be conducted to investigate this possibility because an active selection of man-made artificial habitats by *Diplodus* larvae cannot be excluded, given the low levels of waving and the high trophic productivity often found in marinas (Planes et al. 1999, Dufour et al. 2009). Marinas could also act as light traps for the larvae at night (Doherty 1987). Whatever the case, plasticity in juvenile habitat requirements apparently allows successful settlement and growth of the juvenile fishes of this genus within certain marinas, despite the unavoidable pollution (by noise and by chemicals) associated with these man-made ecosystems. If so, marinas could provide alternative nursery grounds for rocky fishes, at least in highly urbanized areas of the shoreline.

The presence and abundance of *Diplodus* juveniles varied greatly according to the marina investigated. With only 3 juveniles (of *D. vulgaris*) observed during the whole period of our study, the marina of Mèze was barely colonized by the juveniles of this genus in 2013–2014. The environmental conditions in this marina were apparently peculiar, since monthly temperatures during the study period were consistently at least 1°C higher in Mèze than in the 4 other sites investigated (see Fig. S1 in the Supplement). For many fish species, juvenile abundances strongly depend on water temperature, especially at the post-larval stage (e.g. Henderson & Seaby 1994, Félix-Hackradt et al. 2013). However, the juveniles of at least *D. vulgaris*, *D. annularis* and *D. puntazzo* usually settle successfully in environments with large differences in water temperature (18–29°C), salinity (18–39) and dissolved oxygen levels (2.7–9.6 mg l^{-1}) (Vinagre et al. 2010). Therefore, it is quite unlikely that the main reason for the absence of *Diplodus* juveniles in Mèze lies in its environmental conditions. Another explanation could lie in the fact that this marina is located within the Thau lagoon, which the post-larvae must cross before reaching the marina. Indeed, in the nearby lagoon of Salses-Leucate, in which the salinity and temperature conditions are very close to those observed in Thau (Ifremer 2012), a marked reduction in the abundance of *D. sargus* juveniles has been noted over recent decades (Pastor et al. 2013). This phenomenon was attributed either to the increasing collection of *D. sargus* larvae by the artificial constructions built at the entrance of the lagoon, or to an augmentation of local juvenile mortality rates due to the degradation of environmental conditions in the lagoon. All the channels connecting the Thau lagoon to the sea are artificial and the Mèze marina is located at ca. 4 km from the nearest marine entrance. Therefore, the hypotheses proposed to explain the decline of juvenile *D. sargus* in Salses-Leucate (Pastor et al. 2013) could also apply in Thau and explain the lack of juveniles of the *Diplodus* genus in the Mèze marina, which has no direct connection with the sea, where the breeding of the 4 species occurs (Harmelin-Vivien et al. 1995).

Juvenile fish abundances also varied between the 4 other marinas investigated, with almost twice as many individuals counted in Cap d'Agde as in Le Brusc, Port-Vendres and Port-Barcarès. Several hypotheses can be proposed to explain these spatial differences. For example, as the main direction of local currents and the presence of gyres can influence the dispersion or retention of fish eggs and larvae (Cheminee et al. 2011), pelagic larval inputs for each species may differ between marinas, depending on the location of their nearest spawning grounds. Some marinas might also be close to natural nursery areas and indirectly benefit from their attractiveness for the larvae. Another explanation might lie in the differences in mean depth between our marinas, as this factor governs *Diplodus* spp. settlement in natural areas (Harmelin-Vivien et al. 1995). However, *Diplodus* abundances in our study showed no significant relationship with marina depth. For example, the maximum abundances of *D. puntazzo*, a species known to naturally settle in very shallow coastal habitats (Harmelin-Vivien et al. 1995), were observed in the deepest marina (Port-Vendres). Finally, post-settlement mortality rates can differ between locations depending on both the physico-chemical conditions and local inter-specific competition for available resources (Planes et al. 1998). Apparently, of all the sites we studied, the vast (53 ha) and shallow (<3 m) marina of Cap d'Agde is the most favorable for the settlement and growth of *Diplodus* juveniles, despite the fact that, with 58.5 rings ha^{-1} on average, it has the highest density of use after the marina of Le Brusc (99.5 rings ha^{-1}). This might be due to its location on a primarily rocky shore, or to the fact that it is surrounded by several *P. oceanica* meadows (Descamp et al. 2011). However, species composition also depended highly on location, and maximum juvenile abundances were found in Cap d'Agde for *D. vulgaris* only. For the 3 other species, these abundances occurred in other marinas: in Le Brusc for *D. annularis*, in Port-Vendres for *D. puntazzo* and in Port-Barcarès for *D. sargus*. Therefore, the factors responsible for spatial differences in juvenile abundances are probably multiple and depend on the species. They require further investigation to better understand the potential value of marinas as nursery grounds for rocky fishes. However, our results clearly indicate that marinas do not all succeed in providing environmental conditions favorable for the settlement and survival of *Diplodus* juveniles. Thus the location and environmental characteristics of marinas should be considered first when trying to restore the potential nursery function of the littoral ecosystems in which they were built.

Ecological engineering: a tool for improving the nursery potential of marinas

Each marina consists of a mosaic of different artificial habitats, each characterized by specific biotic and abiotic features and supporting functionally different life stages or species. Our results showed that increasing their diversity can have a significant impact on the value of marinas as fish nursery grounds. Indeed, post-settlement stage juveniles were generally found around the added biohut structures, irrespective of whether they were installed on docks or on pontoons. But this result strongly depends on the marina considered because, as a result of their location or physico-chemical conditions they provide, some of them do not seem to meet the environmental requirements for successful *Diplodus* juvenile settlement. Such marinas (e.g. Mèze) probably cannot function as *Diplodus* nursery grounds, and adding biohuts on docks or pontoons does not provide any ecological benefit.

In a natural context, early mortality of *Diplodus* juveniles is driven both by density-dependent processes linked to post-settlement intensity (Doherty 1981, 1991) and by density-independent processes linked to predation and refuge availability (Hixon 1991, Vigliola 1998). Although this has not yet been demonstrated, we can reasonably assume that these 2 types of processes also modulate the abundances of rocky fish juveniles in marinas. For example, differences in abundance between biohuts and controls in our study could be due to a reduction of juvenile mortality on biohuts, since they provide more refuge against predators than the featureless vertical surfaces usually found on docks and pontoons (Ammann 2004, Bulleri & Chapman 2010). In this case, the reason why habitat preference for biohuts in marinas was particularly observable for the youngest stages may lie in the fact that mortality by predation is highest at this period of life (Macpherson et al. 1997). Another explanation could lie in the attraction offered by complex solid structures (in our case, the biohut) for pelagic larvae, a behavior known as thigmotaxis (Ammann 2004). The 2 hypotheses are not mutually exclusive and, even if the biohut was originally designed to protect the youngest juveniles from mobile predators, knowing whether they act on fish production by reducing post-settlement mortality or on fish density by attracting fish larvae by thigmotaxis requires further investigation.

Interestingly, habitat preference at the post-settlement stage was the least marked in *D. sargus*, for which no significant differences in IndVal were observed between DB, PB and PC. This could be due to the higher plasticity in this species' juvenile habitat requirements (Cheminee et al. 2011, Pastor et al. 2013) or to a limitation in the availability of its most favorable habitats (Harborne et al. 2011). Indeed, when pre-settlement *D. sargus* arrive in the marinas (in June–July), biohut habitats are still largely occupied by the post-settlement juveniles of *D. puntazzo* and *D. vulgaris* (see Fig. S2 in the Supplement). This might partly explain why they also settle abundantly under the bare pontoons. Therefore, as in natural habitats, high occupation rates of the most optimal habitats could lead to competitive interactions between species within marinas and force the late-breeding ones to settle on sub-optimal habitats.

Although our results suggest that ecological engineering in some marinas could increase their value as nursery grounds for rocky fishes, this also implies the preservation or improvement of their water and sediment quality. Indeed, to satisfy the definition of nursery area, habitats have to contribute considerably to the adult stock (Beck et al. 2001). Juvenile fish can experience very stressful environmental conditions in marinas (e.g. boat traffic, extensive pollutant loads, dredging, etc.) linked to human activities. Chemical contaminants in particular are known to adversely affect fish physiology, growth, health and behavior, especially at young stages (e.g. Laroche et al. 2002, Marchand et al. 2003, Rowe 2003, Kerambrun et al. 2012). As in other organisms, sub-lethal responses to contaminant exposure in fish commonly involve a decrease in feeding activity (Stephens et al. 2000, Saborido-Rey et al. 2007) and a modification in energy allocation, which is preferentially used to fight chemical stress rather than for body maintenance and growth (Rowe 2003). This can have marked negative effects on global individual fitness, as fish juveniles with slow growth rates and limited energy storage have lower survival rates and contribute less to the adult stock (Sogard 1997). Therefore, heavily contaminated marinas probably cannot function as fish nursery grounds. Because between 337 and 646 *Diplodus* juveniles were observed at all development stages in all but one marina (Mèze) tested for 2 consecutive years, the pollution in these particular locations is probably below critical pollution thresholds. However, our results might overestimate the actual abundances of *Diplodus* juveniles in marinas because the techniques applied in this study (underwater visual census by snorkelers) excluded heavily polluted sites from our investigations. Therefore, the impact of contaminant exposure during juvenile life (high and punctual or limited yet repeated) on the final fitness of fishes will have to be explored before concluding on the real value of marinas as nursery grounds.

Consistency in seasonality and changes in habitat use between natural and artificial habitats

In the Mediterranean, juvenile presence on nursery grounds is known to occur from May–June to late September in *D. sargus*, from July to September in *D. annularis*, from October to May–June in *D. puntazzo* and from November–December to June–July in *D. vulgaris*. Therefore, given our period of survey within marinas (April–August), abundance peaks in juveniles linked to recruitment were expected for *D. annularis* and *D. sargus* only. Similarly, artificial habitat preferences were estimated solely from the individuals present within the marinas from April to August. As a result, they were reliably assessed only for the post-settlement juveniles of *D. annularis* and *D. sargus*, the intermediate juveniles of all 4 species and the pre-dispersal juveniles of *D. puntazzo*, *D. vulgaris* and *D. sargus.* For the other fish groups, preferred habitat estimates should be considered with caution because they were extrapolations based on a reduced number of observations.

Temporal abundance patterns for the post-settlement juveniles of *D. sargus* and *D. annularis* indicated that, during the 2 years studied, their juveniles mainly arrived in the marinas in June and July–August, respectively. This timing is consistent with the information gathered so far on their respective settlement periods in the western Mediterranean, which can show temporal variation of ca. 1 mo between sites and years (see Ventura et al. 2014 for review). For *D. puntazzo* and *D. vulgaris*, post-settlement juveniles were observed only at the beginning of the survey period (April–June) and were consistently accompanied by older juveniles. This suggests that both species settled in the marinas well before the start of the surveys (in April). Thus local adaptations to marina artificial habitats in *Diplodus* spp. apparently do not involve a modification in recruitment dates. It should be noted, however, that the observation of 12 post-settlement juveniles of *D. puntazzo* in several of the marinas investigated in April was relatively unexpected because this species settles in November–December on its natural nurseries (Harmelin-Vivien et al. 1995, Vigliola et al. 1998). Although errors (±3.5 mm) in the estimation of fish size by visual census cannot be excluded (MacPherson 1998), and some of these *D. puntazzo* individuals could be at the boundary between post-settler and intermediate juvenile classes, they were particularly small (<30 mm TL). Therefore, further research should be conducted to investigate the reasons for their presence in the marinas during this period.

In Mediterranean natural coastal areas, ontogenetic shifts in habitat use are well documented for *Diplodus* species (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). In general, morphologic modifications during fish growth in this genus are accompanied by habitat changes, resulting in horizontal and then vertical migrations (MacPherson 1998, Vigliola & Harmelin-Vivien 2001). In *D. annularis*, however, fidelity to *P. oceanica* meadows is usually strong throughout juvenile life, except for the larger individuals that can be found on other substrates such as sandy areas (Ventura et al. 2014). This high habitat fidelity was also observed in the marinas, where the species was almost exclusively found in biohut habitats, irrespective of juvenile stage. Indeed, during the 2 years of our survey, *D. annularis* juveniles were observed only twice on DC and only 3 times on PC, and at very low abundances in both cases. Behavior in the artificial context of marinas is thus close to natural behavior, the juveniles of the species being highly associated with the most sheltered habitat available. Similarly, changes in habitat preferences during juvenile life for *D. sargus*, *D. vulgaris* and *D. puntazzo* juveniles in marinas mirrored those described in natural areas (MacPherson 1998). With increasing body size, juvenile fish are less vulnerable to predation (Houde & Hoyt 1987), so their need for shelter decreases. They also diversify their diet toward bigger and more mobile prey and experience lower inter- or intra-specific competition for food (Ross 1986, MacPherson 1998), driving them to enlarge their territory. Accordingly, in the marinas investigated, the youngest juvenile stages of *D. sargus*, *D. vulgaris* and *D. puntazzo* were generally associated with the most sheltered habitats (PB and/or DB), whereas the oldest stages were found to occur evenly on all types of AH investigated. This was not anticipated because the habitats available within the marinas and in natural environments differ dramatically, and fish species generally adapt their behavior to habitat (Koeck et al. 2013).

CONCLUSIONS

By studying the abundances of *Diplodus* spp. juveniles in 5 marinas located along the French Mediterranean coast, we observed that these man-made littoral ecosystems, designed without considering their potential value as fish habitats, can contain high numbers of juvenile rocky fish, which apparently remain there from settlement to dispersal. This had already been observed for other artificial habitats found in the coastal zone, including the breakwaters commonly found at the entrance of marinas. Nevertheless, and unexpectedly, the docks and pontoons commonly found inside marinas also seem to be suitable for fish settlement and growth, especially if artificial multifaceted devices are added to increase their structural complexity. This has important ecological implications as the entire surface of marina ecosystems might participate in the maintenance of rocky fish stocks along anthropized shorelines. However, water and sediment are often polluted in marinas, and the physical damage caused by the replacement of natural substrates with built infrastructures is irreversible. Therefore, even if some ecological functions can be conserved within man-made habitats, some are definitively lost, and it seems unrealistic to pursue the hope of restoring marinas to pristine conditions. Public policies should therefore manage and protect natural fish nursery grounds prior to considering the potential improvement of marina quality. Whatever the case, the rehabilitation of the nursery function of the zones where marinas have been built cannot rely only on ecological engineering. The immediate and long-term effects of fish exposure to the contaminants found in marinas should also be studied to adequately improve water and sediment quality. Finally, connectivity between artificial and natural habitats must be evaluated to prioritize restoration of the marinas that receive the highest numbers of larvae and contribute most to coastal adult stocks.

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The following supplement accompanies the article

Potential use of marinas as nursery grounds by rocky fishes: insights from four *Diplodus* species in the Mediterranean

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Table S1. Definition of development stages for the four species studied. (a) Data from Ventura et al. (2014). (b), (c) and (d) Data from Vigliola & Harmelin (2001). SL = standard length. TL = total length. Total length (TL) refers to the length of the fish measured from the tip of the snout to the tip of the caudal fin. Standard length (SL) refers to the length of a fish measured from the tip of the snout to the posterior end of the midlateral portion of the hypural plate. Simply put, this measurement excludes the length of the caudal fin. Length used for development stages in Vigliola & Harmelin (2001) are given in SL. We estimated TL in our study. Relation between SL and TL are given in (Vigliola 1998): LT = a. LS with a = 1.257 for *Diplodus puntazzo*. a = 1.290 for *D. sargus*. a = 1.283 for *D. vulgaris*.

Development stage	SL (mm)	TL (mm)
(a) *D. annularis*		
Post-settlement		Settlement - 20
Intermediate		20 - 45
Pre-dispersal		>45
(b) *D. puntazzo*		
Post-settlement	Settlement - 21	Settlement - 26
Intermediate	21 - 43	26 - 54
Pre-dispersal	> 43	> 54
(c) *D. sargus*		
Post-settlement	Settlement - 23	Settlement - 30
Intermediate	23 - 49	30 - 63
Pre-dispersal	> 49	> 63
(d) *D. vulgaris*		
Post-settlement	Settlement - 24	Settlement - 30
Intermediate	24 - 40	30 - 51
Pre-dispersal	> 40	> 51

Fig. S1 Evolution of monthly average temperatures in the five marinas studied during the sampling period (April–August).

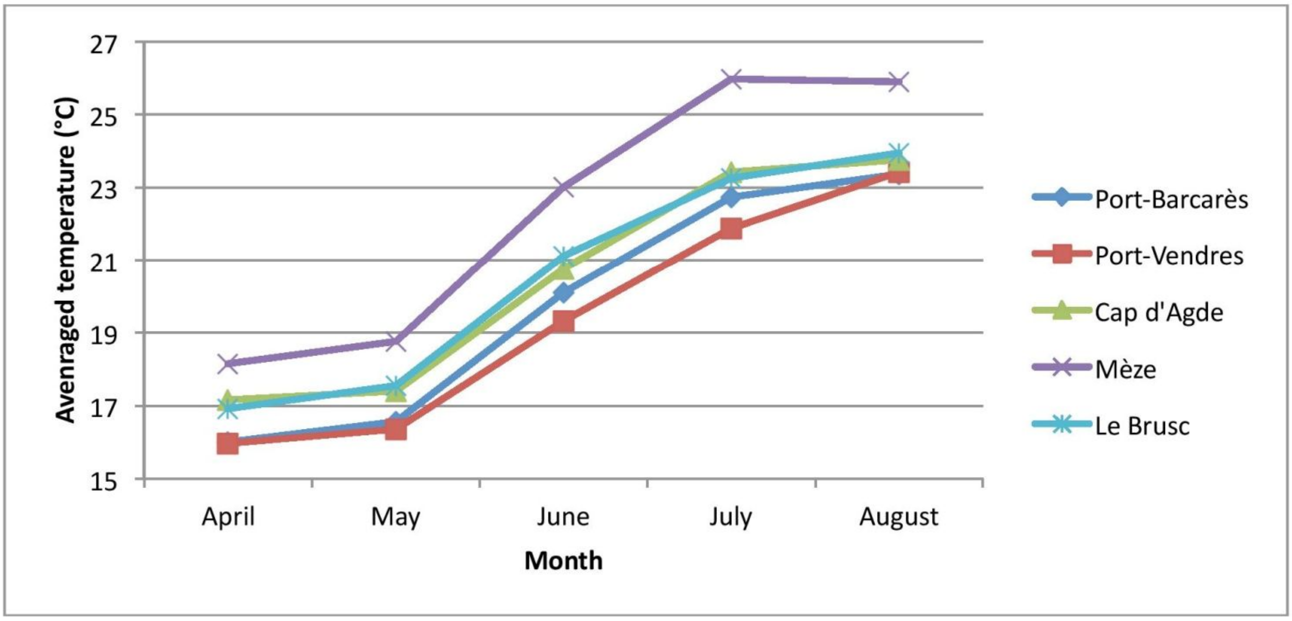
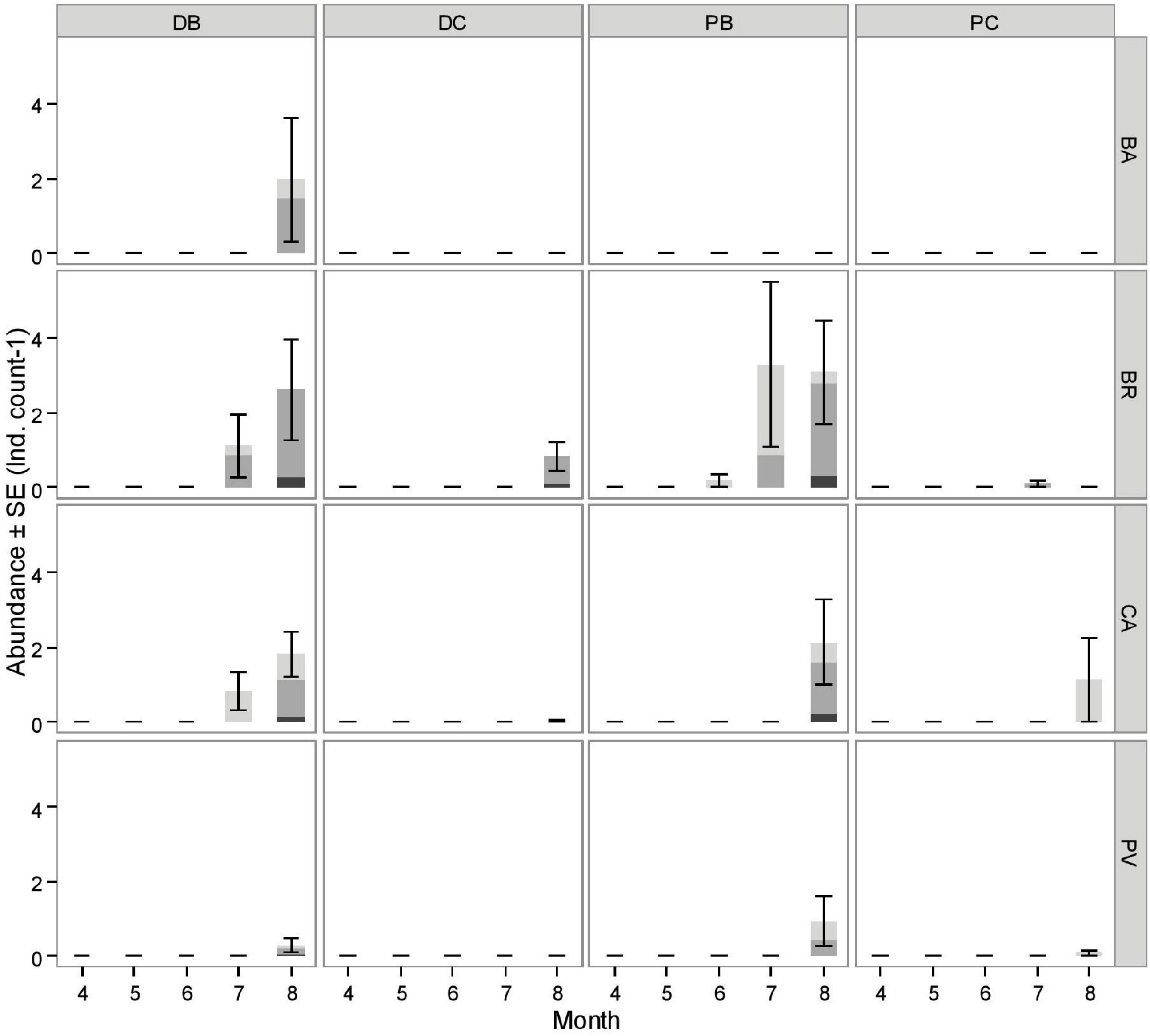
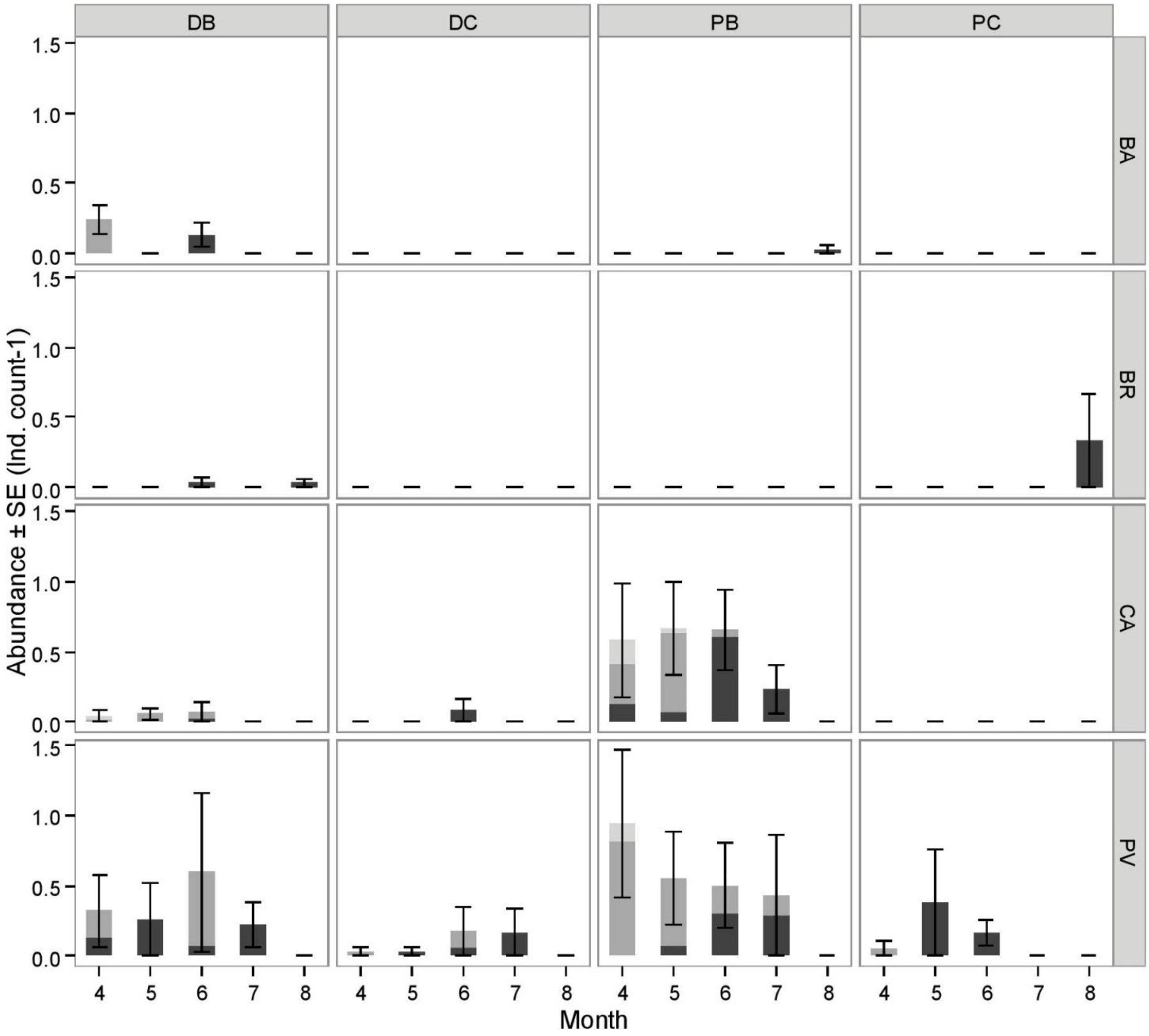


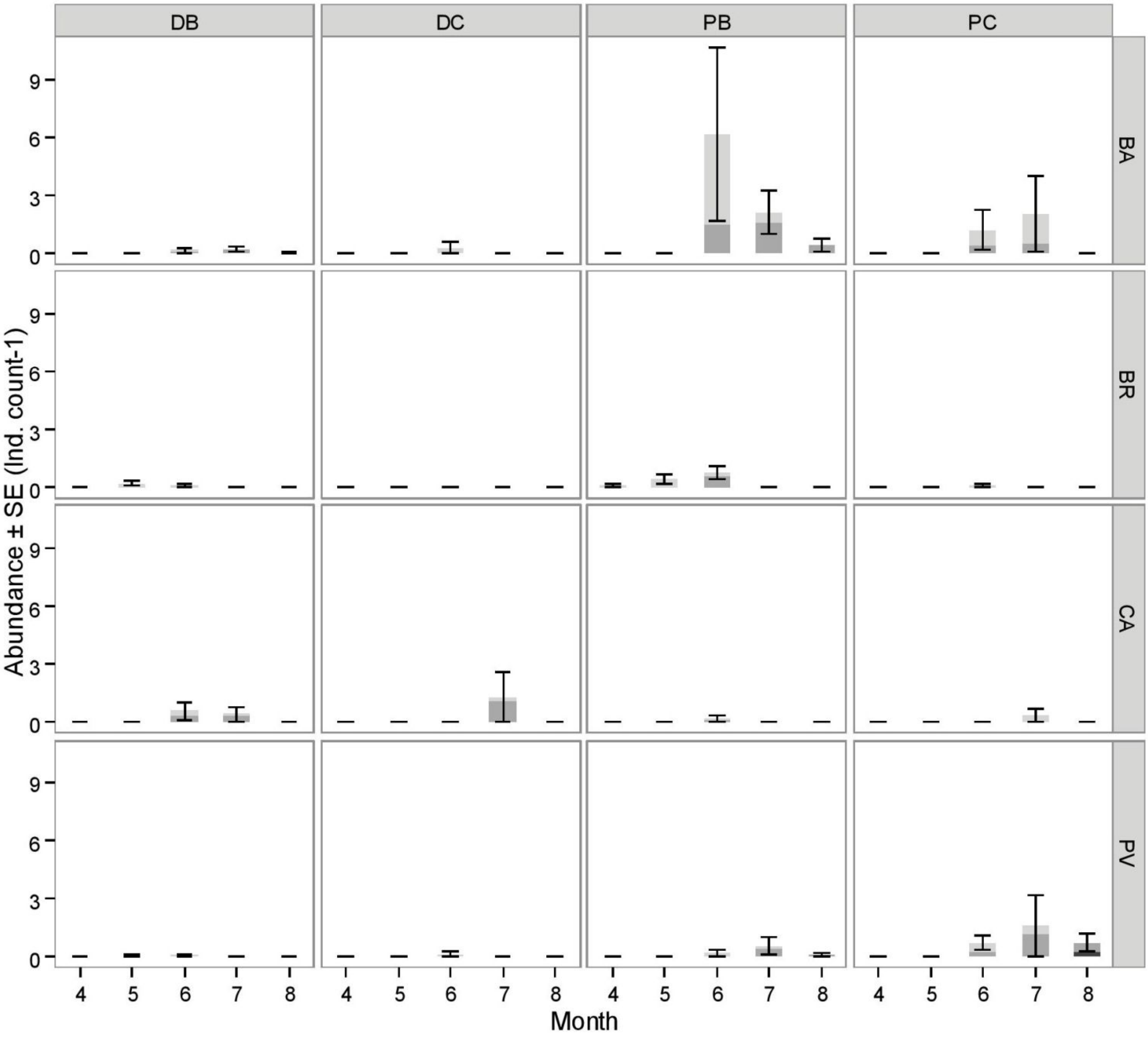
Fig. S2. Mean abundances (ind. count^{-1}) of the juveniles of *Diplodus annularis* (A) , *D. puntazzo* (B) , *D. sargus* (C) and *D. vulgaris* (D) observed per month, marina (Port-Vendres [PV], Port-Barcarès [BA], Cap d'Agde [CA] and Le Brusc [BR]) and habitat type (DB, DC, PB and PC). Results for Mèze are not represented since a total of only 3 individuals were observed in this marina. Colors correspond to the three development stages chosen in this study: post-settlement in light grey, intermediate in dark grey and pre-dispersal in black. Error-bars represent the standard error around the mean abundance found when all development stages were combined.



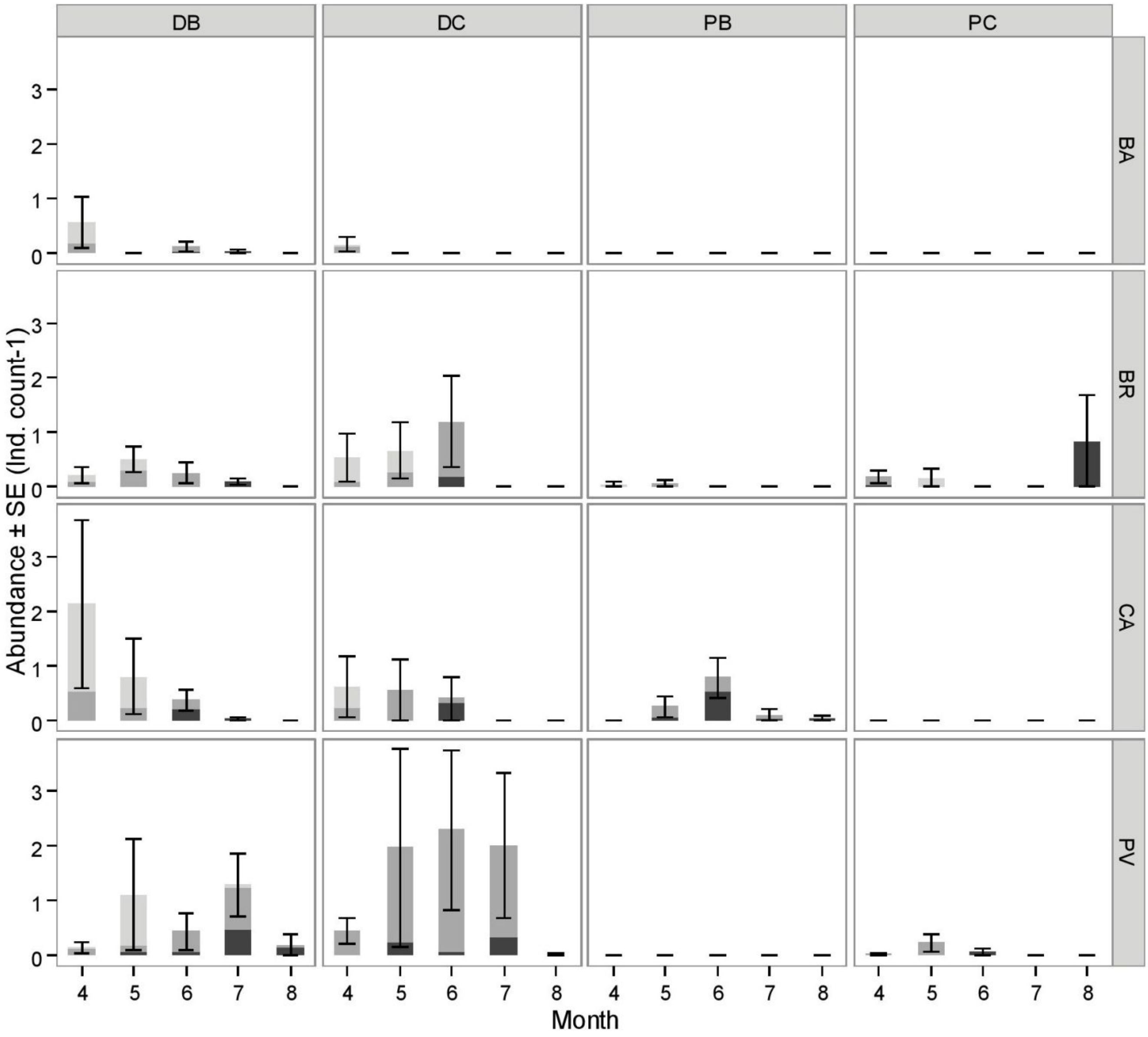
(A): *D. annularis*


DB
DC
PB
PC
BA
BR
CA
PV
Abundance ± SE (Ind. count-1)
0.0
0.5
1.0
1.5
4
5
6
7
8
Month

(B): *D. puntazzo*


DB
DC
PB
PC
BA
BR
CA
PV
0
3
6
9
Abundance ± SE (Ind. count-1)
4
5
6
7
8
Month

(C): *D. sargus*


DB
DC
PB
PC
BA
BR
CA
PV
Abundance ± SE (Ind. count-1)
0
1
2
3
4
5
6
7
8
Month

(D): *D. vulgaris*

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Ventura D, Jona Lasinio G, Ardizzone G (2014) Temporal partitioning of microhabitat use among four juvenile fish species of the genus Diplodus (Pisces: Perciformes, Sparidae). Marine Ecology:1-20

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III.3. Points à retenir :

- Au total, 1 766 observations de juvéniles de sars ont été réalisées en 2013-2014 dans cinq ports répartis sur le long de la façade méditerranéenne,
- L'ensemble des stades de développement juvénile ont été observés pour les quatre espèces (*D. sargus*, *D. vulgaris*, *D. annularis* et *D. puntazzo*),
- Le nombre d'observations variait considérablement entre les ports. Il était quasiment nul dans le port de Mèze (0.04 ± 0.003 ind. comptage^{-1}) et important dans le port du Cap d'Agde (1.08 ± 0.18 ind. comptage^{-1}),
- Les abondances de juvéniles étaient en moyenne deux fois plus importantes sur les micro-structures artificielles (1,02 ± 0.12 ind. comptage^{-1}) que sur les quais et pontons nus (0.52 ± 0.12 ind. comptage^{-1}),
- Une préférence marquée pour les micro-structures artificielles a été mise en évidence pour le stade de développement le plus précoce (stade post-installation),
- Des préférences de micro-habitats préférentiels ont également été trouvées entre les quatre espèces, leurs abondances respectives variant de plus entre les cinq ports.

Conclusions :

➔ L'installation benthique et la croissance des juvéniles de poissons sont possibles en zone portuaire, au moins pour les quatre espèces étudiées,

➔ L'augmentation de la complexité structurale des structures portuaires permet d'améliorer leur qualité en tant qu'habitats juvéniles.

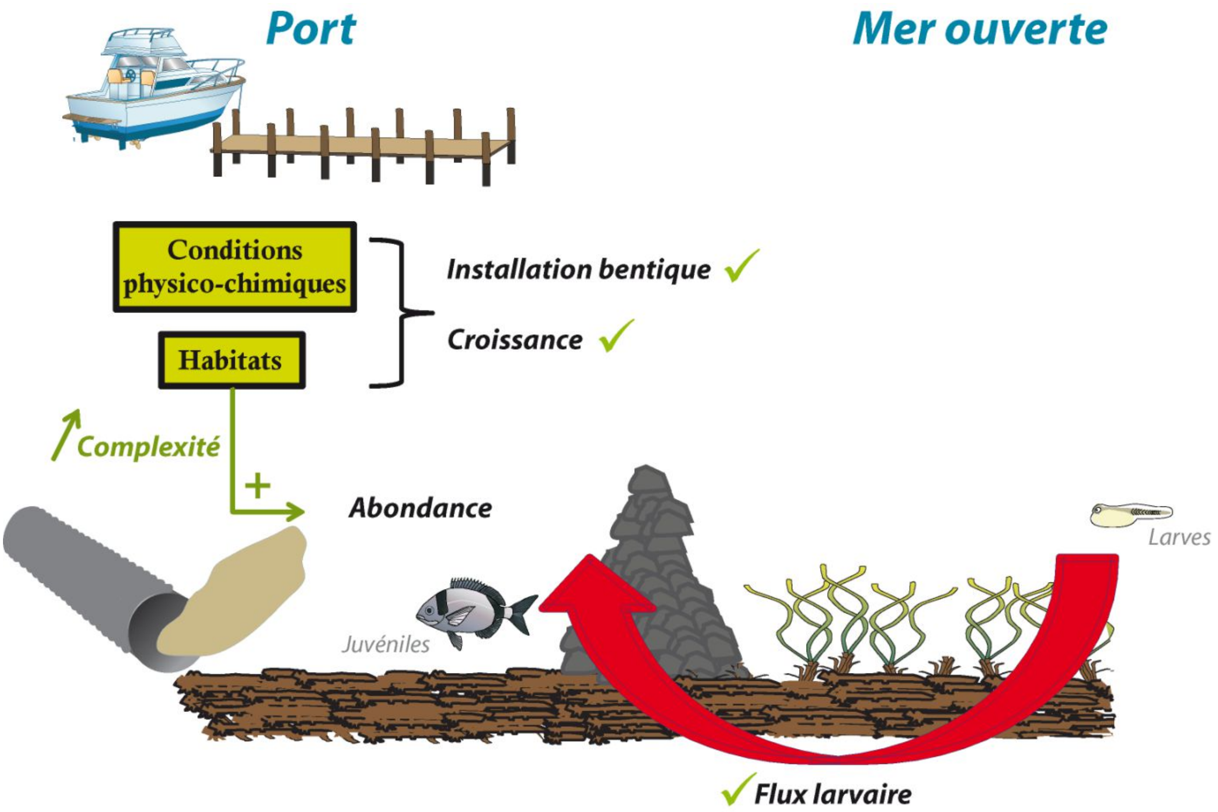
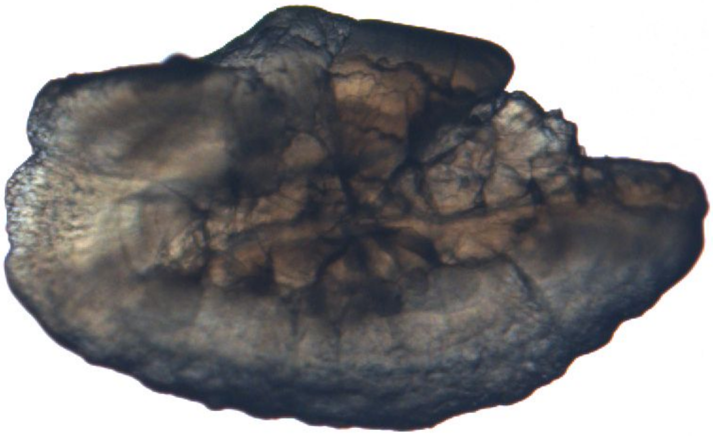


Figure III.1 : Schéma récapitulatif des résultats du chapitre 1. ✓= validé, + = effet positif. Les images proviennent du site http://www.ian.umces.edu.

Chapitre 4. Croissance, condition et contamination des juvéniles de poissons en zone portuaire



F. Chavanon - Ifremer

« La science ne poursuit jamais l'objectif illusoire de rendre ses réponses définitives ou même probables. Elle s'achemine plutôt vers le but infini encore qu'accessible de toujours découvrir des problèmes nouveaux, plus profonds et plus généraux, et de soumettre ses réponses toujours provisoires, à des tests toujours renouvelés et toujours affinés ».

K. Popper

IV.1. Introduction

La mortalité des poissons durant leur vie juvénile est très élevée et dépend de plusieurs facteurs (conditions physiologiques, prédations, etc.) dont leurs conditions de croissance (Gibson 1997, Macpherson et al. 1997). Une croissance rapide permet en effet aux juvéniles non seulement de réduire leur vulnérabilité à la prédation (Halpin 2000, Wennhage 2000) mais également d'exploiter une plus grande gamme de proies (Van Der Veer et al. 1994) et d'augmenter leur résistance aux privations de nourriture (Cowan et al. 2000) ce qui réduit leur mortalité durant leur premier hiver de vie (Sogard 1997, Biro et al. 2004, D'Alessandro et al. 2013). Par ailleurs, même si la croissance des juvéniles de poissons peut être conditionnée par des facteurs génétiques (Planes & Romans 2004) ou maternels (Gagliano et al. 2007), elle dépend fortement des facteurs environnementaux (McCormick 1998). Ainsi, les meilleurs habitats juvéniles (i.e. ceux qui donnent aux juvéniles les meilleures chances de rejoindre les populations adultes) sont généralement ceux où la croissance est la plus élevée (Gibson 1994). C'est pourquoi la croissance juvénile est l'un des critères permettant l'identification des zones de nourriceries (Beck et al. 2001) et qu'elle est très largement utilisée pour caractériser la qualité des habitats juvéniles (e.g. Sogard & Able 1992b, Guindon & Miller 1995, Able et al. 1999, Stunz et al. 2002b, Le Pape et al. 2003). La plupart des études menées sur les nourriceries de poissons concluent que l'utilisation d'un niveau unique d'information n'est pas suffisante pour évaluer de façon pertinente la qualité des habitats juvéniles et recommandent l'utilisation de plusieurs bioindicateurs (Able et al. 1999, Beck et al. 2001, Stunz et al. 2002b). L'utilisation simultanée de plusieurs bioindicateurs dont le temps de réponse varie semble pertinente pour fournir un diagnostic synthétique de la qualité des habitats côtiers des juvéniles poissons (Gilliers et al. 2004, Gilliers et al. 2006, Amara et al. 2007, Kerambrun et al. 2012b). Les indices de condition morphométriques sont simples à acquérir, peu coûteux et complémentaires des indicateurs de croissance (Adams 1999). Parmi eux, l'indice de Fulton est considéré comme représentatif de l'état nutritionnel, des réserves énergétiques des individus et donc de l'état de santé général des individus si on admet l'hypothèse qu'un poisson plus lourd pour une taille donnée a une meilleure condition (Ricker 1975, Suthers 1998, Vasconcelos et al. 2009). Par ailleurs, la condition et la croissance sont deux processus qui peuvent se découpler (Grant & Brown 1999) et donc fournir des informations complémentaires sur des processus physiologiques différents. En effet, en dessous d'un certain seuil critique, les réserves énergétiques sont prioritairement allouées à la croissance au détriment de la condition. Par conséquent, dans un habitat juvénile de piètre qualité, un individu pourrait voir sa taille augmenter et sa condition diminuer. Dans ce cadre, le premier objectif du **chapitre 4** était de mesurer les croissances et les conditions (indice de Fulton) de juvéniles à l'intérieur de zones portuaires et de les comparer avec celles à l'extérieur afin de vérifier si les ports peuvent être des nourriceries pour ces espèces.

S'ils nous donnent une information globale sur la qualité des habitats, les bioindicateurs portant sur la croissance ou la condition des juvéniles ne permettent pas de déterminer les causes de perturbation du système. Généralement intégrés aux villes, à l'interface terre/mer, les ports constituent des écotones très fortement affectés par les rejets industriels et domestiques (Darbra et al. 2004). Leur environnement présente donc souvent des contaminations élevées, notamment en éléments traces métalliques (ETM) (e.g. Schintu & Degetto 1999, Adamo et al. 2005, Tessier et al. 2011, Schintu et al. 2016). L'étude de la contamination par les ETM suscite un grand intérêt au sein de la communauté scientifique (Shulkin et al. 2003). Les ETM sont en effet des constituants naturels de l'environnement à l'état de trace (Bryan 1971), contrairement à de nombreux contaminants organiques (ex. PCB, pesticides). Certains de ces ETM sont essentiels à la vie des organismes et jouent un rôle clé dans leur métabolisme (processus enzymatiques, transport de l'oxygène, etc.). Ces ETM essentiels sont régulés par les organismes. D'autres ETM non-essentiels sont toxiques même en petite quantité. N'étant pas régulés, leur concentration dans les organismes reflète généralement les concentrations environnementales (Amiard et al. 1987). Qu'ils soient essentiels ou non, tous les ETM deviennent toxiques pour les organismes au delà d'un certain seuil (Amiard et al. 1987), avec des conséquences sur la croissance, la condition et la fitness des poissons (cf. **Introduction**). Cependant, la bioaccumulation des ETM dans les poissons est un processus complexe qui dépend d'une part de leur biodisponibilité, et donc de leur spéciation dans les compartiments abiotiques et biotiques des écosystèmes (Bui et al. 2016), et d'autre part de paramètres biologiques des organismes comme l'alimentation, l'âge, la taille, le sexe ou l'habitat (e.g. Harmelin-Vivien et al. 2009, Cresson et al. 2014, Cresson et al. 2015a). Ainsi, il n'existe généralement pas de lien direct entre la mesure d'un ETM dans le milieu et celle dans un organisme vivant supérieur. A notre connaissance, aucun travail n'a décrit à ce jour les niveaux de contamination des juvéniles de poissons ayant grandi en zone portuaire. C'est ce que nous avons tenté de faire dans ce chapitre, afin de mieux évaluer l'influence des contaminants sur la qualité des habitats juvéniles portuaires.

Dans ce contexte, le **chapitre 4** cherchait donc à répondre spécifiquement aux questions suivantes : existe-t-il des différences de croissance, de condition et de niveau de contamination en ETM entre des juvéniles de poissons capturés à l'intérieur et à l'extérieur de ports ? Ces paramètres sont-ils contrôlés par les niveaux de contamination chimique dans le milieu ?

Pour répondre à ces questions, des juvéniles de deux espèces de sars (*D. sargus* et *D. vulgaris*) ont été capturés en fin de vie juvénile dans deux zones portuaires contrastées et deux zones de nourricerie différentes de la rade de Toulon (une naturelle et une artificialisée). Leurs taux de croissance absolue, leurs conditions ainsi que les concentrations en 12 ETM dans leurs muscles ont été comparés, en lien avec la contamination chimique de chaque site. L'estimation de la croissance des poissons peut se faire soit sur les populations naturelles (Gilliers et al. 2004, Amara et al. 2007), soit sur des individus maintenus en cage dans le milieu naturel (Sogard & Able 1992a, Able et al. 1999). Si cette deuxième méthode présente l'avantage de maitriser parfaitement les caractéristiques du lot initial de juvéniles, de connaître avec précision la localisation et la durée d'exposition des individus tout en conservant les conditions environnementales du site étudié (Oikari & Kunnamo-Ojala 1987), elle présente plusieurs inconvénients majeurs qui nous ont amenés à l'écarter. Parmi eux, nous pouvons citer les problèmes d'alimentation des individus en cage, le stress induit par l'enfermement ou encore l'absence de prise en compte des effets de la prédation et par conséquent de la qualité physique de l'habitat. Nous avons donc choisi de mener notre étude sur des populations naturelles. Ceci peut se faire soit par une estimation *in situ* régulière de la taille des juvéniles (Vigliola 1998) soit par analyse des microstructures des otolithes (Encart 2). Ces deux méthodes peuvent fournir des résultats comparables (Vigliola 1998). Néanmoins, la méthode *in situ*, qui nécessite un effort d'échantillonnage conséquent, est très liée aux conditions météorologiques et peut être biaisée par la mortalité si cette dernière est croissance dépendante. L'analyse des microstructures des otolithes, quant à elle, si elle est pratiquée sur des individus capturés en fin de vie juvénile, permet d'intégrer l'impact de l'ensemble des facteurs environnementaux sur la croissance tout au long de la période de résidence des individus sur leur site de capture. En effet, au niveau individuel, la croissance des otolithes est directement liée à la croissance somatique des individus (Campana & Thorrold 2001, Wilson et al. 2009). De plus, différentes marques peuvent être repérées dans la microstructure des otolithes, chacune représentant une transition dans le cycle de vie du poisson (Wilson & McCormick 1999). Chez les sars, une marque reconnaissable se forme au moment la transition entre la vie larvaire pélagique et la vie juvénile benthique (Vigliola et al. 2000). Cette marque permet de repérer précisément l'installation benthique. Il est donc possible d'utiliser la croissance des otolithes durant la vie juvénile benthique et de l'utiliser comme proxy de la croissance juvénile.

IV.2. Article 2 (publié dans Marine Pollution Bulletin) : Growth, condition and metal concentration in juveniles of two *Diplodus* species in ports.

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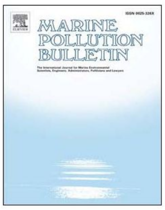

Growth, condition and metal concentration in juveniles of two *Diplodus* species in ports

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ABSTRACT

High abundances of juvenile fish in certain ports suggest they might provide alternative nursery habitats for several species. To further investigate this possibility, post-settlement growth, metal uptake and body condition were estimated in 127 juveniles of two seabream species, collected in 2014–15, inside and outside the highly polluted ports of the Bay of Toulon. This showed that differences in local pollution levels (here in Hg, Cu, Pb and Zn) are not consistently mirrored within fish flesh. Muscle metal concentrations, below sanitary thresholds for both species, were higher in ports for Cu, Pb and V only. Otherwise, fish muscle composition principally differed by species or by year. Juvenile growth and condition were equivalent at all sites. Higher prey abundance in certain ports might therefore compensate the deleterious effects of pollution, resulting in similar sizes and body conditions for departing juvenile fish than in nearby natural habitats.

1. Introduction

Understanding the life cycle of marine fishes is vital for their sustainable exploitation. The juveniles of many coastal species occupy various shallow habitats during their life stages. These habitats include estuaries (e.g. Beck et al., 2001; Vasconcelos et al., 2008; Vinagre et al., 2010), coastal lagoons (e.g. Abecasis et al., 2009; Franco et al., 2006), coral reefs (e.g. Carassou et al., 2009; Doherty, 1981), mangroves (e.g. Nagelkerken and Faunce, 2008), seagrass beds (e.g. Cheminee et al., 2013; Francour, 1999; Jones et al., 2013) and shallow coastal areas (e.g. Cheminee et al., 2011; Harmelin-Vivien et al., 1995; MacPherson, 1998). Since mortality rates in fish are maximal during the early phases of their life cycles, identification of their nursery habitats is particularly important for stock conservation (Jennings and Blanchard, 2004; Macpherson et al., 1997). In theory, fish nursery habitats must fulfill four conditions: they must support high abundances of juveniles, sustain faster somatic growth rates, allow higher survival and their populations must contribute more to the final adult stock (Beck et al., 2001). Therefore defining fish nursery habitats not only requires the identification of habitats with high juvenile densities but also those which enhance survival, growth rates and contribution to adult stocks. During the last few years, several studies suggested that coastal man-made infrastructures, particularly those found inside ports, might provide alternative nursery habitats for several rocky fish species (Bouchoucha et al., 2016; Clynick, 2006; Dufour et al., 2009; Pastor et al., 2013). However, this conclusion was solely based on the high abundances of juvenile fish observed in ports. To our knowledge, the impact of juvenile fish settlement in ports on their subsequent growth and physiological condition remains to be investigated.

Ports are among the most common man-made infrastructures found on the shoreline. Because they are semi-closed, calm and protected areas, they might provide favorable conditions for juvenile growth and survival (Harmelin-Vivien et al., 1995). However, they are generally integrated within cities or towns, and their influence on the environment is unavoidable (Darbra et al., 2005). Indeed, the very existence of a port already implies a certain loss of natural habitat. Furthermore, the industrial and yachting activities associated with ports result in chronic biological and chemical pollution of both the sediment and the water column inside and in the vicinity of port areas (Darbra et al., 2004). Chemical contaminants are well known to adversely affect fish physiology, growth and health, especially at young stages (e.g. Able et al., 1999; Amara et al., 2007; Kerambrun et al., 2013; Kerambrun et al., 2012). A commonly observed sub-lethal response of fish chronically exposed to contaminants is the modification of their energy allocation:

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it is used preferentially to resist chemical stress rather than for maintenance and growth (Rowe, 2003). This decreases global individual fitness as fish juveniles with slower growth and limited energy storage have lower survival rates and contribute less to the adult stock (Sogard, 1997). Juvenile fish exposure to chemical contaminants in ports is therefore expected to result in slower growth and poorer condition. Consequently, it is questionable that ports effectively correspond to the definition of fish nursery areas. Yet, many coastal habitats under high anthropogenic influence, like most estuaries and coastal lagoons, have been shown to sustain important densities of juvenile fish with high growth rates (Beck et al., 2001; Franco et al., 2006; Gibson, 1994) and are, as such, listed as nursery habitats for many species. As recipients of industrial and domestic wastes, these systems are subjected to moderate to high pollution (Amara et al., 2007; Courrat et al., 2009; Vasconcelos et al., 2011), which does not seem to alter their nursery function.

In this context, we measured and compared the post-settlement growth rates and the final body conditions and muscle metal concentrations of the juveniles of two sparids of the same genus (*Diplodus* Raffinesque, 1810) captured after at least 4.5 months of residency in two contrasted port areas of the Bay of Toulon (North-West Mediterranean) and in nearby coastal habitats matching their nursery area criteria. Further comparison of this data with concomitant in situ records of the environmental and pollution conditions experienced at each site allowed better assessment the value of port habitats as fish nursery areas and improved understanding of the potential consequences of their construction in terms of coastal fish stock dynamics.

1.1. M & M

1.1.1. Ethics statement

Sampling for this work was carried out in strict accordance with French legislation. After collection, juvenile individuals were immediately euthanized in ice slurry. The sampling activity did not involve endangered or protected species.

1.1.2. Model species

Two coastal rocky fish species of the same genus were selected for this study: the white seabream *D. sargus sargus* (Linnaeus, 1758), hereafter *D. sargus*, and the two-banded seabream *D. vulgaris* (Geoffroy Saint-Hilaire, 1817). These two sparids are common in the Mediterranean and have high ecological and commercial value (Coll et al., 2004; Lloret et al., 2008; Morales-Nin et al., 2005). They are highly abundant in both natural and artificial rocky coastal areas (Tortonese, 1965) and their juvenile habitat use is fairly well known (Bouchoucha et al., 2016; Cheminee et al., 2011; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Ventura et al., 2014; Vigliola et al., 1998): *D. sargus* settles in one pulse only, in June–July, and usually leaves its nursery grounds in September; conversely *D. vulgaris* settles in two pulses, one in November–December and one in January–February, and leaves its nursery grounds in June–July. Moreover, as migration is very limited in *Diplodus* juveniles (Macpherson et al., 1997) and given the distance between our sampling sites (between 1.5 and 8 km), the post-settlement growth, body condition and contamination levels of the juveniles of the two species should correctly reflect the quality of the sites in which they were collected. Given the complementarity of the periods of residency of the two species over the year, investigating their respective reactions to different habitat types should allow reaching more general conclusions regarding habitat suitability with regards juvenile fish growth, condition and contamination.

1.1.3. Study area and fish sampling

Our study was carried out within the Bay of Toulon, located in the northwest French Mediterranean (Fig. 1) and surrounded by the city of Toulon (ca. 600,000 inhabitants). The Bay of Toulon is divided into the “Large Bay” (42.2 km^2) and the “Small Bay” (9.8 km^2), separated by a breakwater (1200 m) built in the nineteenth century (Fig. 1). The Small Bay harbors one of the largest industrial ports of France and six marinas. Almost all natural habitats have disappeared from this area. Its semi-enclosed morphology, micro-tidal conditions and intermittent freshwater inputs (Nicolau et al., 2012), lead to relatively long water residence times (Dufresne et al., 2014). Consequently, local historic (e.g. World War II) and present anthropogenic activities have resulted in strong multi-contamination of its sedimentary compartment (Dang et al., 2015; Pougnet et al., 2014; Tessier et al., 2011) and water column (Dang et al., 2015; Jean et al., 2012). Conversely, the Large Bay opens onto the Mediterranean and is little affected by human activities (Tessier et al., 2011). Its shoreline, about 13 km in length, is rocky and natural, except for two small marinas and three artificial beaches.

In this work, four contrasting sampling sites were selected: two as representative of the different types of ports present in the Bay of Toulon and two as representative of the other types of coastal habitats available for the juveniles of local rocky fishes. Previous observations had confirmed the regular presence of the juveniles of the two species at the four sites, where they had repeatedly been seen in abundance and at different sizes (personal observation). The first sampling site (STM) was positioned in the Saint Mandrier marina, within the Small Bay (Fig. 1). This port, representative of the marinas found in the Bay of Toulon, harbors 800 boats and pleasure craft and its average depth varies between 2.5 and 4 m. It is protected by two breakwaters that separate it from the rest of the bay. Sampling at this site was made inside the port, on the landward side of its eastern breakwater. The second site (TLN) was positioned further within the Small Bay (Fig. 1), in one of the most contaminated parts of the Bay of Toulon (Tessier et al., 2011; Wafo et al., 2016) located at about 500 m from the biggest naval port of the Mediterranean (the port of Toulon, which harbors around 30 warships and nuclear submarines) and < 200 m from a large ferry terminal serving the Corsica island (ca. 1000 rotations and 1.2 million passengers per year). As for STM, sampling was carried out on the landward side of a breakwater. The third sampling site (DLE) was positioned on the seaward side of the main breakwater that separates the Small Bay from the Large Bay (Fig. 1), in an area that is very little impacted by port pollution (Tessier et al., 2011; Wafo et al., 2016). In the Mediterranean, the seaward sides of peripheral breakwaters have been shown to be colonized by the juvenile of numerous fish species and are generally considered as favorable habitats for juvenile fish growth (Clynick, 2006; Dufour et al., 2009; Guidetti, 2004; Pastor et al., 2013; Pizzolon et al., 2008; Ruitton et al., 2000). Therefore, the DLE site was chosen as a representative of the non-polluted artificial nursery habitats available for rocky fishes within the Bay of Toulon. Physical habitat characteristics (substrate, depth, etc.) are equivalent in the STM, TLN and DLE sampling sites. The last sampling site (MAG) was positioned within the Large Bay (Fig. 1), in a natural cove (Anse Magaud) whose physical habitat characteristics match those identified as the most suitable for the benthic settlement of *Diplodus* species, i.e. shallow coastal habitats (between 0 and 2 m) protected from prevailing winds and characterized by gentle slopes covered with sand, pebbles and boulders (Cheminee et al., 2011; Harmelin-Vivien et al., 1995). Therefore, this site was chosen as a representative of the natural rocky fish nursery habitats available in the Bay of Toulon.

Fish sampling for this study was to be carried out in 2014 and 2015, during the month preceding juveniles' departure dates for each species, i.e. after at least 4.5 months of residency in each habitat. Unfortunately, we failed to collect *D. sargus* juveniles in 2015. Therefore, *D. sargus* juveniles in this work were collected in late August- early September 2014 only, whereas *D. vulgaris* juveniles were collected both in 2014 and in 2015, in early July for both years. At each location, fish were sampled between 0 and 2.5 m depth using hand-nets. The juveniles of the two species were discriminated following the morphometric and size criteria of Vigliola and Harmelin-Vivien (2001).

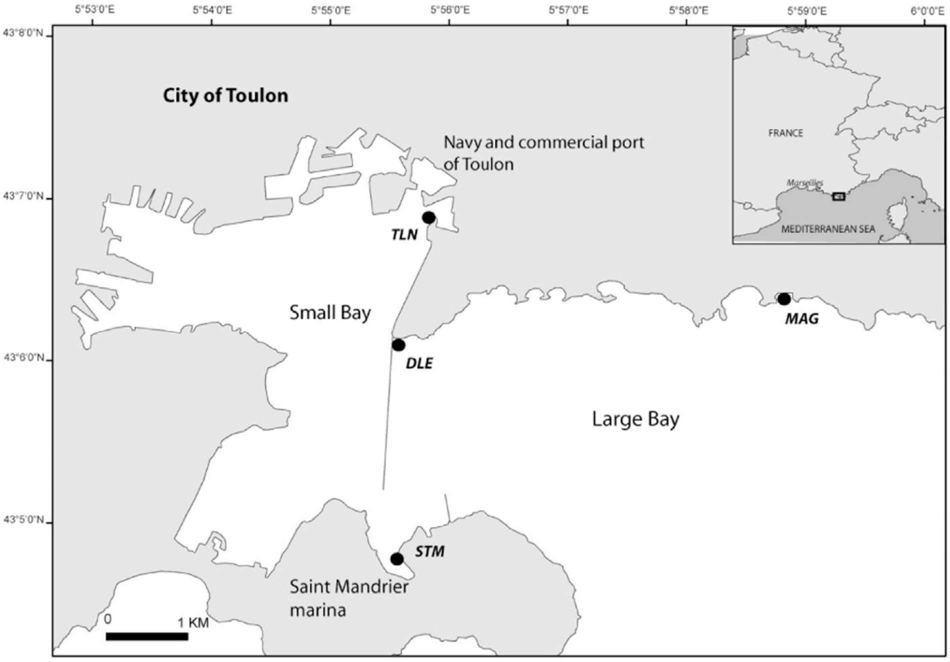

Fig. 1. Location of the 4 sites (●) sampled in the Bay of Toulon (Northwestern Mediterranean).

1.1.4. Environmental and chemical contamination data

Metal bioavailability in the environment can be estimated by various methods. Among them, the use of Diffusive Gradient on Thin film devices (DGT) allows gathering integrative values of water concentrations in the most labile dissolved metal species (Davison and Zhang, 1994). DGTs concentrate the most highly labile dissolved cations, as defined operationally (hydrated ions, mineral complexes, and weak or rapidly dissociable organic complexes). Indeed, during their immersion period, DGT accumulate ionic forms and weakly dissociable complexes (hereafter named the DGT-labile fraction) on a Chelex 100 resin, proportionally to their water concentration over the entire exposure time. This DGT-labile fraction is considered more representative of the fraction potentially bioavailable than the total metal concentration (Odzak et al., 2002; Twiss and Moffett, 2002; Zhang and Davison, 2001).

For this study, three DGT were immersed at 1.5 m depth for 15 days each month, from January to July 2015, in order to record local metal concentrations at each of the four sampling sites over 7 consecutive months. During this period, water temperature and salinity were also recorded at each site using a CTD probe (YSI Pro30), and monthly samples of surface water were taken to investigate local variations in primary productivity (Chlorophyll *a* concentrations). Three DGT devices were selected as control and not immersed in the seawater.

To quantify the DGT-labile fraction bioavailable at each site for each month, the Chelex 100 resin of the DGT probes was peeled off in the laboratory and trace elements were extracted in 1.8 ml of 1 M ultrapure nitric acid (24–48 h). Concentrations in the acid extracts were analyzed for seven trace elements (Cr, Pb, Mn, Zn, Cu, Fe and Al) using ICP-MS to determine the mass of metal (M) accumulated by the DGT. Then, for each trace element, the average labile concentrations in water (C_{DGT}) were calculated using the following equation (Zhang et al., 1995):

$$C_{DGT} = (M \cdot \Delta g)/(D_m \cdot t \cdot A)$$

where M is the mass of the trace element accumulated in the resin, Δg is the diffusive layer thickness, Dm is the diffusion coefficient of the trace element provided by DGT Research (www.dgtresearch.com), t is the immersion of the DGT probe, and A is the exposure area.

Chlorophyll a (Chl *a*) concentrations for each site and month were estimated by filtering 1 L of water through Whatman GF/F filters (pore diameter = 0.7 µm) under vacuum conditions. The resulting filters were placed in glass tubes and stored separately at − 20 °C until they could be analyzed. For this, each filter was ground separately in acetone 90% and the resulting solution was incubated for 24 h in the dark at 4 °C before measurement of pigment concentrations by spectrofluorimetry (Neveux and Lantoine, 1993).

1.1.5. Fish post-settlement growth and final condition

Upon collection, the juveniles of the two species were transported on ice to the laboratory, measured (total length TL, in mm), weighed (total mass M, in g) and stored at − 20 °C. Their body condition was estimated based on the Fulton's index K (Ricker, 1975):

$$K = 10^5 M/TL^3$$

where M is the total wet mass in g and TL the total length in mm.

This morphometric index assumes that heavier fish for a given length are in better condition (Ricker, 1975).

Fish post-settlement growth rates for this study were derived from otolith (ear stones) reading. Otoliths are paired calcified structures located in the inner ear of teleost fishes. Their use has become standard in marine ecology and fishery research. They provide a great deal of information on the life histories of fishes, particularly at the juvenile stage (Campana, 1999). Many studies reported the daily formation of otolith increments in larvae and juveniles of various species. As a result, counts of increments in otoliths have enabled the determination of juvenile fish ages on a daily basis (Campana and Jones, 1992; Pannella, 1971). Moreover, at the individual level, otolith growth rate is directly related to somatic growth rate (Campana and Thorrold, 2001; Wilson et al., 2009). Therefore, the length of the otolith radius can be used as a proxy of fish somatic growth.

For each fish, the left sagital otolith was extracted, washed and prepared for daily ring counts. Otoliths were embedded individually in Crystalbond resin and ground in the transversal plane using 1200, 2400 and 4000 grit silicate paper until the core (primordium) was exposed. Then, the otolith sections were flipped over and polished down to reach an average thickness of 20 µm. As daily otolith increment deposition has been validated for both *D. sargus* and *D. vulgaris* (Vigliola, 1997), daily rings count can be used for age estimation in their juveniles. Moreover, the sagital otoliths of both *D. sargus* and *D. vulgaris* exhibit a benthic settlement mark, described as a series of shaded daily increments (Di Franco et al., 2011; Vigliola et al., 2000). Therefore, within each otolith, it is possible to discriminate between the larval pelagic and the juvenile benthic periods of growth. Post-settlement increments were counted from the settlement mark to the edge of the otolith.

Table 1
Environmental parameters for the four sampling sites studied, inside (STM and TLN) and outside (DLE and MAG) ports in the Bay of Toulon.

	Mean temperature (°C)		Mean salinity		Mean Chloropyll *a* concentration ($\mu g \cdot l^{-1}$)	
Site	Mean ± SD	Min-max	Mean ± SD	Min-max	Mean ± SD	Min-max
DLE	17.1 ± 3.9	12.6–23.6	38.0 ± 0.8	35.8–39.0	0.27 ± 0.17	0.02–0.58
MAG	17.4 ± 4.1	13.2–25.5	38.0 ± 0.5	37.2–39.1	0.27 ± 0.20	0.13–0.86
STM	17.7 ± 4.9	12.0–25.4	37.8 ± 1.3	34.4–39.5	0.37 ± 0.23	0.16–0.80
TLN	17.5 ± 4.3	12.8–24.8	37.7 ± 1.0	35.1–38.8	0.48 ± 0.33	0.17–1.16

Corresponding distances (in µm) were also measured along the maximum otolith growth axis. Finally, the post-settlement daily absolute growth rate (AGR, Panfili, 2002) was calculated for each fish using the equation:

$$AGR = D/T$$

where D is the distance (in µm) and T the number of daily increments (in day) between the settlement mark and the edge of the otolith.

1.1.6. *Trace element concentrations in fish muscle tissue*

For each sampling site, ca. 5 individuals of each species and year were selected randomly for analysis of their body concentrations in 12 trace elements (Al, As, Cr, Cu, Fe, Hg, 004Dn, Pb, Se, Ti, V and Zn). All the materials used for muscle dissection and sample preparation were previously decontaminated by 4% ultrapure nitric acid baths, triple rinsed with ultrapure water (18.2 MΩ) and dried under a class 100 clean bench.

For each individual a dorsal muscle sample was dissected, freeze-dried and ground into powder. Total mercury (hereafter Hg) analyses were carried out directly on 10–100 mg sub-samples of fish muscle powder (untreated) using an Advanced Mercury Analyzer (ALTEC AMA 254). For Hg determination, the metal was evaporated by progressive heating up to 800 °C, then kept in an oxygen atmosphere for 3 min, and amalgamated on a gold net. Afterwards, the net was heated to release the collected Hg which was finally measured by atomic absorption spectrophotometry. Hg analyses were run according to a thorough quality control program including periodic analysis of a certified reference material DORM-4 (fish protein, CNRC-NRC) chosen in accordance with the assumed Hg content of the sample.

For the other trace elements, aliquots (100–200 mg) of muscle powder were first placed in a microwave oven (MARS-5, CEM Corporation) to be digested with 8 ml of ultrapure nitric acid under controlled temperature and pressure conditions. After cooling, the digests were diluted to 50 ml with milli-Q water. The concentrations of Al, As, Cr, Cu, Fe, Mn, Pb, Se, Ti,V and Zn were determined using an ICP-Q-MS (iCAP Qc, ThermoFisher Scientific) equipped with a Peltier-cooling system, a quartz cyclonic spray chamber, a 200 $\mu l \cdot mn^{-1}$ PFA nebulizer and Nickel standard cones with insert. Elemental concentrations (in $mg \cdot kg^{-1}$ of dry mass, dm) were determined using external calibration (4 to 6 points) in diluted HNO_3 (3%). A known amount of internal standard solution (^{45}Sc, ^{89}Y, ^{115}In and ^{209}Bi) was added to all the solutions to monitor for instrumental drift and matrix effects. Depending on the element, measurements were performed using standard (STD) or Kinetic Energy Dispersion (KED) modes. ICP-MS analyses were run according to a thorough quality control program including repeated analysis of certified reference material DORM-4 (fish protein, CNRC-NRC) and IAEA-407 (fish tissue, IAEA). Detection limits (LODs) were estimated at 0.50, 0.05, 0.05, 0.25, 0.25, 0.05, 0.05, 0.25, 0.10, 0.10 and 1.00 $mg \cdot kg^{-1}$ dm for Al, As, Cr, Cu, Fe, Mn, Pb, Se, Ti, V and Zn, respectively. Element concentrations below LODs were set to zero.

1.1.7. *Statistical analyses*

All statistical analyses were performed using the PRIMER 6 software with the PERMANOVA add-on (Clarke and Warwick, 2001). The significance level for the tests was consistently set at $\alpha = 0.05$.

Spatial variations in age, total length, juvenile growth rate and final fish body condition and trace element concentrations were analyzed for the two species, separately or grouped, according to the sampling site. Interspecific and inter-annual variations were tested using data from *D. sargus* and *D. vulgaris* in 2014 and from *D. vulgaris* in 2014 and 2015, respectively. Differences in ambient environmental conditions (temperature, salinity and Chl *a* levels) and in water elemental composition among sampling sites (TLN, STM, DLE or MAG) were tested separately. To do this PERMANOVAs were performed. They allow handling complex, unbalanced and multiple-factor designs, and considering interactions between factors. In addition, they do not assume normal error distributions (Anderson, 2001). Euclidean distance similarity matrixes were generated and the factors Species (with two levels: *D. sargus* and *D. vulgaris*), Year (with two levels: 2014 and 2015) and Site (with four levels: TLN, STM, DLE and NAT) were treated as fixed. Data were log(X + 1) transformed prior to statistical analyses. In each case, *p*-values were calculated by 9999 random permutations of residuals (Anderson, 2001).

2. Results

2.1. *Differences in environmental conditions among sites*

Temperature and salinity conditions were similar ($p > 0.695$) at all sampling sites (Table 1), the average values over the seven months surveyed ranging from 17.1 ± 3.9 °C (at DLE) to 17.7 ± 4.9 °C (at STM) for temperature, and from 37.7 ± 1.0 (at TLN) to 38.0 ± 0.8 (at DLE) for salinity. Conversely, primary production levels differed significantly ($p > 0.02$) among sites (Table 1), with 1.5–1.7 times higher average water concentrations in Chl *a* in the two ports (0.48 ± 0.33 $\mu g \cdot l^{-1}$ at TLN and 0.37 ± 0.23 $\mu g \cdot l^{-1}$ at STM) than at the DLE (0.27 ± 0.17 $\mu g \cdot l^{-1}$) and MAG (0.27 ± 0.20 $\mu g \cdot l^{-1}$) sites.

With regards contamination, only the water concentrations in Cu, Pb and Zn differed significantly ($p < 0.026$) according to the sampling site (Fig. 2), with consistently lower water concentrations at MAG, and higher ones in the ports. However, water concentrations in Cu were maximal at STM (2971 ± 997 $ng \cdot l^{-1}$), while for Pb, the highest values were recorded at TLN (328 ± 107 $ng \cdot l^{-1}$). For Zn, water concentrations were similar at the two port sites, with average values of 3.3 ± 0.78 $\mu g \cdot l^{-1}$ at STM and 3.1 ± 1.7 $\mu g \cdot l^{-1}$ at TLN. For the other trace elements investigated (Al, Cr, Fe and Mn), spatial differences in water concentrations were not significant ($p > 0.078$) due to important variations at certain sites. However, the highest local water concentrations in Fe (0.69 ± 1.0 $\mu g \cdot l^{-1}$) and in Mn (1.5 ± 1.2 $ng \cdot l^{-1}$) were interestingly both observed at DLE, and Al and Cr concentrations were the lowest in a port, at STM (averages of 0.61 ± 0.18 $\mu g \cdot l^{-1}$ and 49 ± 15 $ng \cdot l^{-1}$, respectively).

2.2. *Body condition and juvenile growth rate*

For the 127 individuals included in this work, post-settlement growth rate (AGR) and body condition (K) ranged from 4.3 ± 0.8 to 6.9 ± 0.9 $\mu m \cdot d^{-1}$ and from 1.44 ± 0.12 to 1.83 ± 0.10, respectively (Table 2). For both parameters, significant variations were found both by species ($p < 0.001$) and by year ($p < 0.001$), with higher

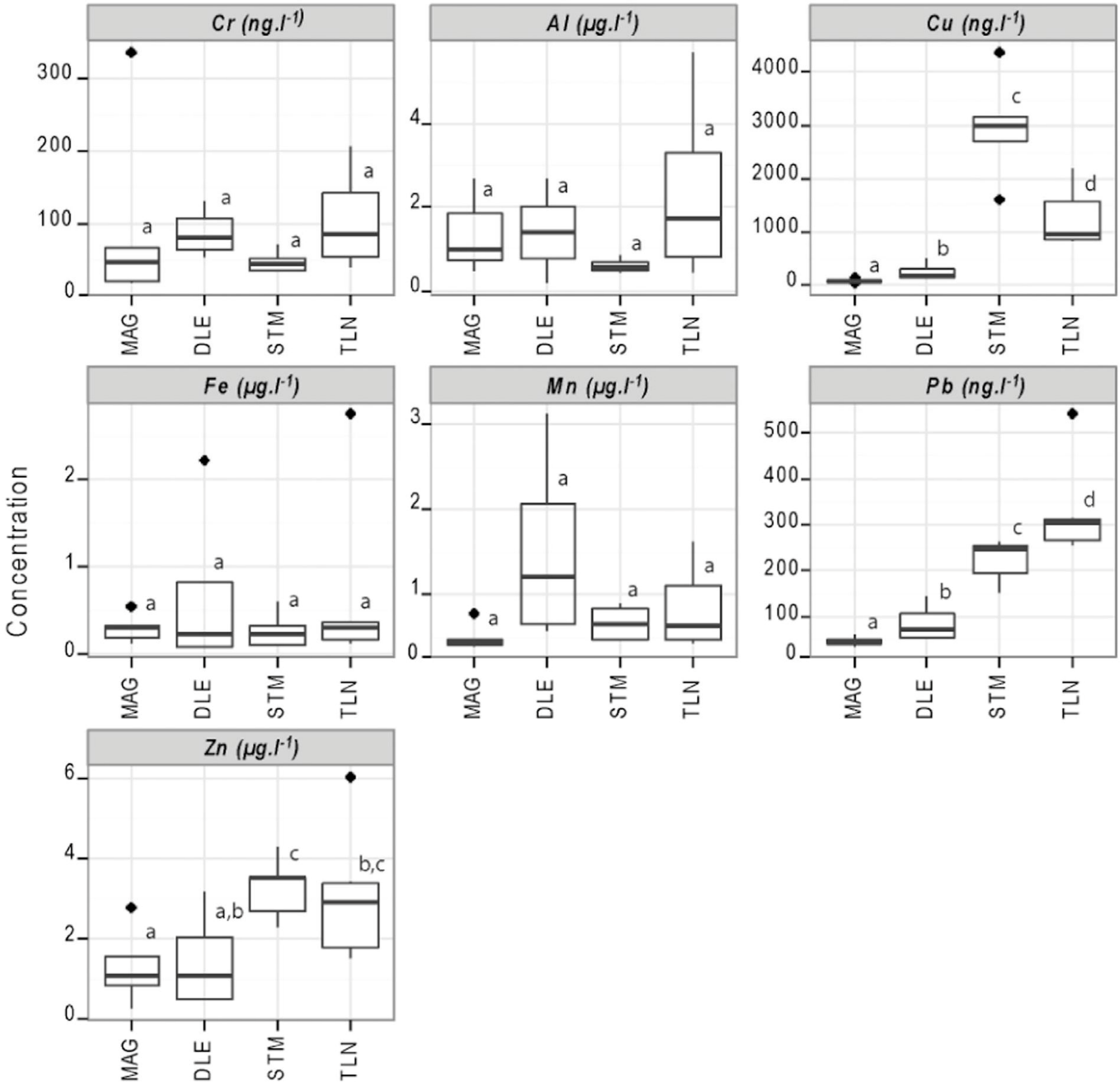

Fig. 2. Comparisons of trace element contamination in the water column among the four sampling sites studied, inside (STM and TLN) and outside (DLE and MAG) ports in the Bay of Toulon. Letters indicate significant differences ($p < 0.05$) between sites.

Table 2
Growth and body condition (mean ± SD) of the juveniles of *D. sargus* and *D. vulgaris* at the four sampling sites studied, inside (STM and TLN) and outside (DLE and MAG) ports in the Bay of Toulon.

	Site	Total length (mm)	Total mass (g)	Total age (day)	Absolute growth rate (μm·day^{-1})	Fulton's K
D. sargus	DLE (n = 10)	60.6 ± 12.3	4.4 ± 2.6	125.9 ± 28.5	6.8 ± 0.9	1.74 ± 0.13
Year = 2014	MAG (n = 16)	70.0 ± 9.3	6.4 ± 2.3	139.3 ± 15.8	6.9 ± 0.9	1.79 ± 0.10
	STM (n = 12)	66.7 ± 7.4	5.5 ± 1.7	145.8 ± 16.9	6.5 ± 0.6	1.81 ± 0.06
	TLN (n = 14)	59.0 ± 4.3	3.8 ± 0.8	132.3 ± 10.2	6.1 ± 0.7	1.83 ± 0.10
D. vulgaris	DLE (n = 10)	57.9 ± 9.6	3.1 ± 1.6	173.9 ± 15.3	4.6 ± 0.7	1.44 ± 0.12
Year = 2014	MAG (n = 10)	57.2 ± 10.9	3.2 ± 2.1	192.4 ± 17.9	4.3 ± 0.8	1.52 ± 0.21
	STM (n = 10)	62.6 ± 9.0	4.1 ± 2.1	188.5 ± 31.9	4.7 ± 0.6	1.57 ± 0.12
	TLN (n = 13)	64.3 ± 10.3	4.2 ± 2.1	192 ± 13.4	4.8 ± 1.0	1.46 ± 0.05
D. vulgaris	DLE (n = 9)	59.4 ± 8.3	3.5 ± 1.5	169.3 ± 18.0	5.6 ± 0.6	1.58 ± 0.08
Year = 2015	MAG (n = 3)	59.3 ± 2.1	3.6 ± 0.6	165.7 ± 12.7	5.5 ± 0.3	1.71 ± 0.17
	STM (n = 11)	58.1 ± 7.5	3.2 ± 1.3	184.8 ± 10.8	5.2 ± 0.8	1.58 ± 0.12
	TLN (n = 9)	65.3 ± 6.4	4.8 ± 1.4	178.3 ± 7.0	5.4 ± 0.4	1.69 ± 0.10

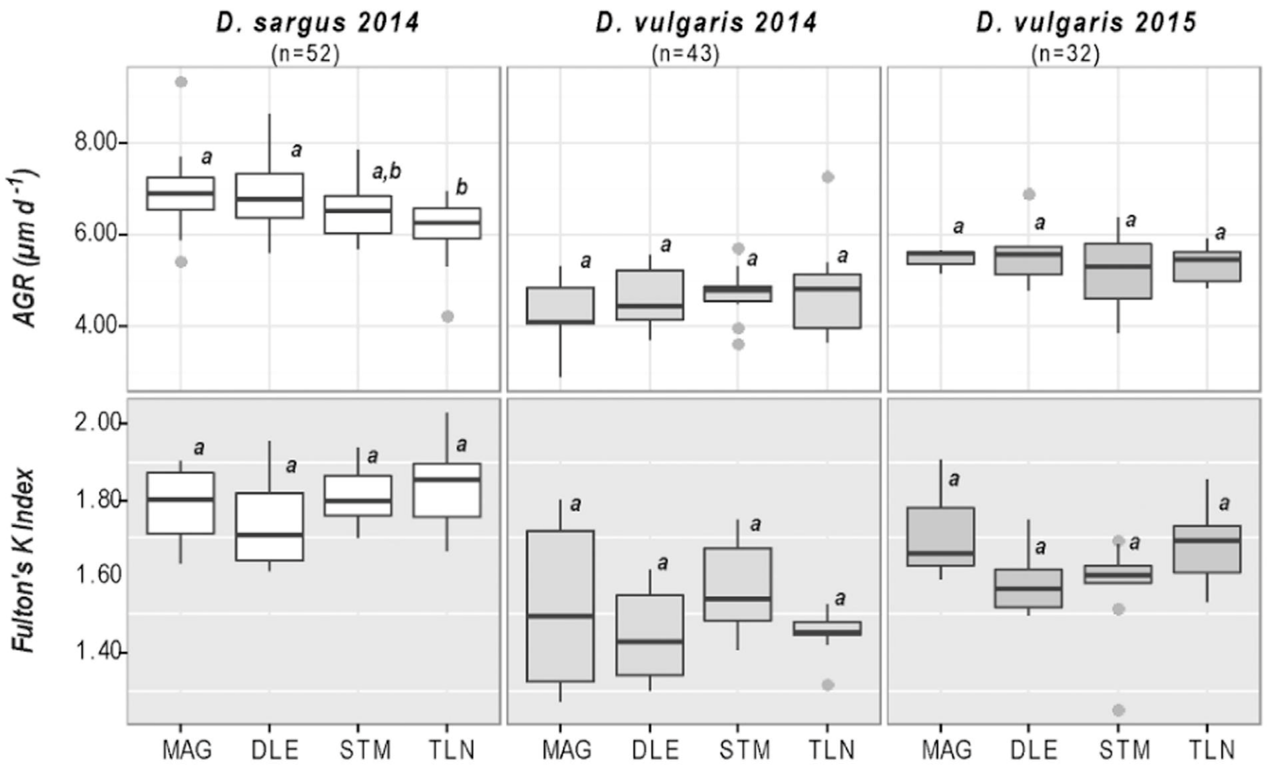

Fig. 3. Comparisons of AGR and Fulton's K index in *D. sargus* and *D. vulgaris* juveniles. For each species and year, letters indicate significant differences ($p < 0.05$) among the four sampling sites studied, inside (STM and TLN) and outside (DLE and MAG) ports in the Bay of Toulon. Statistical comparisons between species or years are not presented.

($p < 0.001$) growth rates and body conditions for *D. sargus* in 2014 (AGR = 6.6 ± 0.8 $\mu m \cdot d^{-1}$ and K = 1.80 ± 0.10) and *D. vulgaris* in 2015 (AGR = 5.4 ± 0.6 $\mu m \cdot d^{-1}$ and K = 1.62 ± 0.12) than for *D. vulgaris* in 2014 (AGR = 4.6 ± 0.8 $\mu m \cdot d^{-1}$ and K = 1.49 ± 0.14). Variations according to the sampling site were less marked (Table 2, Fig. 3). They only concerned *D. sargus* in 2014, with significantly ($p < 0.042$) lower growth rates in TLN (6.1 ± 0.7 $\mu m \cdot d^{-1}$) than in DLE (6.8 ± 0.9 $\mu m \cdot d^{-1}$) and in MAG (6.9 ± 0.9 $\mu m \cdot d^{-1}$), while STM showed intermediate values (6.5 ± 0.6 $\mu m \cdot d^{-1}$). Body condition did not differ significantly among sampling sites for this species and year ($p = 0.184$) and, for *D. vulgaris*, both parameters were similar at all sites, irrespective of the year considered ($p > 0.087$).

2.3. Trace element concentrations in fish muscle

For the 12 element investigated, muscle concentrations were over detection limits in all the fish analyzed (Table 3). Contamination levels in Al, As, Cr, Hg, Mn, Pb and V differed significantly between the two species ($p \leq 0.025$), with higher muscle concentrations in *D. sargus* for As and Hg ($p \leq 0.020$) and in *D. vulgaris* for Al, Cr, Mn, Pb and V ($p \leq 0.025$). However, elemental concentrations in the flesh of the fish also apparently depended on the year: for *D. vulgaris*, muscle concentrations in As and Cr were higher in 2014 ($p \leq 0.009$), whereas those in Cu, Mn, Ti and V were higher in 2015 ($p \leq 0.003$) (Table 3, Fig. 4, Fig. S1).

When considering both species grouped, muscle concentrations only varied significantly ($p \leq 0.037$) according to the sampling site for Cu, Mn, Pb and V (Table 3, Fig. 4). The highest muscle concentrations were observed in STM for Cu (3.8 ± 1.9 $mg \cdot km^{-1}$ dm) and V (1.1 ± 1.0 $mg \cdot km^{-1}$ dm), in DLE for Mn (1.8 ± 1.2 $mg \cdot km^{-1}$ dm), and indifferently ($p = 0.268$) in TLN (0.21 ± 0.09 $mg \cdot km^{-1}$ dm) or in DLE (0.17 ± 0.11 $mg \cdot km^{-1}$ dm) for Pb (Table 3, Fig. 4). Differences in element concentrations among sites depended both on the species and the year ($p < 0.001$). Spatial variations for *D. sargus* in 2014 were significant for Cu, Fe, Mn, Pb, Zn and V ($p \leq 0.041$), but for *D. vulgaris* they concerned only Al, Hg and V in 2014 ($p \leq 0.031$) and Al, Cu, Hg, Mn, Se, Ti and V in 2015 ($p \leq 0.013$) (Fig. 4, Fig. S1). For all these elements, when spatial variations existed, the highest concentrations were systematically observed in a port site, TLN or STM, with exception of Mn, for which the highest concentrations were found in DLE (Table 3, Fig. 4, Fig. S1).

3. Discussion

Very few studies so far have simultaneously assessed the condition, growth history and contamination levels of fish juveniles captured in ports. To our knowledge, this is the first time that this has been investigated this thoroughly. Unfortunately, due to technical and logistic constraints, solely seven trace elements out of 12 were measured in the water column in this work, and environmental parameters could only be recorded during the seven months of *D. vulgaris* presence in the four juvenile habitats. However, this time period also covered the first month of juvenile residency for *D. sargus*. Therefore, matching the environmental data gathered in this work in both the port areas and at nearby coastal sites with the physiological and contamination response of the two fish species on these contrasted juvenile habitats allowed improving our understanding about port use by rocky fishes and their value as nursery sites. Notwithstanding the limitations inherent to small samples (in terms of number of species, individuals and sites studied) that might weaken certain generalizations, our results demonstrate that higher levels of environmental pollution in ports do not necessarily result in higher muscle contamination, reduced growth or poorer condition for the fish juveniles that inhabit them.

3.1. Environmental contamination and fish contamination

Contamination levels in fish are generally estimated from liver samples because, for all metals but Hg, concentrations are usually the highest in this tissue (Henry et al., 2004). In the present study, muscle tissue was used instead. Indeed, the small size of the fish sampled did not allow collection of enough liver material for metal concentration analyses. Moreover, in exploited species like *D. sargus* and *D. vulgaris*,

Table 3
Trace metal concentrations (in mg kg^{-1} dm) measured in fish muscle tissue at each site (DLE, MAG, STM and TLN).

	Al (mg·kg^{-1} dm)		Ti (mg·kg^{-1} dm)		V (mg·kg^{-1} dm)		Cr (mg·kg^{-1} dm)		Mn (mg·kg^{-1} dm)		Fe (mg·kg^{-1} dm)	
	Mean ± sd	Min − Max	Mean ± sd	Min − Max	Mean ± sd	Min − Max	Mean ± sd	Min − Max	Mean ± sd	Min − Max	Mean ± sd	Min − Max
D. Sargus 2014												
DLE (n = 5)	3.5 ± 1.5	1.6–5.4	6.9 ± 1.3	5.4–8.2	0.10 ± 0.06	0.00–0.13	0.34 ± 0.40	0.1–1.0	0.91 ± 0.13	0.82–1.1	11 ± 2.3	8.9–15
MAG (n = 5)	2.8 ± 2.0	1.4–6.3	7.8 ± 1.5	6.3–10	0.20 ± 0.06	0.13–0.27	0.21 ± 0.17	0.00–0.47	0.74 ± 0.10	0.64–0.87	15 ± 1.8	14–18
STM (n = 5)	6.6 ± 3.5	2.7–10.1	9.9 ± 2.3	5.7–13	0.20 ± 0.04	0.13–0.25	0.34 ± 0.38	0.14–1.0	0.70 ± 0.09	0.55–0.79	22 ± 11	13–41
TLN (n = 5)	3.9 ± 2.1	2.0–7.3	11 ± 5.6	5.6–21	0.34 ± 0.08	0.22–0.43	0.28 ± 0.21	0.12–0.61	0.64 ± 0.07	0.55–0.71	15 ± 3.8	11–19
D. vulgaris 2014												
DLE (n = 4)	3.5 ± 0.8	2.5–4.2	11 ± 2.6	7.1–13	0.58 ± 0.25	0.35–0.88	1.5 ± 1.6	0.58–3.9	1.7 ± 0.98	0.92–3.1	18 ± 4.5	14–24
MAG (n = 5)	7.2 ± 2.4	4.1–10.5	13 ± 4.2	7.9–18	0.53 ± 0.09	0.43–0.63	0.65 ± 0.42	0.27–1.4	1.1 ± 0.57	0.80–2.1	19 ± 4.1	14–25
STM (n = 4)	3.9 ± 1.6	1.8–5.4	6.8 ± 4.2	1.7–11	1.2 ± 0.81	0.48–2.4	0.83 ± 0.59	0.40–1.7	0.71 ± 0.31	0.46–1.1	14 ± 9	1.6–22
TLN (n = 4)	11 ± 7.6	6.1–22	7.8 ± 0.90	7.3–9.2	0.43 ± 0.07	0.39–0.54	0.43 ± 0.10	0.32–0.56	0.85 ± 0.04	0.80–0.89	18 ± 3.8	15–24
D. vulgaris 2015												
DLE (n = 5)	16 ± 26	1.4–62	13 ± 3.2	10–18	1.1 ± 0.68	0.63–2.3	0.43 ± 0.87	0.00–2.0	2.9 ± 1.12	1.9–4.5	29 ± 26	7.0–64
MAG (n = 3)	1.2 ± 0.20	1.0–1.4	14 ± 3.6	12–18	1.0 ± 0.28	0.77–1.3	0.13 ± 0.14	0.00–0.29	1.4 ± 0.04	1.4–1.5	16 ± 7.5	10–24
STM (n = 5)	22 ± 20	7.0–57	16 ± 3.4	12–20	2.0 ± 0.89	1.32–3.6	0.15 ± 0.10	0.00–0.28	1.1 ± 0.20	0.87–1.3	25 ± 12	15–45
TLN (n = 6)	2.3 ± 0.80	1.5–3.5	9.3 ± 1.9	6.1–12	0.46 ± 0.04	0.41–0.54	0.61 ± 1.13	0.0–2.9	1.2 ± 0.30	0.78–1.6	18 ± 9.1	11–36

	Cu (mg·kg^{-1} dm)		Zn (mg·kg^{-1} dm)		As (mg·kg^{-1} dm)		Se (mg·kg^{-1} dm)		Pb (mg·kg^{-1} dm)		Total Hg (mg·kg^{-1} dm)	
	Mean ± sd	Mean ± sd	Min − Max	Mean ± sd	Mean ± sd	Min − Max	Mean ± sd	Mean ± sd	Mean ± sd	Min − Max	Mean ± sd	Min − Max
D. Sargus 2014												
DLE (n = 5)	1.6 ± 0.32	1.2–2.0	24 ± 3.8	20–29	22 ± 5.6	17–29	1.3 ± 0.19	0.98–1.5	0.10 ± 0.07	0.00–0.17	0.55 ± 0.37	0.13–1.1
MAG (n = 5)	2.3 ± 0.40	1.8–2.8	31 ± 1.9	29–34	25 ± 5.4	17–30	1.3 ± 0.15	1.2–1.6	0.05 ± 0.04	0.00–0.08	0.47 ± 0.36	0.17–1.1
STM (n = 5)	2.9 ± 1.4	1.6–5.1	32 ± 5.7	24–40	19 ± 8.3	8.6–31	1.4 ± 0.16	1.2–1.6	0.07 ± 0.03	0.05–0.11	0.44 ± 0.11	0.34–0.59
TLN (n = 5)	2.2 ± 0.21	1.9–2.4	28 ± 2.5	25–32	16 ± 6.1	11–26	1.4 ± 0.17	1.1–1.6	0.20 ± 0.09	0.12–0.36	0.40 ± 0.05	0.35–0.48
D. vulgaris 2014												
DLE (n = 4)	1.8 ± 0.42	1.5–2.4	45 ± 11	35–61	20 ± 16	9.4–44	1.9 ± 0.36	1.3–2.2	0.19 ± 0.09	0.11–0.30	0.27 ± 0.08	0.19–0.39
MAG (n = 5)	2.2 ± 0.24	1.8–2.4	39 ± 12	26–57	17 ± 6.8	7.2–26	1.8 ± 0.11	1.7–1.9	0.15 ± 0.07	0.11–0.27	0.12 ± 0.03	0.08–0.17
STM (n = 4)	2.9 ± 1.0	2.0–4.3	31 ± 24	1.7–60	11 ± 7.7	1.3–20	1.7 ± 0.17	1.5–1.9	0.12 ± 0.04	0.09–0.17	0.23 ± 0.02	0.21–0.26
TLN (n = 4)	2.1 ± 0.73	1.6–3.2	34 ± 3.5	30–38	13 ± 2.9	9.6–16	1.5 ± 0.17	1.4–1.7	0.19 ± 0.04	0.13–0.22	0.29 ± 0.04	0.24–0.33
D. vulgaris 2015												
DLE (n = 5)	2.7 ± 0.63	1.8–3.3	26 ± 3.1	21–29	8.4 ± 1.2	6.8–9.8	2.3 ± 0.45	1.9–3.0	0.22 ± 0.13	0.12–0.44	0.25 ± 0.03	0.21–0.28
MAG (n = 3)	3.1 ± 0.28	2.8–3.3	31 ± 4.6	26–35	8.0 ± 2.6	5.3–11	2.4 ± 0.23	2.2–2.6	0.09 ± 0.05	0.05–0.14	0.1 ± 0.01	0.09–0.11
STM (n = 5)	5.6 ± 1.9	4.3–8.9	30 ± 2.6	26–33	7.8 ± 1.9	6.2–11	2.6 ± 0.57	1.9–3.4	0.13 ± 0.06	0.09–0.24	0.25 ± 0.04	0.21–0.31
TLN (n = 6)	2.6 ± 0.54	1.7–3.3	27 ± 2.8	24–32	8.4 ± 1.0	6.4–9.5	1.6 ± 0.17	1.3–1.8	0.23 ± 0.11	0.10–0.36	0.29 ± 0.02	0.26–0.32

the Mediterranean (Tessier et al., 2011). Our measurements in the water column (for Cu, Pb and Zn) are consistent with these observations. Apparently, spatial differences in fish contamination in the Bay of Toulon therefore reflect differences in environmental contamination levels between the Small and the Large Bay. However, when considering each trace element individually, spatial variations in environmental contamination did not always match those observed in the flesh of the *Diplodus* juveniles.

The metals analyzed here differ fundamentally in their metabolic role and their regulations by aquatic organisms. Elements like Cu, Fe, Mn, Se and Zn are essential in fish metabolism and cannot be synthesized (Amiard et al., 1987). They are generally efficiently regulated by marine animals, and present a narrow range of variation in their tissues, except when ambient concentrations in seawater or food reach very high concentrations (Amiard et al., 1987; Chapman, 1996; Vallee and Auld, 1990). This can explain why spatial variations in muscle Zn concentrations were low irrespective of the species or the year although concentrations in the water for this element were ~3 times higher at the two port sites (Fig. 2). By contrast, fish muscle concentrations were found to be 1.6 times higher for Cu in the Saint Mandrier marina (STM) and 2.2 times higher for Mn along the breakwater that separates the Small Bay from the Large Bay (DLE), than in the three other sites. Because this pattern is consistent with water concentrations in Cu and Mn at all sites (Fig. 2), it is likely that local contamination levels for these elements at STM and DLE probably exceed the regulatory levels for juvenile fish.

On the contrary, As, Cr, Hg, Pb and V are not essential for marine life and their concentrations in the organisms depend mainly on their environmental levels (Amiard et al., 1987). This is consistent with our findings for As and Cr: similar environmental contamination levels for these two elements at the four sites (Tessier et al., 2011) explain the absence of spatial variation in their concentrations in fish muscles. Similarly, the high Pb concentrations recorded in the muscle of both species at TLN are consistent with our measurement in the water column (Fig. 2), and with the high Pb contamination levels reported in the sediments of this area (Tessier et al., 2011). Therefore, the most likely explanation for the higher V concentrations measured in the flesh of the *D. vulgaris* juveniles captured at the STM site in 2015 is that of an accidental oil spill in this port, since V is one of the most abundant metals in petroleum (Ball et al., 1960).

Unfortunately, technical constraints prevented us from measuring water concentrations for Hg during this study. However, the results for this element suggest that its contamination levels in ports are not directly reflected in fish flesh. Indeed, although Hg concentrations in the sediment have been reported to be 45 times higher at TLN than at MAG (Tessier et al., 2011), spatial variations for this metal in the muscle of the two species were surprisingly limited, and significant for *D. vulgaris* only. An explanation for this may lay in the role of food webs in the dynamics of metal accumulation. Indeed, food is a major route for metal uptake in fish, in particular Hg (e.g. Hall et al., 1997). Metals mainly enter the food chains through their uptake by the phytoplankton, their concentrations in this trophic compartment reflecting their specific uptake rates but also the phytoplankton growth (Blackmore and Wang, 2004). Processes of ‘biomass dilution’ in highly productive waters thus result in lower trace metal concentrations at the base of food webs (Cresson et al., 2015; Harmelin-Vivien et al., 2009). Because in this study, water Chl *a* concentrations were much higher at TLN and STM than at MAG and DLE, it is likely that high mean primary production in these two ports resulted in lower contamination of their phytoplankton by metals. This partially explains why spatial variation in fish Hg contamination levels were so limited, and probably contributed to the fact that fish muscle concentrations in Pb were higher at DLE than at STM when water concentrations for this metal suggested the opposite (Fig. 2). However, as copepods are the most common prey of *Diplodus* juveniles (Altin et al., 2015), the structure of the zooplankton community and its level of contamination also need to be considered when trying to explain fish contamination patterns. In the Bay of Toulon, zooplankton communities differ between the Large Bay and the Small Bay (Jamet et al., 2005) but the spatio-temporal fluctuations of their metal content are large and irregular (Rossi and Jamet, 2008). These fluctuations could explain the variations in fish contamination we observed, not only between the two years sampled, but also between the two species studied. Indeed, the seasons for fish presence on the juvenile habitats differ between *D. vulgaris* (winter/spring) and *D. sargus* (late spring/summer), with limited overlap between them. As a result, the higher Cu and Pb concentrations found in the flesh of *D. sargus* partially reflect the fact that highest concentrations in these two elements in the zooplankton are observed during the summer (Rossi and Jamet, 2008).

3.2. Fish growth, body condition and health in ports

Body condition and growth are physiological indicators that have been regularly and successfully used to compare nursery habitat quality for fish (e.g. Amara et al., 2007; Gilliers et al., 2006; Isnard et al., 2015; Sogard and Able, 1992). The use of growth and condition as indices of habitat quality is based on the assumption that larger, faster growing fish are healthier and are hence exposed to more favorable environmental conditions than smaller slower-growing ones. For many juvenile fishes, the first winter is a critical period (Fullerton et al., 2000; Miranda and Hubbard, 1994), with severe conditions in the open-sea such as low temperatures, limited food resources and elevated risk of predation. Many studies have shown that fish that grow faster, or have higher levels of energy reserves, are less vulnerable to predation when they leave their juvenile habitats than those in poor condition; they also are more apt to survive the first winter of life and thereby contribute to the renewal of adult stocks (Biro et al., 2004; D'Alessandro et al., 2013; Sogard, 1997).

In *Diplodus* juveniles, growth and body condition of are mainly controlled by environmental parameters (Planes et al., 1999). In our study, post-settlement growth and final condition indexes were lower in *D. vulgaris,* which mostly occupies the juvenile habitats during the autumn and the winter, than in *D. sargus*, which occupies them during throughout the spring and the summer. Although inter-specific differences in growth rates cannot be excluded, this confirms that temperature and food availability account significantly in the variation of juvenile growth and condition regardless of the juvenile habitat (Planes et al., 1999; Vigliola et al., 2000). Chemical contaminants also induce various biological responses in juvenile fish, affecting their physiology and their growth, but also their health and their behavior (e.g., Kerambrun et al., 2012; Laroche et al., 2002; Marchand et al., 2003; Rowe, 2003). As in other organisms, sub-lethal responses to contaminant exposure in fish commonly involve a decrease in feeding activity (Saborido-Rey et al., 2007; Stephens et al., 2000) and a modification in energy allocation, which is preferentially used to fight chemical stress rather than for body maintenance and growth (Rowe, 2003). This should have marked negative effects on both individual growth rate and body condition. However, spatial variations for these two parameters were limited in our study, and were not consistent between species or years. The significantly lower growth of *D. sargus* juveniles at TLN may be associated with the general exposure of their organisms to metal contaminants in this heavily polluted area, but, in general fish physiological status in this study seemed to be similar among all the sites studied, even if these included two heavily contaminated port sites (STM and TLN) and a natural nursery area under limited human influence (MAG). Therefore, environmental pollution seems to have a lesser influence than temperature or food availability on the growth and condition of *Diplodus* juveniles.

Although regularly used for evaluating fish health, growth rate and body condition are often less sensitive to environmental stressors than molecular biomarkers (Adams, 2002). Indeed, they both are subject to a variety of regulating influences, and are largely driven by water temperature and food abundance in juvenile fish (Planes et al., 1999). In our study area, high primary production in ports is probably the cause for substantial juvenile fish growth and condition despite pollution: by sustaining the development of zooplankton (Jamet et al., 2005) on which *Diplodus* juveniles feed (Altin et al., 2015), it reduces trophic competition and energy requirements for feeding, while the biodilution at the base of the food web that it induces probably lowers metal uptake by the fish. Both processes foster juvenile fish growth and condition and thereby offset the negative effects of chemical contaminants. However, the apparently low impact of local contamination on fish health in ports will need to be confirmed by investigations of fish physiological stress levels. Combining several molecular biomarkers (e.g. ethoxyresorufin-O-deethylase activity, glutathione S-transferase activity, catalase activity) for this should allow a comprehensive assessment of port environmental quality (Gilliers et al., 2006; Kerambrun et al., 2011; Vasconcelos et al., 2009).

3.3. Ports: potential nursery areas for coastal fishes?

The link between environmental pollution and juvenile fish contamination and health is not a straightforward one. During the last few years, certain studies have shown that the abundances of juveniles of the most common rocky species inside ports also seem to be similar to those found in natural habitats (Bouchoucha et al., 2016; Clynick, 2008; Dufour et al., 2009). These observations strongly suggest that ports could serve as nursery habitats at least for some rocky fishes, providing them with shelter and enhanced feeding conditions. This is all the more likely that our results unexpectedly showed that the condition and growth of *Diplodus* juveniles within highly polluted ports can be equivalent to those measured in nearby natural and artificial habitats that match the criteria for *Diplodus* spp. nursery grounds (Harmelin-Vivien et al., 1995; Pastor et al., 2013). Of course, our results will have to be confirmed for more fish species and other ports before reaching a general conclusion with regards to ports value as potential nursery areas for rocky fishes. Our results might also underestimate the actual impact of contaminants on fish juveniles in ports since the information gathered here is based only on survivors. Lastly, contaminants and their effects may accumulate over long periods of time prior to the onset of significant biological responses (Rowe, 2003). Therefore, for comprehensive assessment of the value of ports as nursery grounds, the impact of contaminant exposure during juvenile life (high and punctual or limited yet repeated) on the final mortality rates of fish and their capacity to reproduce will have to be explored. Investigations into the contribution of individuals that use ports as juvenile habitats to the adult stocks are also needed before one can reach a robust conclusion about the importance of ports in the maintenance of rocky fish stocks along anthropized shorelines.

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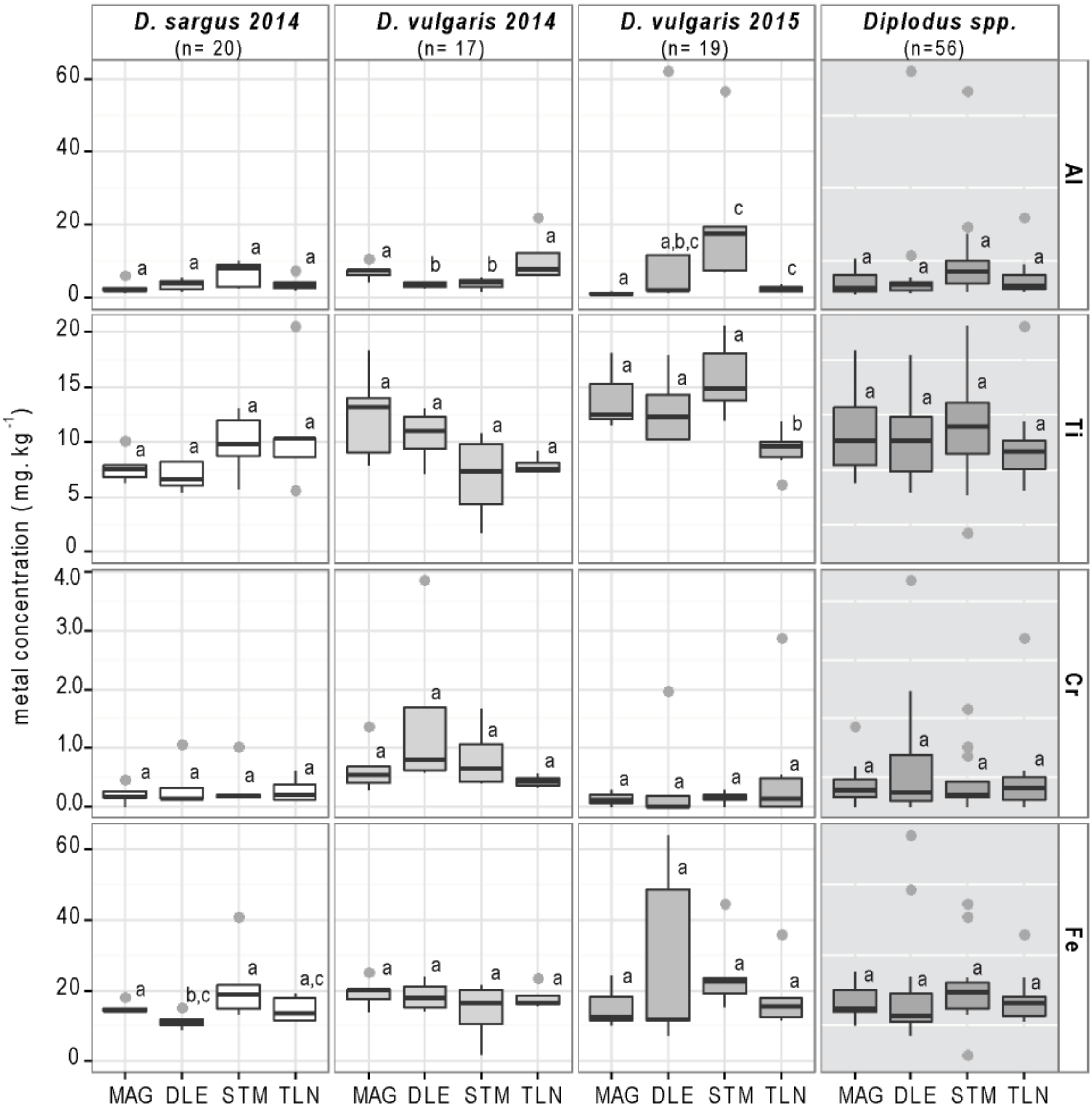
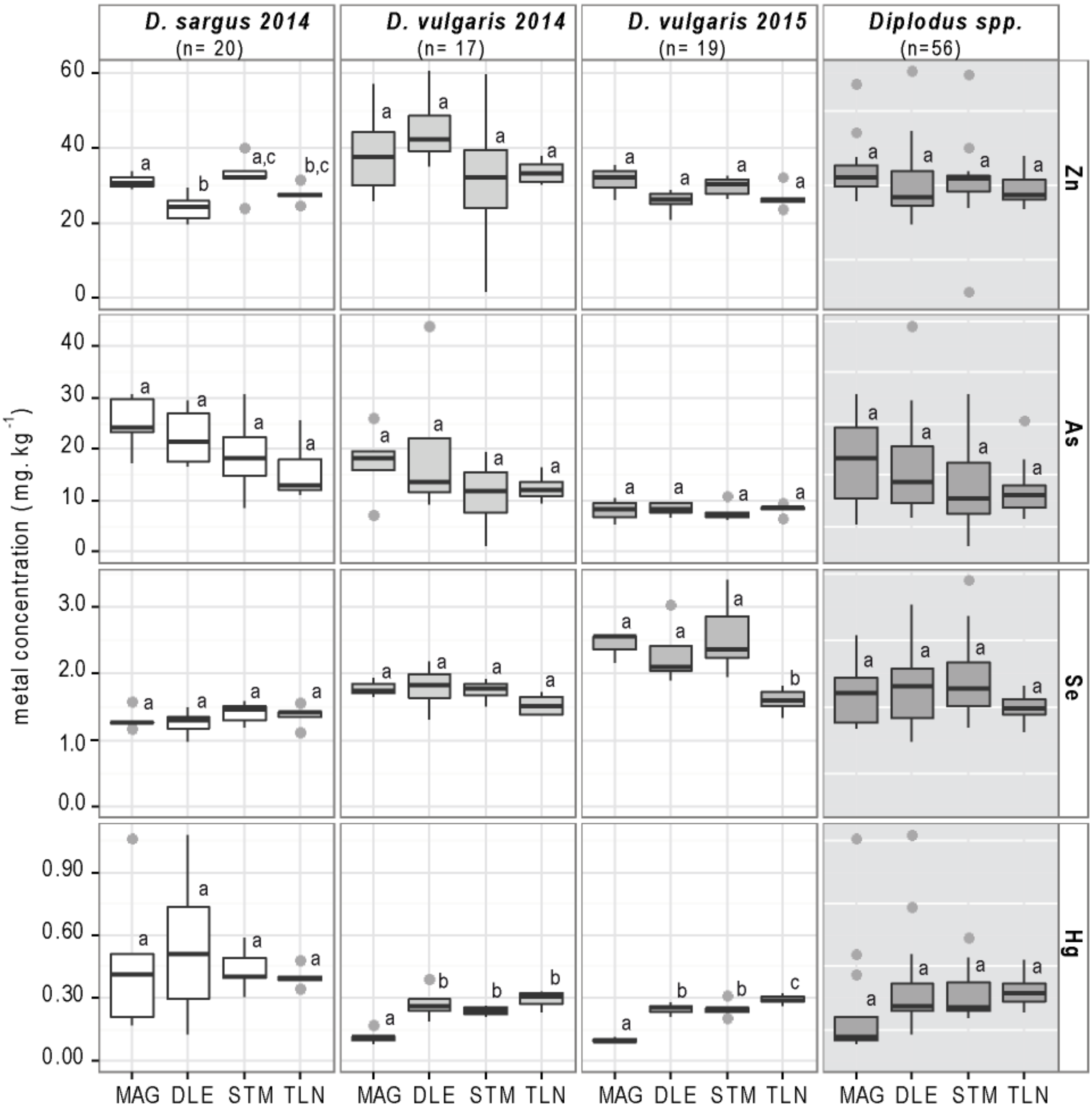
Supplementary material

Figure S1: Variation of Al, As, Cr, Fe, Hg Zn, Se and Ti concentrations in the muscle tissue of juvenile *D. sargus* and *D. vulgaris*. For each species and year, letters indicate significant differences ($p < 0.05$) among the four sampling sites studied, inside (STM and TLN) and outside (DLE and MAG) ports in the Bay of Toulon. Statistical comparisons between species or years are not presented.




D. sargus 2014
(n= 20)
D. vulgaris 2014
(n= 17)
D. vulgaris 2015
(n= 19)
Diplodus spp.
(n=56)
metal concentration (mg. kg^{-1})
Zn
As
Se
Hg
0
20
40
60
0
10
20
30
40
0.0
1.0
2.0
3.0
0.00
0.30
0.60
0.90
MAG DLE STM TLN
MAG DLE STM TLN
MAG DLE STM TLN
MAG DLE STM TLN
a
b
a,c
b,c
c

IV.3. Points à retenir :

- Les concentrations en éléments traces métalliques (ETM) mesurées dans le muscle des juvéniles des deux espèces de sars étaient faibles, de 5 à 7,5 fois inférieures aux seuils de sécurité sanitaire (Hg et Pb),
- Lorsque des différences spatiales existaient, les concentrations les plus importantes étaient mesurées chez des juvéniles issus de zones portuaires (V, Cu et Pb),
- Cependant, les concentrations en ETM dans le muscle des juvéniles de sar ne reflétaient pas directement les concentrations environnementales (Hg, Pb et Zn),
- La croissance et la condition des juvéniles issus des ports étaient globalement équivalentes à celles des individus capturés à l'extérieur.

Conclusions :

➔ Des zones portuaires très polluées peuvent, au moins dans certains cas, permettre des croissances et conditions juvéniles équivalentes à celles des zones naturelles,

➔ La contamination chimique dans la chair des juvéniles issus des ports est faible et ne devrait pas présenter de risque pour l'Homme,

➔ L'impact sur la biologie et la fitness des futurs adultes reste à déterminer.

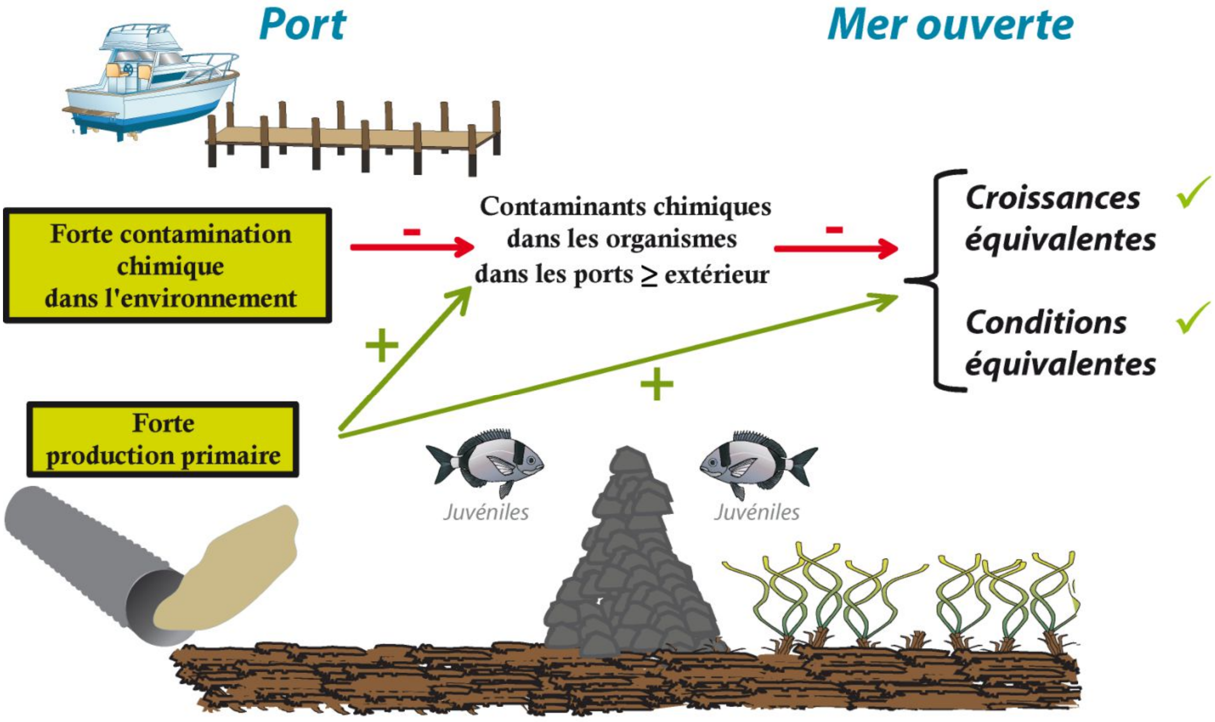


Figure IV.1 : schéma conceptuel des hypothèses vérifiées dans le chapitre 4. ✓= validé, + = effet positif, - = effet négatif. Les images proviennent du site http://www.ian.umces.edu.

Chapitre 5. Composition chimique des otolithes

« Je marche plus sur et plus ferme à mont qu'à val »

Montaigne

V.1. Introduction

La quantification de la contribution relative de chaque habitat juvénile au stock d'adultes est essentielle pour compléter l'identification des nourriceries (Beck et al. 2001). En effet, la connectivité entre les stades de vie juvénile et adulte est nécessaire au recrutement et un habitat juvénile qui ne serait pas connecté serait un piège écologique[4] et ne pourrait être considéré comme une zone de nourricerie (Beck et al. 2001, Gillanders et al. 2003). A notre connaissance, aucun travail n'a décrit à ce jour les déplacements des juvéniles de poissons depuis les zones portuaires vers les habitats adultes naturels. Pour initier ce travail, l'objectif global du **chapitre 5** était de tester la pertinence de l'analyse microchimique des otolithes pour estimer la contribution relative des ports aux stocks d'adultes.

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[4] Un « piège écologique » désigne une situation dans laquelle une modification anthropique de l'environnement conduit certains organismes à être attirés par un habitat de qualité médiocre à mauvaise, et à ne pas pouvoir le quitter, même si cela met l'individu ou l'espèce en péril (Robertson et al. 2017).

De nombreuses méthodes existent pour reconstituer les migrations des poissons au cours de leur vie (voir revue Gillanders et al. 2003). Historiquement, les méthodes de capture-marquage-recapture ont été très utilisées car elles sont susceptibles de fournir une information directe sur les mouvements des individus (Cunjak et al. 2005, Bradshaw et al. 2007, Greenwood 2008). Ces méthodes présentent néanmoins plusieurs inconvénients. Premièrement, l'extrapolation du déplacement ne peut se faire qu'entre l'endroit du marquage et celui de la recapture, sans pouvoir connaître le trajet parcouru par les individus entre ces deux points ni leur temps de résidence dans les différents habitats. Par ailleurs, les taux de recaptures sont souvent faibles (< 5 % - Hansen & Jacobsen 2003), ce qui nécessite de marquer un nombre important de poissons rendant ainsi ces expérimentations généralement coûteuses (Barnes & Gillanders 2013). Au cours des dernières années, avec les avancées technologiques, de nouveaux types de marques ont été développés pour permettre de suivre les mouvements individuels (Nielsen et al. 2009, Pastor et al. 2009) tout en apportant des données complémentaires sur les caractéristiques physico-chimiques des habitats marins fréquentés (Block et al. 2005, Aarestrup et al. 2009) ou encore d'état physiologique des individus (Lutcavage et al. 1999, Block et al. 2005). Grâce à ces méthodes, notre compréhension de la structuration spatiale des populations et du comportement migratoire des individus a fait un véritable bond en avant (Righton et al. 2010, Block et al. 2011). Cependant, malgré les avancées récentes dans leur miniaturisation, ces marques artificielles demeurent peu adaptées à l'étude des mouvements des juvéniles de poissons, principalement pour des raisons de taille et de fortes mortalités subséquentes aux marquages (Dorval et al. 2005). Pour s'affranchir de ces problèmes, plusieurs méthodologies indirectes ont été développées, toutes basées sur l'utilisation de marqueurs biologiques ou biogéochimiques individuels. Ces "tags naturels" regroupent différents marqueurs génétiques et/ou moléculaires (e.g. Planes & Lemer 2011), morphométriques (e.g. Morat et al. 2012), les charges en parasites des individus (e.g. Sequeira et al. 2010), les compositions chimiques de leurs tissus mous (isotopes stables, profils lipidiques, signature en acides aminés, contamination chimique) (e.g. Cresson et al. 2015b) ainsi que la composition chimique ou isotopique de diverses structures calcifiées, notamment les otolithes et les écailles (Campana 1999, Panfili 2002). Parmi ces techniques, la méthode la plus communément utilisée pour suivre les déplacements des poissons, notamment entre les habitats juvéniles et adultes, est l'analyse de la composition élémentaire de leurs otolithes (e.g. Dorval et al. 2005, Gillanders 2005, Vasconcelos et al. 2008, Tournois et al. 2017).

L'utilisation de la composition chimique de certaines régions des otolithes pour identifier rétrospectivement les zones de nourriceries de poissons adultes (e.g. Gillanders & Kingsford 2000, Vasconcelos et al. 2008) se déroule en deux phases distinctes. Dans un premier temps, les signatures élémentaires des différents habitats juvéniles ainsi que leur variabilité temporelle sont caractérisées à partir des otolithes de juvéniles issus de chacun d'entre eux (e.g. Vasconcelos et al. 2007, Tournois et al. 2013). Puis, dans un second temps, la partie des otolithes d'adultes correspondant à la vie juvénile est analysée et comparée aux signatures disponibles pour chacun des différents habitats. Ces études se déroulent généralement sur plusieurs années afin d'obtenir une signature multi-annuelle stable des habitats juvéniles fréquentés avant de prélever les adultes des cohortes correspondantes pour les réassigner suivant la signature de leurs otolithes. Pour des raisons matérielles, au cours de cette thèse, nous nous sommes concentrés sur la première étape et avons cherché à tester la pertinence de la méthode pour identifier la vie juvénile dans les zones portuaires.

La composition chimique des otolithes a été utilisée très souvent et avec succès pour discriminer des habitats juvéniles très contrastés en termes de propriétés physico-chimiques, en particulier du point de vue de la salinité (Bourret et al. 2014, Tournois et al. 2017). Par contre, pour les espèces fréquentant des habitats aux salinités proches, en particulier pour les espèces totalement marines, la discrimination n'est pas toujours évidente (Gillanders et al. 2001, Sturrock et al. 2012). En effet, pour être incorporés, les éléments et les ions présents dans l'eau et/ou dans l'alimentation vont traverser plusieurs compartiments liquides (le plasma sanguin et l'endolymphe) et donc plusieurs barrières physiques (système branchial, paroi intestinale, otosac…). Ils entrent donc dans des processus de régulation physiologique (e.g. osmorégulation) plus ou moins importants selon les éléments avant de précipiter pour former l'otolithe (Campana 1999). Ainsi, la composition chimique des otolithes dépend de mécanismes endogènes et exogènes complexes et encore mal appréhendés et ne reflète pas directement celle de l'environnement (e.g. Gauldie 1996, Geffen et al. 1998, Morales-Nin et al. 2007). Par ailleurs, du fait de l'importance des processus de régulation dans l'incorporation des éléments dans les otolithes ainsi que des variations naturelles de leurs concentrations dans l'environnement, les signatures multi-élémentaires des habitats juvéniles varient entre les espèces (Geffen et al. 1998, Hamer & Jenkins 2007, Barnes & Gillanders 2013), dans l'espace (Vasconcelos et al. 2007, Tanner et al. 2011) et dans le temps (Reis-Santos et al. 2012, Tournois et al. 2013). Ces variations sont aujourd'hui très largement reconnues et ont conduit de nombreux chercheurs à recommander la création d'une bibliothèque de signatures pour tous les habitats possibles afin de prédire la contribution de chacun d'entre eux au stock d'adultes (Gillanders 2002, Schaffler et al. 2014).

Dans ce contexte, l'objectif du **chapitre 5** était de déterminer si la composition chimique des otolithes de juvéniles issus des zones portuaires diffère de celle de juvéniles issus de zones naturelles adjacentes et existe une signature unique permettant d'identifier rétrospectivement l'origine portuaire, ce qui permettrait de quantifier la contribution relative des ports aux stocks adultes.

Plus précisément, le **chapitre 5** cherchait à répondre spécifiquement aux questions suivantes : la composition chimique des otolithes de juvéniles issus des ports et des zones naturelles adjacentes diffère-t-elle ? Existe-t-il une signature chimique caractéristique des zones portuaires ?

Pour cela, des juvéniles de deux espèces de sars (*D. sargus* et *D. vulgaris*) ont été capturés en fin de vie juvénile sur deux années consécutives dans trois zones portuaires contrastés et deux zones extérieures de la rade de Toulon. La composition chimique de leurs otolithes a été analysée et comparée.

V.2. Article 3 (soumis le 11 décembre 2017 dans Estuarine Coastal and Shelf Science) : Investigation of the use of otolith fingerprints as natural tag for identification of juvenile fish life in ports.

Title: **Investigation of the use of otolith fingerprints as natural tags to identify juvenile fish life in ports**

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Abstract

The construction of ports has caused substantial habitat destruction in coastal areas previously used as nursery grounds by many fish species, with consequences on fish stocks. Regarding juvenile fish abundances and growth in ports, it was recently suggested that these artificial coastal areas might provide alternative nursery habitats for several species, although their contribution to adult stocks had never been estimated. Here, we investigated the variability of otolith composition in the juveniles of two *Diplodus* species collected from three contrasting port areas and two adjacent coastal juvenile habitats of the Bay of Toulon (northwestern Mediterranean) in order to determine the possible use of otolith fingerprints as natural tags for the identification of juvenile fishes in ports. The global accuracy of discrimination between ports and coastal areas was very high (94%) irrespective of species, suggesting that otolith fingerprints can be used with confidence to retrospectively identify past residency in the ports of this bay. However, Ba was systematically the most discriminating element, since its concentrations in otoliths were generally higher outside ports than in inside them, probably due to river runoff. Moreover, otolith signatures varied greatly by species and between sampling sites. Furthermore, although Cu and Pb concentrations in water were at least 2.3 to 34-fold higher inside ports than outside, this was not consistently reflected in fish otoliths, confirming that spatial differences in otolith concentrations depend on the species and do not directly reflect differences in environmental contamination levels. Therefore, it seems unlikely that otolith microchemistry could provide a universal fingerprint capable of discriminating ports from other coastal areas. Nevertheless, the contribution of ports to adult fish populations can be determined well by establishing a library of otolith fingerprints for all juvenile habitats.

Keywords: Coastal areas, nursery habitats, fish, LA-ICPMS, contamination.

Introduction:

Identifying and protecting fish nursery habitats is crucial for the long-term conservation of fish stocks (Wilson et al., 2017).Shallow coastal areas is used as nursery habitats by many fish species because they are highly productive environments (Beck et al., 2001; Harmelin-Vivien et al., 1995; Macpherson et al., 1997). However, they are increasingly threatened by urbanization (Airoldi and Beck, 2007; Halpern et al., 2008; Lotze et al., 2006). Many different types of man-made structures now dominate the world's shorelines, yet ecological issues related to their development have received little attention so far (Bulleri and Chapman, 2010; Chapman and Blockley, 2009) and we are just beginning to understand their impact on marine organisms and especially on juvenile fish (Duffy-Anderson et al., 2003).

Ports are among the most common man-made infrastructures found on the shoreline (Rodríguez-Rodríguez et al., 2015). When a port is constructed, the intrinsic patchiness of the heterogeneous subtidal environment is replaced by homogeneous and less complex artificial habitats (Mercader et al., 2017). This reduction of structural complexity may alter habitat quality (Dahlgren and Eggleston, 2000) and impair the fish nursery function of coastal areas (Cheminée et al., 2016; Connell and Jones, 1991; Piko and Szedlmayer, 2007).

During the last few years, several studies have suggested that coastal man-made infrastructures, particularly those found inside ports, might provide suitable alternative nursery habitats for certain fish species (e.g. Bouchoucha et al., 2016; Mercader et al., 2017; Pizzolon et al., 2008). However, these conclusions were solely based on fish abundance (Bouchoucha et al., 2016; Mercader et al., 2017) or post-settlement growth and condition (Bouchoucha et al., 2018) in ports when, in theory, fish nursery grounds are defined according to four parameters: they support high abundances of juveniles, they sustain faster somatic growth rates and they also enhance fish survival so their populations contribute more to the final adult stock (Beck et al., 2001). Therefore, the correct estimation of the nursery role played by ports implies estimating the relative contribution of port juvenile habitats to adult stocks.

Among the tools available for this purpose, otolith microchemistry is increasingly used (Campana et al., 2000; Dierking et al., 2012; Elsdon et al., 2008). Otoliths are paired calcified structures located in the inner ear of teleost fishes. They have been widely used in marine ecology and fishery research to describe population age structure, assess connectivity between fish stocks and study individual migration patterns (Campana, 1999). Otoliths are particularly well suited for these applications because of three key properties. Firstly, they grow continuously throughout fish life, by the centrifugal deposition of aragonite and protein layers that can be used to estimate fish age (Campana and Neilson, 1985). Secondly, as otoliths are acellular and metabolically inert, they are neither reworked nor resorbed, even during times of starvation (Campana and Neilson, 1985). Chemical fingerprints are thus retained permanently within the microstructure (Panfili, 2002). Thirdly, otolith chemical composition is often different in fish collected from areas with distinct water chemistry (Elsdon and Gillanders, 2003; Sturrock et al., 2012). The chemical composition of the inner region within adult fish otoliths can thus be used as a natural tag to retrospectively assign their juvenile origin (e.g. Gillanders and Kingsford, 2000; Tournois et al., 2017; Vasconcelos et al., 2008).

To achieve this, the habitats must differ sufficiently in their environmental conditions, whether because of varied anthropogenic influences or due to natural variations (Barnes and Gillanders, 2013; Sturrock et al., 2015). As the recipients of industrial and domestic wastes, ports are generally subject to high chemical contaminations (Darbra et al., 2004) and seem particularly suited for studies using elemental fingerprints in otoliths as natural tags. However, the incorporation of elements in otoliths is more complex than their mere concentration in the ambient water as it is affected by their bioavailability, the physiological state of individual fish (Sturrock et al., 2015) and the synergetic/concomitant effects of temperature, salinity and water chemistry (Elsdon and Gillanders, 2004). While some elements (e.g., Sr, Ba) appear to directly reflect ambient water concentrations, others (e.g. Cu, Zn) are physiologically regulated and less likely to reflect surrounding environmental conditions (Campana, 1999; Sturrock et al., 2012). Moreover, some elements (e.g. Cu, Pb) can affect fish condition and metabolic rates leading to variations in their incorporation in otoliths (Geffen et al., 1998; Hamer and Jenkins, 2007).

In this context, the specific aim of this study was to investigate differences in otolith composition among fish juveniles captured after several months of residency in varied habitats located inside and outside ports. Using two *Diplodus* species with different recruitment periods and five contrasting sites (three inside ports and two outside them, in adjacent juvenile habitats) located in the Bay of Toulon (Northwestern Mediterranean), we tested whether otolith elemental fingerprints could be used with confidence to retrospectively identify previous fish residency in ports. This would allow the reliable assessment of the contribution of ports to adult fish populations and thus better evaluation of the potential consequences of port infrastructures for fish stock dynamics. The hypothesis tested here was that the otoliths of fish captured inside ports would contain consistently higher concentrations of port related trace elements (such as Pb, Cu, Zn, etc.) than those of fish from the other coastal areas.

M&M

Model species

Two *Diplodus* species, *D. sargus sargus* (Linnaeus, 1758), hereafter *D. sargus*, and *D. vulgaris* (Geoffroy Saint-Hilaire, 1817) were chosen for this study. Both are very common in the Mediterranean (Coll et al., 2004; Lloret et al., 2008; Morales-Nin et al., 2005) and their juveniles are found in high abundances inside ports (Bouchoucha et al., 2016; Clynick, 2006). However the two species differ in their juvenile habitat use (Bouchoucha et al., 2016; Cheminee et al., 2011; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Ventura et al., 2014; Vigliola et al., 1998): *D. sargus* settles in one pulse, in June-July, and usually leaves its nursery grounds in September while *D. vulgaris* settles in two pulses, in November-December and in January-February, the first pulse being predominant, and leaves its nursery grounds in June-July. Moreover, migrations between nursery areas is very limited for both species (Macpherson et al., 1997). Therefore, investigating variations in otolith chemical composition in these two species should allow reaching conclusions regarding the temporal stability of the otolith elemental fingerprints if any.

Study area, fish sampling and environmental data

This study was carried out in the Bay of Toulon (Northwestern Mediterranean, Fig. 1) which is divided into the “Large Bay” (42.2 km²) and the “Small Bay” (9.8 km²), separated by a breakwater (1,200 m) built in the nineteenth century (Fig.1). The “Small Bay” harbors one of France’s largest industrial ports, the biggest naval port of the Mediterranean, and several marinas. Both the historic and present activities pursued in this part of the bay result in the heavy multi-contamination of its sedimentary compartment (Dang et al., 2015; Pougnet et al., 2014; Tessier et al., 2011) and water column (Dang et al., 2015; Jean et al., 2012). For example, sediment concentrations of Pb and Cu within the naval port of Toulon are among the highest ever measured in a marine area (Tessier et al., 2011). Conversely, the “Large Bay” is only slightly impacted by human activities and offers shallow rocky areas whose characteristics correspond to suitable nursery areas for many juvenile fishes (Cheminee et al., 2011; Harmelin-Vivien et al., 1995). Contamination levels in this part of the bay are low (Tessier et al., 2011). Therefore, the Bay of Toulon is particularly suited for investigating differences in fish otolith composition between juvenile habitats located within and outside ports.

In this work, five contrasting sampling sites were selected in the Bay of Toulon: three representative of the different types of port present in the Bay of Toulon and two representative of the other types of coastal habitats available for the juveniles of local rocky fishes. The first sampling site (STM) was located in the Saint-Mandrier marina. This marina, representative of the marinas found in the Small Bay of Toulon, harbors 800 boats and pleasure craft and its average depth varies between 2.5 and 4 m. The second site (TLN) was located about 500 m from the port of Toulon, which is the biggest naval port in the Mediterranean (30 warships and nuclear attack submarines) and a major ferry terminal (around 1,000 rotations and 1.2 million passengers a year). The area around the TLN sampling site is one of the most contaminated of the Bay of Toulon (Tessier et al., 2011; Wafo et al., 2016). The third site (IFR) was positioned further in the Small Bay (fig. 1), within a port harboring a part of the French oceanographic fleet. The fourth sampling site (DLE) was located on the seaward side of the breakwater that separates the Small from the Large Bay (Fig. 1), in an area considered as slightly impacted by port pollution (Tessier et al., 2011; Wafo et al., 2016). As the seaward sides of peripheral breakwaters are generally considered favorable juvenile fish habitats (Clynick, 2006; Dufour et al., 2009; Guidetti, 2004; Pastor et al., 2013; Pizzolon et al., 2008; Ruitton et al., 2000), the DLE site was considered in this study as representative of the non-polluted artificial juvenile habitats available for rocky fishes within the Bay of Toulon. Physical habitat characteristics (substrate, depth, etc.) are equivalent in the STM, TLN, IFR and DLE sampling sites. The last sampling site (MAG) was located in a natural cove (Anse Magaud) whose characteristics match those of the successful benthic settlement of *Diplodus* species*,* i.e. shallow water habitats (between 0 and 2 m) protected from prevailing winds and characterized by gentle slopes covered with sand, pebbles and boulders (Cheminee et al., 2011; Harmelin-Vivien et al., 1995). Therefore, this site is considered as representative of the natural rocky fish nursery habitats available in the Bay of Toulon.

Sampling for this work took place in September 2014 for *D. sargus* and late June / early July 2015 for *D. vulgaris*, i.e. during the month preceding the departure of the juveniles of each species. Between 9 and 14 juveniles per species were sampled from each site using hand-nets. Juveniles were discriminated following the size and morphometric criteria given by Vigliola and Harmelin-Vivien (2001).

Trace element concentrations in the water column were assessed at each sampling site using the diffusive gradient in thin film (DGT) device which allows gathering integrative values of the most labile dissolved concentrations of metal species in water (Davison and Zhang, 1994). By accumulating ionic forms and weakly dissociable complexes (hereafter named the DGT-labile fraction) on a Chelex 100 resin, proportionally to their water concentration and exposure time, “Standard" DGTs "concentrate" the most highly "labile" dissolved cations, as defined operationally (hydrated ions, mineral complexes, and "weak" or "rapidly dissociable" organic complexes). This DGT- labile fraction is generally considered more representative of potentially bioavailable fraction than the total metal concentration (Odzak et al., 2002; Twiss and Moffett, 2002; Zhang and Davison, 2001). In our study, three DGTs were immersed at 1.5m depth for 15 days each month, from January to July 2015, at each of the five sampling sites. Three DGTs were selected as controls and not immersed in the seawater. During this period, temperature and salinity data were also recorded monthly at each site using a CTD probe (YSI Pro30).

Otolith analyses

Fish juveniles were transported on ice to the laboratory, measured (Total length TL, in mm), weighed (total mass, in mg) and stored at -20°C until otolith extraction. In accordance with Campana et al. (2000), all the materials used for otolith extraction and handling were decontaminated in 4% ultrapure nitric acid baths, triple rinsed with ultrapure water (18.2 MΩ) and dried on a Class 100 clean bench. *Diplodus* sagital otoliths were extracted using plastic forceps under binocular lens, rinsed with ultrapure water and cleaned of adhering tissues. They were then sonicated for 5 min in ultrapure water, triple rinsed again and dried on the same laminar clean bench.

Right otoliths from all fish were embedded separately in epoxy resin (Araldite 2020, Escil) and cut in the transverse plane using a saw with a diamond coated blade (Buehler IsoMet 1000 precision saw). Individual otolith sections were then polished using 1200, 2400 and 4000 silicate papers to expose the core (average thickness ≈ 300 µm). A final sonication was carried out for surface decontamination before storage in dust-free conditions until analysis.

In addition to ^{43}Ca, otolith elemental compositions of nine elements (^{24}Mg, ^{51}V, ^{55}Mn, ^{63}Cu, ^{66}Zn, ^{88}Sr, ^{118}Sn, ^{138}Ba and ^{208}Pb) were assessed using a 257 nm high repetition rate femtosecond (fs) Laser Ablation system (Lambda 3, Nexeya, France) coupled with a High Resolution Inductively Coupled

Plasma Mass Spectrometer(HR-ICPMS) fitted with a jet interface (Element XR, Thermo Bremen) (fsLA-HRICPMS). The laser in this system delivers 360 fs pulses at a wave-length s of 257 nm and can be operated at high repetition rates (up to 100 kHz). By combining the high repetition rate (500 Hz) of the laser with a fast back and forth movement (1 mm.s^{-1}) of its beam (diameter 20 µm, energy 45 µJ.pulse^{-1}), an elongated virtual beam shape (width 150 µm) was simulated at a speed of 5 µm.s^{-1}. For each otolith analyzed, a linear raster of 150 µm length consisting of ca. 30 sequential measures, was taken along the longest radius, starting at 200 µm after the settlement mark. This portion of the otolith corresponds approximately to the third month of fish juvenile life, based on daily increment counts (Vigliola, 1997). For each otolith, the laser was used to preclean the otolith surface of interest prior to ablation. To do this, the laser was operated at a lower repetition rate (100 Hz) and a faster stage movement (400 µm.s^{-1} instead of 5 µm.s^{-1}) in order to prevent excessive in-depth removal (resulting ablation depth = 2-5 microns).

The ablation cell was flushed with Helium (700 ml.min^{-1}) to carry the particles to the ICPMS, and argon (300 ml.min^{-1}) was mixed with the helium stream using a Y-piece to adjust the optimal particle atomization conditions in the plasma. The plasma was also fed with nitrogen (10 ml.min^{-1}) to enhance signal sensitivity.

As light elements are prone to interference from polyatomic and double charged isotopes, the mass spectrometer was used in medium resolution mode (R = 4000) to optimize interference removal during analysis. Calcium was used as an internal standard for each ablation to correct for instrumental error (in terms of ablation yield and detection). The quantification of elements in the otoliths was achieved by external calibration using three NIST glass standards (610, 612 and 614). Two otolith Certified Reference Materials (NIES22 and FEBS 1 were also pelletized and used to control the quality of the analysis of selected elements in the fish otoliths. The average limits of detection (LOD) over a three month-session based on the threefold standard deviation of blank gas were 2.0, 0.8, 0.8, 4.2, 13.2, 1.6, 8.1, 0.3 and 0.6 µg.g^{-1} in the otoliths for ^{24}Mg, ^{51}V, ^{55}Mn, ^{63}Cu, ^{66}Zn, ^{88}Sr, ^{118}Sn, ^{138}Ba and ^{208}Pb, respectively.

Water analyses

Following the deployment of the DGTs, the Chelex resin of the probes was peeled off in the laboratory and trace elements were extracted in 1.8 ml of 1 M ultrapure nitric acid (24 – 48 h). Concentrations in the acid extracts were analyzed for four trace elements (Pb, Mn, Zn and Cu) using ICP-MS to determine the mass of metal (M) accumulated in the Chelex 100 resin. These elements were chosen because they can be measured using DGT and are representative of port and human activities in the Bay of Toulon (Tessier et al., 2011).

For each trace element, the average labile concentrations in water (CDGT) were calculated using the following equation (Zhang et al., 1995):

$CDGT = (M.\Delta g) / (Dm.t.A)$

where M is the mass of the trace element accumulated in the resin, Δg is the diffusive layer thickness, Dm is the diffusion coefficient of the trace element provided by DGT Research (www.dgtresearch.com), t is the immersion of the DGT probe, and A is the exposure area.

Statistical analyses

Otolith concentrations for all elements were transformed to their ratio to Calcium (element:Ca ratio) and checked for normality and homoscedasticity prior to statistical analyses. Since none of the assumptions were satisfied, even after transformation, Mann-Whitney tests and Kruskall-Wallis tests followed by Steel-Dwass-Chritchlow-Fligner post-hoc tests were used. For each species spatial variation in elemental ratios were analyzed according to habitat type (inside or outside a port) and the sampling site, respectively. Spatial variation in the elemental composition of water was also tested using Kruskall-Wallis tests followed by Steel-Dwass-Chritchlow-Fligner post-hoc tests.

In accordance with Mercier et al. (2011), accuracy in habitat type and sampling site identification using otolith elemental fingerprints were investigated for each species using the Random Forest (RF) algorithm (Breiman, 2001). RF is a machine-learning classification method which requires no a priori assumptions regarding data distribution and can extract signals from complex datasets. Therefore it is very effective for discriminating local coastal habitats based on otolith elemental fingerprints (e.g. Mercier et al., 2012; Regnier et al., 2017; Tournois et al., 2017) even in the presence of skewness (Jones et al., 2017; Mercier et al., 2011). Details of the method are provided in Mercier et al. (2011)and Tournois et al. (2013). For each of the individual measures performed on the otoliths, the RF predicts habitat origin by running it through 5000 trees of a classifier (built from known signatures from all habitats) and then using "majority rules" to reach a consensus between all the trees (Tournois et al., 2017). In our case, to identify the list of elements needed to reach maximum accuracy in habitat discrimination, a portion of the dataset (75%) was randomly selected to build the RF classifier and the remaining portion (25%) was used to calculate the global classification accuracy and the percentage of correct re-assignments for each location (cross validation procedure). This cross-validation procedure was applied to all the possible combinations of two to nine of the nine elements measured in the otoliths (Ca was used as an internal standard).

Once the optimal RF classifier had been identified, values for True Skill Statistics per habitat (TSS, Allouche et al., 2006) were calculated to evaluate the successful discrimination for each location. Contrary to habitat accuracy, TSS accounts for true negative prediction, namely for fish whose absence from a given site was correctly predicted. TSS ranges from -1 to 1, where 1 indicates 100% correct prediction of presence or absence in a given habitat (Tournois et al., 2017). Finally, the contribution of each element to the global success of discrimination was evaluated using the mean decrease in the Gini index (Archer and Kimes, 2008): the higher it is, the more discriminative the element (Tournois et al., 2013).

All data processing and statistical analyses were performed using the R software (R Core Team, 2014) and PRIMER 6 software with the PERMANOVA add-on (Clarke and Warwick, 2001).

Results

Water concentrations in Cu and Pb differed significantly ($p < 0.0001$) according to the sampling sites (Table 1), with consistently lower values at MAG and higher ones in ports. However, water concentrations in Cu were maximal at STM (2 971 ± 997 $ng.l^{-1}$), while for Pb, the highest values were recorded at TLN (328 ± 107 $ng.l^{-1}$). No significant differences ($p > 0.06$) in Mn and Zn concentrations in water were observed among the sites (Table 1).

Spatial differences in otolith elemental concentrations were not consistent for all elements and between species (Fig.2). Ba, Mn and Sr values were always significantly higher ($p < 0.001$) outside ports while for Mg and Sn otolith concentrations were consistently higher inside them ($p < 0.018$). For Cu, the values in ports were significantly higher for *D. sargus* ($p < 0.001$) but lower for *D. vulgaris* ($p < 0.0001$). For Pb, no significant variation ($p > 0.063$) was observed between the two habitat types (inside or outside ports), irrespective of species. Finally, for Zn, variations were not significant between habitat types for *D. sargus* ($p = 1$) whereas, for *D. vulgaris* the values were higher outside ports ($p < 0.001$). This pattern was inversed for V.

For both species, discrimination accuracy using RF was always maximal when including eight elements out of nine, V and Sr apparently contributing more noise than signal to the discrimination for *D. sargus* and *D. vulgaris,* respectively (Fig. 3).

The global discrimination accuracy between ports and adjacent juvenile habitats reached 94% with TSS > 0.87 irrespective of species (Fig. 3, Table 2). However, the list of elements included in the RF classifier differed between the two species, the three most useful elements being Ba, Mn and Sn for *D. sargus* and Ba, Zn and Mn for *D. vulgaris* (Fig. 3).

When considering the five sampling sites separately, using the optimal RF classifier for each species allowed reaching high overall accuracy for both *D. sargus* (90%) and *D. vulgaris* (89%). Yet again, the most useful elements differed between species, the three most discriminating elements being Ba, Sn and Mn for *D. sargus* and Ba, Sn and Cu for *D. vulgaris* (Fig. 3). For both species, misclassification errors mostly concerned the STM sampling site (TSS < 0.84) which was to some extent confused with the MAG, DLE and IFR sites due to similar values for Mn, Sr, Cu, Mg, Sn and Zn (Table 2, Fig. 2).

Discussion

As expected from similar studies on other coastal habitats in the Mediterranean (e.g. Di Franco et al., 2011; Fortunato et al., 2017) and elsewhere (e.g., Correia et al., 2011; Hamer et al., 2005), our study showed differences in otolith elemental composition between the five sites sampled. This is not particularly surprising as the sampling sites in this work are highly contrasted in terms of contaminant concentrations (Fig. 2), which are known to influence fish otolith composition (Campana, 1999; Sturrock et al., 2012).

In our study area, otolith signatures inside ports differed markedly from those outside them (especially for Ba and Mn), which should allow accurate the identification of port origin in local adult *D. sargus* and *D. vulgaris*. For both species, the global classification accuracy obtained between habitat types (inside ports vs. outside) was even higher (94%) than those found in other coastal systems (Gillanders, 2005; Tanner et al., 2011; Tournois et al., 2013; Vasconcelos et al., 2008). However, considering all five sampling sites separately also led to very high global classification accuracies (≥ 89%) and correct re-assignment rates for all of them (≥76%). Therefore, although port habitats could be confidently identified here for both species, the variability of elemental fingerprints was high among port sites and among adjacent juvenile habitats. This variability has already been pointed out in natural coastal areas and is largely exploited in studies of the dispersal/connectivity of fully marine fishes (Di Franco et al., 2011).

However, this work also showed that otolith elemental concentrations in ports do not consistently reflect their high concentrations in the environment. The relationship between environmental exposure and otolith final concentrations was even inversed for some trace elements. For example, in *D. sargus*, otoliths from MAG were 1.4-fold more contaminated in Cu than those from STM (Fig. 3) whereas Cu concentration was found to be 34-fold higher in the water of MAG (Fig. 2). Similarly, in *D. vulgaris*, otolith concentrations in Pb were significantly higher in DLE than in TLN (1.3-fold, $p = 0.017$) whereas this element was 2.6-fold more concentrated in the water at TLN than at DLE (Fig. 2, Fig. 3). Therefore, although the three ports studied were more contaminated than adjacent juvenile habitats, in particular for Pb and Cu (Fig. 2), we failed to find at least one trace element for which otolith concentrations would be consistently higher in ports. Up to now few studies have focused on the link between the accumulation of elements in fish otoliths and their bioavailable concentrations in the aquatic environment (e.g., Daverat et al., 2012; Geffen et al., 1998; Ranaldi and Gagnon, 2009), yet those that have done so generally suggested that for many trace elements stored in fish otoliths, in particular Cu and Pb (Friedrich and Halden, 2010, 2011; Søndergaard et al., 2015), otolith concentrations largely reflect concentrations in water. This led some authors to conclude that trace element analyses in otoliths could be considered a valuable method for assessing time-resolved trace element exposure due to anthropogenic pollution (Selleslagh et al., 2016; Søndergaard et al., 2015). Several hypotheses can be proposed to explain the inconsistency between our results and these conclusions. Firstly, due to differences in metabolism and otolith formation, trace element accumulation in otoliths differs among species (Geffen et al., 1998; Hamer and Jenkins, 2007; Vasconcelos et al., 2007). Therefore, it is possible that otolith trace element incorporation is lower in *D. sargus and D. vulgaris* juveniles than in the sand goby *Pomatoschistus minutus* (Geffen et al., 1998), black bream *Acanthopagrus butcheri* (Ranaldi and Gagnon, 2008), flounder *Platichthus flesus* (Selleslagh et al., 2016) and common sculpin *Myoxocephalus scorpius* (Søndergaard et al., 2015), which were all suggested to be adequate for monitoring pollution from point sources. This hypothesis is supported by the fact that lower otolith accumulation rates have already been pointed out for certain trace elements in *Diplodus vulgaris*, when compared to other species like sole and flounder (Vasconcelos et al., 2007). Secondly, the accumulation of trace elements in fish otoliths not only depends on several factors, including their concentration in the environment and their bioavailability, but also on the physiological state of the fish (affecting the exchange rate between the external and internal environments), and on the mechanisms they use for detoxifying different metals or controlling their growth rate (affecting the rate of accumulation of otolith material). Although juvenile growth for both species is equivalent inside and outside the ports of this area (Bouchoucha et al., 2018), the consequences of juvenile life in ports on their individual physiological state still remain unclear. The influence of anthropogenic stressors on fish metabolism may explain differences in otolith trace element incorporation between the two types of habitat. However, further research is needed to investigate the respective influences of element concentrations in water and spatial variations in fish metabolism on their accumulation in the otoliths of juvenile *Diplodus*. Nonetheless, our initial hypothesis was wrong: the otoliths of the juvenile *Diplodus* captured inside ports, even at the most polluted sites, did not contain higher concentrations of port-related trace elements (such as Pb, Cu, Zn, etc.) than those from the juveniles captured in less polluted coastal areas. Therefore, otolith concentrations in these elements cannot be used to retrospectively identify the past residency of adult fish in ports, at least for the two species studied.

For both species, Ba was the most discriminating element among our sampling sites and between the two types of habitat, as its concentration in the otoliths, with one exception, was consistently higher outside ports than inside them (Fig. 3). This result is surprising as Ba is routinely used to distinguish residence in brackish habitats (reviewed by Elsdon et al., 2008), as its incorporation in otoliths falls when salinity increases (Bath et al., 2000; Elsdon and Gillanders, 2004). Nonetheless, the three port sites investigated here had lower salinities than the two others (Table 1). However, Ba concentrations in otoliths can be modulated by endogenous factors (e.g. fish condition - Izzo et al., 2015), and generally reflect ambient environmental concentrations (Campana, 1999; Elsdon et al., 2008). The DLE and MAG sites are located in the Large Bay of Toulon, close to the two outlets of the Eygoutier river (Fig. 1). As Ba is closely bound to fluvial sediments (Coffey et al., 1997), ambient Ba concentrations may be higher in DLE and MAG than in the three other sampling sites, explaining differences in juvenile fish otolith compositions. Therefore, it is likely that the pattern observed here with regard to otolith Ba concentrations is particular to the Bay of Toulon and cannot be extrapolated to other ports and coastal areas.

Finally, the trace elements responsible for the discrimination among the five sampling sites differed according to species, which might suggest that otolith fingerprints should be determined for each species independently and cannot be extrapolated from one species to another. The differences in otolith environmental records between our two species may be due to endogenous processes like physiological regulation (Sturrock et al., 2015) as well as to exogenous ones. Indeed, *D. vulgaris* hatches in two pulses, in October-November and in December-January, whereas *D. sargus* hatches only in May-June (Vigliola et al., 1998). Since we analyzed otolith portions corresponding approximately to the third month of life for both species, the environmental signals recorded by the two species do not overlap: for *D. vulgaris*, the otolith fingerprints correspond to winter/spring conditions while for *D. sargus*, they correspond to summer ones. Temporal variability in the elemental fingerprints must therefore be evaluated before concluding on the differences in environmental recording capacities among species.

In conclusion, our results showed that otolith microchemistry cannot provide a unique and reliable fingerprint discriminating all ports from other coastal areas. Nevertheless, we showed that, as with natural habitats, otolith microchemistry can provide an effective natural tag for determining the contribution of each port individually, at least in the two species studied. Therefore, in order to assess the contribution of ports to adult fish populations, a library of otolith fingerprints from all juvenile habitats should be established, by species and probably by cohort, and matched against fingerprints from adult otoliths (Thorrold et al., 2001).

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Figure 1: Map of the Bay of Toulon (Northwestern Mediterranean) showing the location of the five sites sampled for this study. The sites located inside ports are represented by black circles while those located outside are represented by white circles.

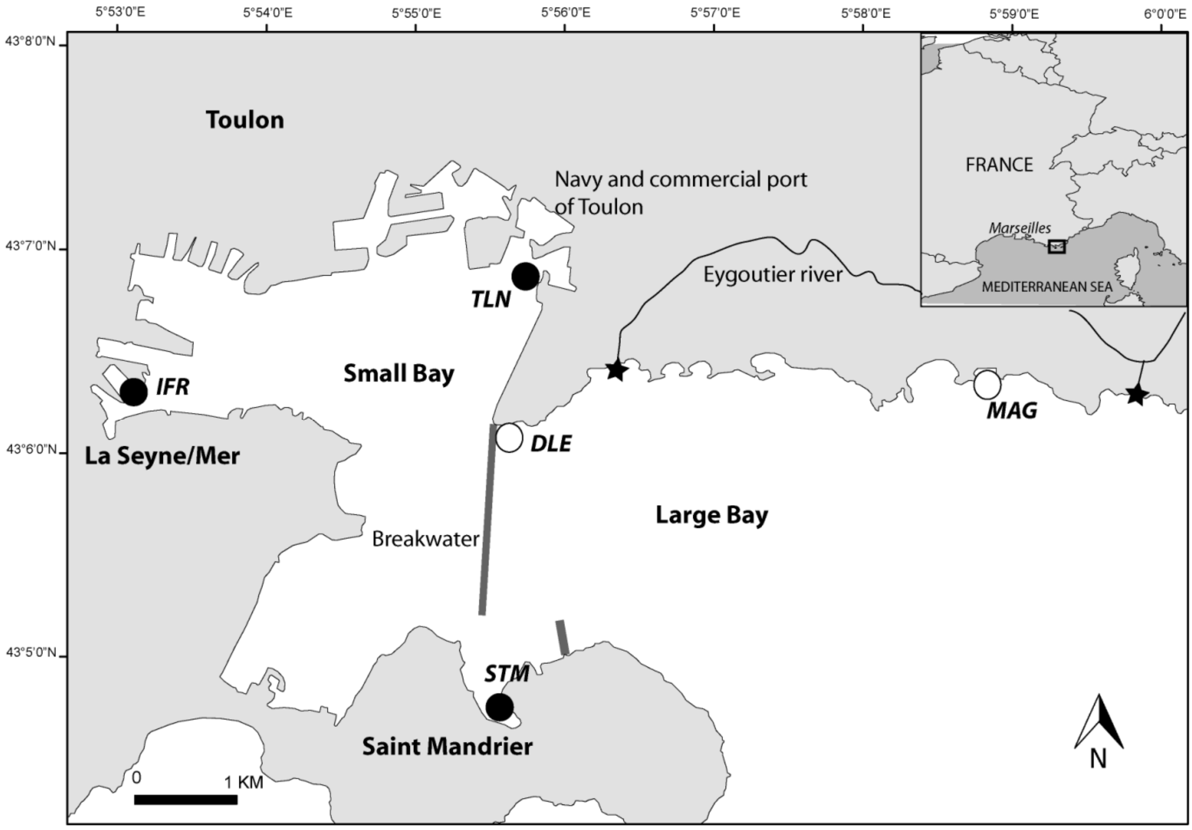


Figure 2: Mean otolith element:Ca ratios (± SE) measured for Ba, Mn, Sr, Cu, Pb, V, Mg, Sn and Zn in the juveniles of *D. sargus* and *D. vulgaris* from the two habitat types (In, inside ports , Out, outside ports) and the five sampling sites (M, MAG ; D, DLE ; S, STM ; T, TLN ; I, IFR). For each species, letters indicate significant differences ($p < 0.05$) between habitat types or sampling sites (see M&M for details).

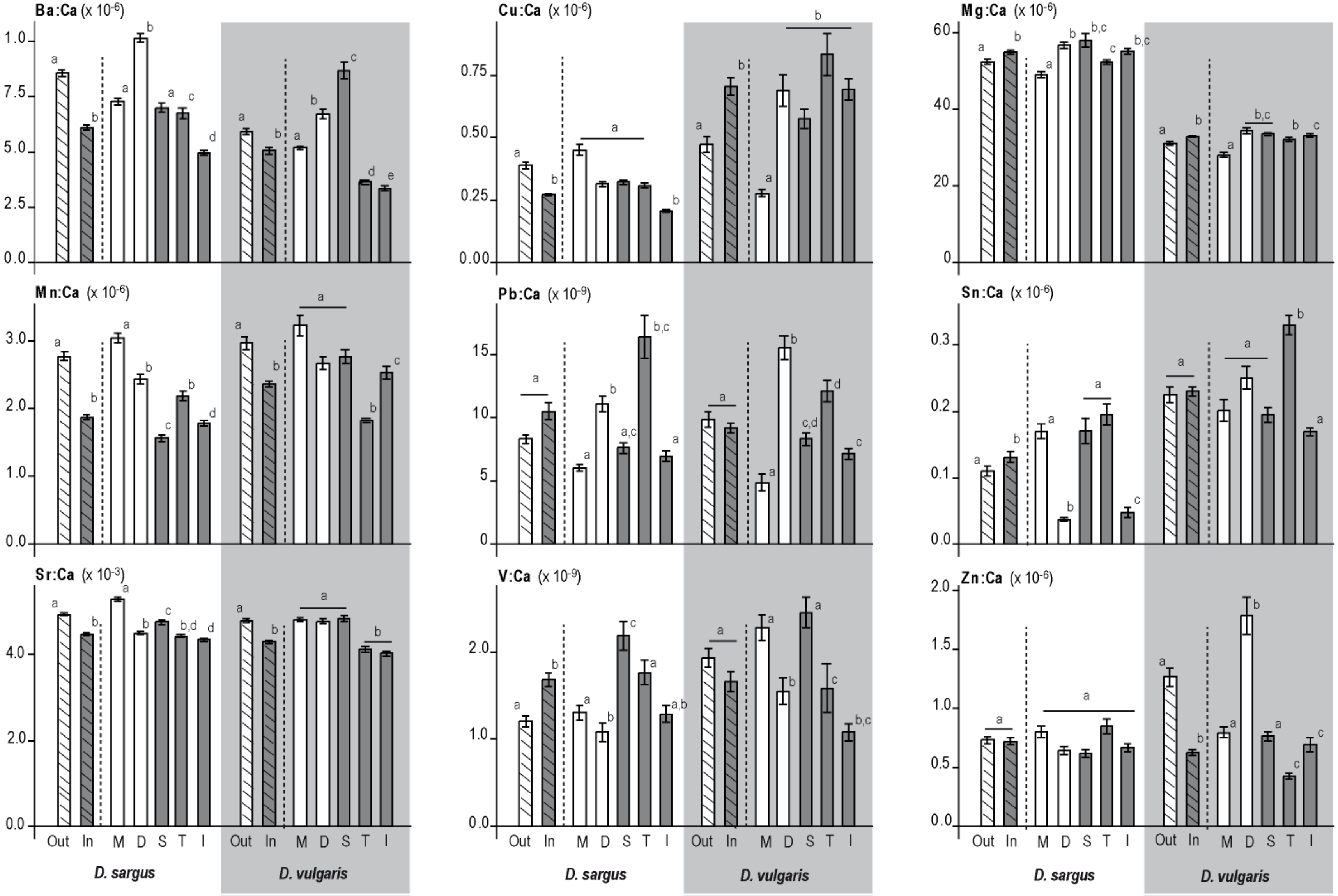
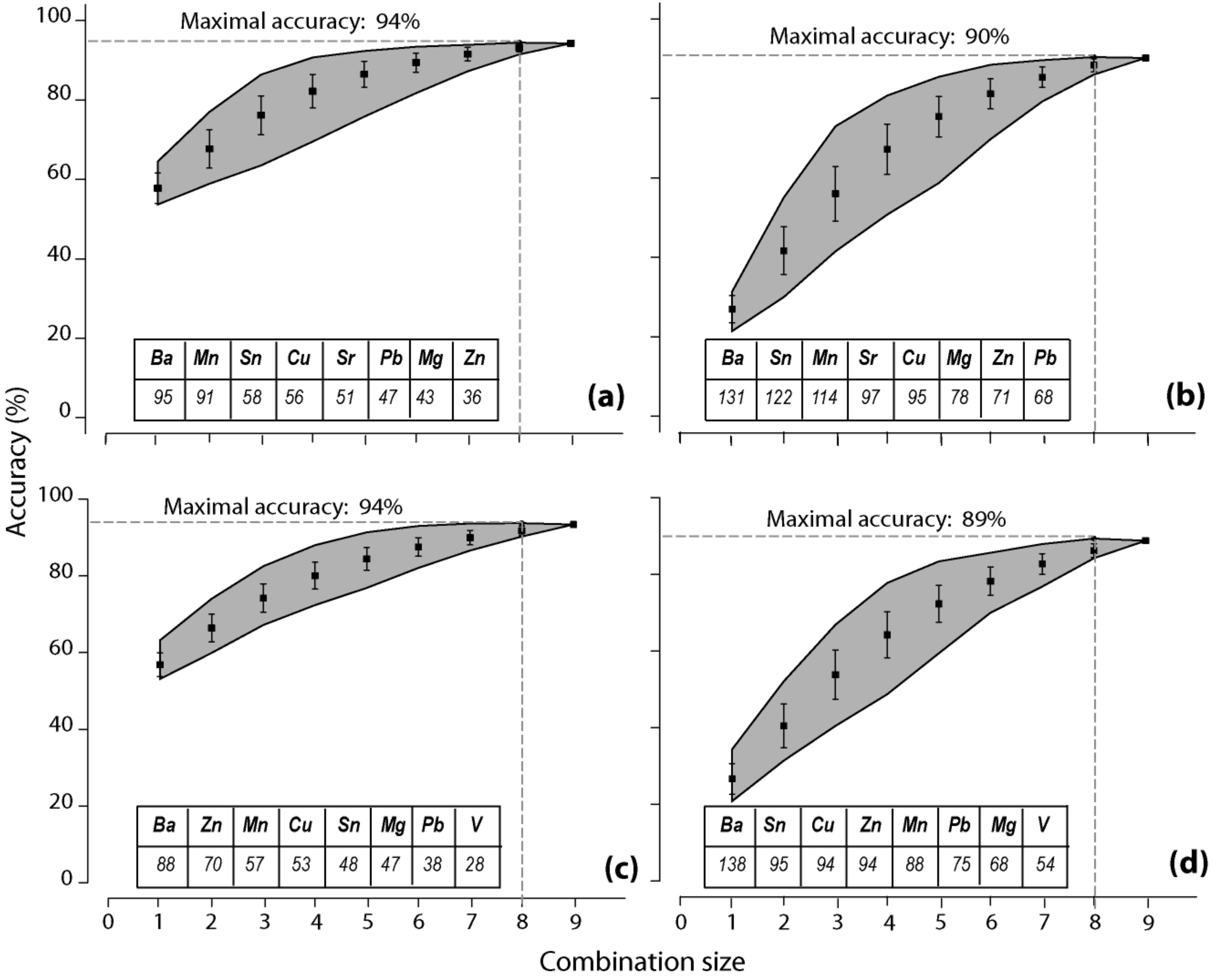

Ba:Ca (x 10^{-6})
1.0
7.5
5.0
2.5
0.0
Cu:Ca (x 10^{-6})
0.75
0.50
0.25
0.00
Mg:Ca (x 10^{-6})
60
40
20
0
Mn:Ca (x 10^{-6})
3.0
2.0
1.0
0.0
Pb:Ca (x 10^{-9})
15
10
5
0
Sn:Ca (x 10^{-6})
0.3
0.2
0.1
0.0
Sr:Ca (x 10^{-3})
4.0
2.0
0.0
V:Ca (x 10^{-9})
2.0
1.0
0.0
Zn:Ca (x 10^{-6})
2.0
1.5
1.0
0.5
0.0
Out In M D S T I
Out In M D S T I
D. sargus
D. vulgaris

Figure 3: Effect of elemental combination size and composition on the discrimination accuracy obtained using the RF method: (a) between the two habitat types for *D. sargus*, (b) among the five sampling sites for *D. sargus*, (c) between the two habitat types *for D. vulgaris* and (d) among the five sampling sites for *D. vulgaris* (d). The grey area on the graph represents the range between the minimal and maximal accuracies reached for each combination size while the corresponding average accuracy (±SD) in represented by the black square. The table gives the list of elements that achieved the maximal discrimination with the corresponding mean decreases in Gini index (see text for details).



(a)

Ba	Mn	Sn	Cu	Sr	Pb	Mg	Zn
95	*91*	*58*	*56*	*51*	*47*	*43*	*36*

(b)

Ba	Sn	Mn	Sr	Cu	Mg	Zn	Pb
131	*122*	*114*	*97*	*95*	*78*	*71*	*68*

(c)

Ba	Zn	Mn	Cu	Sn	Mg	Pb	V
88	*70*	*57*	*53*	*48*	*47*	*38*	*28*

(d)

Ba	Sn	Cu	Zn	Mn	Pb	Mg	V
138	*95*	*94*	*94*	*88*	*75*	*68*	*54*

Table 1: Concentrations in trace elements in the water column for the five sampling sites measured with DGT. Letters indicate significant differences ($p<0.05$) between sites if any

	Temp. (°C)		Salinity (psu)		Cu (ng.l^{-1})		Mn (µg.l^{-1})		Pb (ng.l^{-1})		Zn (µg.l^{-1})	
site	Mean ± sd	Min-Max	Mean ± sd	Min-Max	Mean ± sd	Min-Max	Mean ± sd	Min-Max	Mean ± sd	Min-Max	Mean ± sd	Min-Max
TLN	17.5 ± 4.3	12.8 – 24.8	37.1 ± 1.0	35.1 – 38.8	1268 ± 572 (a.b)	842 - 2203	0.83 ± 0.49 (a)	0.43 - 1.62	328 ± 107 (a)	206 - 540	3.05 ± 1.67 (a)	1.52 - 6.03
IFR	17.6 ± 4.8	12.0 – 25.7	37.2 ± 1.9	32.2 – 38.7	879 ± 261 (b)	589 -1205	1.28 ± 0.59 (a)	0.76 - 2.22	203 ± 85 (a.b)	132 - 337	3.44 ± 1.42 (a)	1.72 - 5.36
STM	17.7 ± 4.9	12.0 – 25.4	37.8 ± 1.3	34.4 - 39.5	2972 ± 997 (a)	1593 - 4375	0.67 ± 0.20 (a)	0.48 - 0.90	222 ± 47 (a)	153 - 261	3.27 ± 0.78 (a)	2.32 - 4.30
DLE	17.1 ± 3.9	12.6 – 23.6	38.0 ± 0.8	35.8 – 39.0	257 ± 166 (c)	142 - 498	1.52 ± 1.18 (a)	0.57 - 3.12	86 ± 44 (b.c)	52 - 145	1.47 ± 1.26 (a)	0.50 - 3.17
MAG	17.4 ± 4.1	13.2 – 25.5	38.0 ± 0.5	37.2 – 39.1	87 ± 38 (c)	39 - 145	0.50 ± 0.16 (a)	0.40 - 0.78	47 ± 10 (c)	36 - 61	1.31 ± 0.96 (a)	0.26 - 2.79

Table 2: Classification accuracy and True Skill Statistics (TSS) per habitat type or per sampling site reached for *D. sargus* and *D. vulgaris* with RF using the optimal elemental combination.

	Inside ports	TLN	IFR	STM	**Outside ports**	DLE	MAG
a) D. sargus							
Inside ports	**95.3**				**6.7**		
TLN		88.1	2.6	4.4		0.6	0.8
IFR		6.7	88.7	6.3		1.1	0.9
STM		1.1	2.4	76.1		0.8	0.7
Outside Ports	**4.7**				**93.3**		
DLE		1.4	3.2	6.1		97.2	0.3
MAG		2.7	3	7.2		0.3	97.3
TSS	***0.89***	*0.86*	*0.85*	*0.75*	***0.89***	*0.95*	*0.94*
b) D. vulgaris							
Inside ports	**95.3**				**8.6**		
TLN		91.7	5.7	0.5		1.0	1.3
IFR		4.3	88.8	3.0		1.5	1.4
STM		0.4	1.7	85.9		4.6	1.4
Outside ports	**4.7**				**91.4**		
DLE		1.7	2.1	4.3		86.3	2.8
MAG		1.8	1.8	6.4		6.5	93.1
TSS	***0.87***	*0.90*	*0.86*	*0.84*	***0.87***	*0.84*	*0.89*

V.3. Points à retenir :

- La composition chimique des otolithes de 2014-2015 permettait une très bonne discrimination (94 %) entre les zones portuaires et extérieures,
- Cependant, la discrimination entre les différents sites de prélèvement était également très importante (> 89 %), avec des signatures chimiques aussi différentes entre les ports qu'entre ces derniers et les autres zones côtières,
- Le Ba était l'élément le plus discriminant,
- Malgré des concentrations dans l'eau en Pb et Cu de 2,3 à 34 fois supérieures dans zones portuaires par rapport aux zones naturelles, les concentrations en ces éléments dans les otolithes n'étaient pas supérieures chez les juvéniles de *D. sargus* et *D. vulgaris* issus des ports.

Conclusions :

➔ Il est peu probable que nous soyons en mesure d'identifier dans les otolithes une signature élémentaire unique caractéristique d'une vie juvénile portuaire,

➔ La composition chimique des otolithes peut néanmoins être utilisée pour évaluer, à terme, la contribution relative des ports de la rade de Toulon aux stocks de *D. sargus* et *D. vulgaris* adultes à condition de caractériser la signature de l'ensemble de leurs habitats juvéniles potentiels, dans et en dehors des ports.

Chapitre 6. Discussion générale et perspectives

VI.1. Discussion

Ce travail de thèse est l'un des premiers à s'intéresser au rôle potentiel des ports comme nourriceries alternatives pour certaines espèces de poissons marins côtiers. L'approche choisie, basée sur quatre espèces modèles de sars (*D. sargus*, *D. vulgaris*, *D. puntazzo* et *D. annularis*) et une zone atelier (la rade de Toulon) a permis de démontrer que la qualité des habitats portuaires pour les juvéniles de poissons est, dans certains cas, nettement supérieure à celle supposée jusqu'ici, notamment en termes d'installation benthique, d'abondance, de croissance et de condition des juvéniles dans les ports. Ces résultats ont d'importantes implications pour la conservation des espèces marines côtières et pour la gestion des zones littorales.

VI.1.1. Installation benthique et schémas d'abondance inter-ports

Chez les poissons marins côtiers, l'intensité du recrutement est en partie dépendante de celle de l'installation benthique (Vigliola 1998) et tout facteur venant perturber le succès de cette dernière peut potentiellement avoir des conséquences importantes sur les populations adultes. A macro (10-100 km) et méso-échelle (0,1-1 km), le succès de l'installation benthique dépend de la distribution des larves dans la colonne d'eau et de facteurs environnementaux (e.g. les sons, les odeurs, la lumière, etc.) influençant la sélection de l'habitat (Sale 1969, Carr 1991, Wellington 1992). Celui-ci est donc conditionné à la fois par les conditions hydrodynamiques qui influencent le transport larvaire (Félix-Hackradt et al. 2013) et par le comportement des larves (Leis et al. 2014, Faillettaz et al. 2015). Par corollaire, toute modification des courants locaux (Munday et al. 2008) ou des facteurs environnementaux influençant la sélection de l'habitat juvénile (Leis 2007) peut avoir d'importantes conséquences sur l'installation benthique des juvéniles de poissons côtiers. Or, la construction d'un port modifie profondément ces deux paramètres (Martin et al. 2005).

Au cours de notre travail, nous avons observé des abondances non négilgeables de juvéniles de quatre espèces de sars (*D. sargus*, *D. vulgaris*, *D. puntazzo* et *D. annularis*) à l'intérieur de cinq ports, choisis pour représenter la diversité des ports de plaisance de Méditerranée (**chapitre 3**). Des constats similaires ont été faits pour *D. sargus* et *D. vulgaris* dans les trois sites portuaires contrastés étudiés dans la rade de Toulon : la marina de Saint-Mandrier-sur-Mer, le port de l'Ifremer et un grand port militaire et de commerce fortement pollué, le port de Toulon. La présence de juvéniles de sars dans les ports avait déjà été signalée (Clynick 2006). Elle a par ailleurs été récemment relevée dans un grand port de commerce méditerranéen, le grand port maritime de Marseille (Mercader et al. 2017). De plus, d’autres espèces de poissons côtiers, comme *Coris julis* (Clynick 2006), *Dicentrarchus labrax* (Dufour et al. 2009), *Symphodus ocellatus* (Clynick 2006) ou encore *Symphodus sp.* (Mercader et al. 2017), ont été observées au stade juvénile dans des ports. Les modifications physico-chimiques engendrées par une construction portuaire ne sont donc pas de nature à limiter totalement les flux larvaires et l'installation benthique des juvéniles de poissons dans les ports.

Cependant, au cours de ce travail, de fortes variations d’abondances de juvéniles de sars ont été montrées entre les ports (**Article 1**, figure S2) ; allant de la quasi-absence dans le port de Mèze à des densités particulièrement importantes (1,08 ± 0,18 individus par comptage visuel en moyenne dans le port du Cap-d’Agde). La structure spatio-temporelle des assemblages de juvéniles de poissons résulte d’une combinaison entre les variations dans l’intensité de l’installation benthique (Doherty 1991) et les processus déterministes de mortalité post-installation (Doherty et al. 2004, Lecchini et al. 2006). Deux hypothèses peuvent donc être avancées pour expliquer ces différences spatiales : (i) des différences d’intensité d’installation benthique entre les zones portuaires et/ou (ii) des taux de mortalité post-installation différents. Les courants marins influencent la dispersion des œufs et des larves (Cheminee et al. 2011, Cheminée et al. 2017). L'apport larvaire de chaque espèce peut varier en fonction de la localisation des ports par rapport aux zones de ponte. Par ailleurs, certains ports peuvent être proches de zones de nourriceries naturelles et donc bénéficier de l'attraction qu’elles exercent sur les larves. Une autre hypothèse peut être l’existence d’une différence dans l’intensité de la mortalité post-installation entre les différents ports pour ces espèces (Öhman et al. 1998, Doherty 2002, Macpherson & Raventos 2005) en lien avec la qualité des habitats juvéniles qu’ils offrent (Planes et al. 1998). Il n’est pas possible à ce stade de séparer l'effet des apports de larves de celui du différentiel de mortalité entre les ports sur les abondances de juvéniles. En effet, la mortalité juvénile étant maximale dans les premières heures qui suivent l’installation benthique (Doherty et al. 2004), le pas de temps de 15j entre les comptages du **Chapitre 3** n’était pas adapté à l’appréciation correcte des cinétiques de mortalité dans les différents ports. Cependant, les ports suivis dans le **chapitre 3** présentaient des caractéristiques équivalentes en termes de micro-habitats. Donc, même si ces caractéristiques sont bien connues pour influencer l’installation benthique des poissons (Mellin 2007), ce facteur ne peut pas expliquer à lui seul la variabilité dans l’installation benthique des sars entre ports. Ainsi, malgré les incertitudes sur les processus responsables des différences spatiales d’abondances, il apparaît clairement que tous les ports ne peuvent pas fournir des conditions équivalentes pour l’installation benthique ou la survie des juvéniles de poissons et que par conséquent, tous n’ont pas le même potentiel pour fournir des nourriceries alternatives aux poissons marins côtiers. Compte tenu des phénomènes pré et post-installation, ce potentiel peut varier suivant les espèces mais également entre les années pour une même espèce.

VI.1.2. Influence du micro-habitat sur les abondances dans les ports

A micro-échelle (1-100m), l'installation benthique dépend fortement des caractéristiques des micro-habitats (Mellin 2007, Ventura et al. 2014). L'observation régulière de juvéniles de poissons confirme que ces derniers trouvent généralement dans les ports des micro-habitats aux caractéristiques compatibles avec le succès de leur installation benthique. Par ailleurs, cette dernière n'est pas conditionnée par la réalisation ou non de projets d'ingénierie écologique. L'observation de juvénile de sars dans les sites étudiés dans les **chapitres 4 & 5** sans aménagement particulier l'illustre parfaitement. Il est néanmoins à noter que, dans les ports comme en milieu naturel (Ventura et al. 2014), les différentes espèces ont des préférences en termes de micro-habitats à l'installation benthique. Par exemple, dans le **chapitre 3**, les plus jeunes stades de *D. sargus* et *D. puntazzo* (stade post-installation) ont plutôt été observés sous des pontons alors que ceux de *D. vulgaris* l'ont été sur des quais (**Article 1**, figure 4). Pour ces espèces, la spécificité de micro-habitat à l'installation benthique était même très importante et les abondances observées dans tous micro-habitats hormis l'habitat préférentiel étaient quasiment nulles. Ceci laisse supposer qu'un port ne présentant aucun micro-habitat favorable à une espèce ne peut être colonisé par cette dernière. Ceci est néanmoins à nuancer. En effet, nous avons souligné dans le **chapitre 3** qu'il existe chez les poissons, du moins chez les sars, une certaine plasticité dans les besoins en termes d'habitats juvéniles. Cette plasticité est parfaitement illustrée dans le cas de *D. annularis*. En milieu naturel, les juvéniles de cette espèce sont très fortement associés aux herbiers de posidonie (Gordoa & Moli 1997, Garcia-Charton et al. 2004, Ventura et al. 2014) et se retrouvent entre 6 et 8 m de profondeur (Harmelin-Vivien et al. 1995). Au cours de notre travail, nous les avons observés en abondance dans des ports, à moins d'1m de profondeur, indifféremment sur des quais et sous des pontons (**Article 1**, figures 4 et S2). Cette plasticité a également été notée chez d'autres espèces (Guidetti 2004, Martin et al. 2005, Clynick 2006). Les capacités d'adaptation des poissons à de nouveaux habitats juvéniles sont donc certainement plus importantes que ce que nous pouvions imaginer jusqu'à présent et nous pouvons nous demander si ces espèces ne pourraient pas modifier leur habitat préférentiel en fonction de ceux qu'elles trouvent dans les ports.

Par ailleurs, l'influence de la complexité structurale des habitats sur les cinétiques de mortalité des juvéniles de poissons a été démontrée à maintes reprises (Holbrook et al. 2000, Holbrook & Schmitt

2002, Mellin 2007). La majorité des linéaires portuaires est constituée de quais et de pontons offrant aux juvéniles de poissons des surfaces lisses, *a priori* moins propices à leur installation benthique (Chapman & Blockley 2009) et à leur survie (Bulleri & Chapman 2010) que des surfaces complexes. Au cours de ce travail de thèse, nous avons vu que les abondances de juvéniles de sars étaient en moyenne doublées lorsque des micro-structures artificielles complexes étaient fixées sur les ouvrages portuaires (quais et pontons). Il semble donc évident que la faible complexité structurale des micro-habitats portuaires limite fortement leur qualité en tant qu'habitat juvénile. Ainsi, toute opération conduisant à l'augmentation de cette complexité pourrait permettre d'améliorer la qualié des ports comme nourriceries alternatives de poissons. Les projets d'ingénierie écologique actuellement développés dans les ports méditerranéens sont en ce sens prometteurs. Ce résultat doit néanmoins être considéré avec précaution. Deux hypothèses peuvent en effet expliquer l'augmentation de l'abondance des juvéniles de sars lorsque des micro-structures artificielles complexes sont fixées sur les ouvrages portuaires : (i) une diminution réelle de la mortalité juvénile liée à la création d'abris (Bulleri & Chapman 2010) et/ou (ii) un phénomène d'attraction/concentration par la nouvelle structure solide (phénomène de thigmotaxisme – Ammann 2004). Dans le cadre de l'hypothèse d'attraction/concentration, la régulation de la mortalité pré-recrutement n'est pas liée à la disponibilité en refuges dans les ports mais peut être soit due à de la compétition pour de la nourriture, soit à des processus denso-indépendant comme l'influence de la contamination chimique. Les micro-structures artificielles fixées sur les ouvrages portuaires sont alors assimilées à des dispositifs de concentration de poissons attirant les juvéniles des zones adjacentes et leur déploiement n'engendre pas une augmentation de la contribution des ports équipés au recrutement. Plusieurs études ont montré que, en milieu naturel, la compétition pour la nourriture n'est pas le processus qui explique la mortalité des sars durant leur phase juvénile benthique (Macpherson et al. 1997, Vigliola 1998, Cuadros et al. 2017). Les ports étant des milieux généralement productifs et riches d'un point de vue trophique (e.g. Jamet et al. 2005), il semble peu probable que la compétition pour la nourriture soit la cause principale de la mortalité juvénile en zone portuaire. Le rôle des phénomènes denso-indépendants ne peut, par-contre pas être écarté à ce stade. A l'inverse, dans le cadre de l'hypothèse diminution de la mortalité, la fixation de micro-structures artificielles sur les ouvrages portuaires permet une augmentation réelle de la qualité de l'habitat qui se traduit par une augmentation de l'abondance de juvéniles sur les zones équipées sans influence sur les zones adjacentes. Il est certain que le processus d'attraction/concentration intervient autour des micro-structures artificielles fixées sur les ouvrages portuaires puisque des individus juvéniles y plus sont observés que dans les zones adjacentes dès leur immersion (**chapitre 3**). Par contre, l'hypothèse de la réduction de la mortalité reste à vérifier. Cette controverse a fait l'objet d'importants débats dans un autre contexte, opposant deux modèles conceptuels de fonctionnement des récifs artificiels : attraction vs. production (e.g. Bohnsack 1989, Polovina 1989, Grossman et al. 1997). Aujourd'hui, il est généralement admis que ces deux hypothèses ne sont pas mutuellement exclusives et que les structures mises en place peuvent à la fois attirer et protéger les poissons (Svane & Petersen 2001). Il est raisonnable de penser que cette conclusion doit également s'appliquer aux micro-structures artificielles fixées dans les zones portuaires.

VI.1.3. Croissance et condition des juvéniles de poissons dans les zones portuaires

De très nombreuses études ont démontré l'effet négatif des contaminants chimiques sur la physiologie des juvéniles de poissons, au travers notamment de la diminution de leur croissance ou de leur condition (e.g. Rowe 2003, Gilliers et al. 2006, Kerambrun et al. 2013) avec des conséquences potentielles sur leur recrutement futur. Comment envisager alors que des zones fortement contaminées puissent être des nourriceries de poissons ? Cette question anime systématiquement les débats portant sur la réhabilitation de la fonction de nourricerie en zone portuaire. Elle n'est cependant pas propre aux ports et peut être posée pour l'ensemble des systèmes côtiers fortement anthropisés et soumis à des pollutions parfois importantes comme par exemple certains estuaires (Hamzeh et al. 2016, Robinson et al. 2017) ou encore certaines lagunes littorales (Accornero et al. 2008, Ben Mna et al. 2017). Pourtant, ces milieux sont souvent identifiés comme étant les principales zones de nourriceries de diverses espèces poissons marins côtiers (Beck et al. 2001, Franco et al. 2006, Vasconcelos et al. 2008). L'étang de Mauguio, par exemple, fait partie des lagunes les plus dégradées du Languedoc-Roussillon (Witkowski et al. 2017). Néanmoins, des travaux récents ont mis en évidence qu'il avait non seulement une contribution significative au stock de daurades (*Sparus aurata*) adultes (Tournois et al. 2017) mais également que les juvéniles de cette espèce y grandissant avaient des croissances et conditions juvéniles supérieures à celles observées dans d'autres lagunes moins dégradées (Isnard et al. 2015).

Les quelques travaux portant sur la croissance et la condition de juvéniles de poissons dans des zones portuaires ou à leur proximité immédiate présentent des résultats contradictoires. Les études menées sur des individus en cage ou élevés en conditions contrôlées montrent que même une courte exposition (quelques semaines) à un environnement portuaire affecte les performances biologiques des juvéniles (e.g. Kerambrun et al. 2012a, Kerambrun et al. 2013). En conditions naturelles, des résultats équivalents ne sont généralement pas mis en évidence. Par exemple, aucune différence de performances biologiques n'a été observée entre des juvéniles prélevés à proximité des zones portuaires (Dunkerque, Calais, Boulogne) et d'autres capturés à bonne distance (Gilliers et al. 2004). Cette variabilité dans les réponses observées ne remet pas en cause l'existence d'une influence négative des contaminants chimiques sur les performances biologiques des poissons juvéniles mais relève plutôt de l'interférence au niveau local de facteurs naturels et anthropiques qui interagissent sur les conditions de vie des individus (Whitfield & Elliott 2002). Par exemple, la production primaire a un effet positif direct sur la croissance et la condition des poissons (Le Pape et al. 2013, Morrongiello et al. 2014) et donc sur la fonction de nourricerie (Kostecki et al. 2012). Ceci a déjà été souligné pour les estuaires (Gilliers et al. 2006, Amara et al. 2007) y compris certains fortement contaminés (Courrat et al. 2009). Par ailleurs, une plus forte production primaire contribue à la dilution de la concentration des contaminants à la base des réseaux trophiques (Harmelin-Vivien et al. 2009, Cresson et al. 2015a) limitant ainsi leurs effets délétères.

Malgré les niveaux de contamination environnementale élevés observés dans les ports, cette thèse a montré que les juvéniles de quatre espèces de sars (*D. sargus*, *D. vulgaris*, *D. annularis* et *D. puntazzo*) étaient susceptibles d'y survivre et d'y grandir jusqu'à la fin de leur période de résidence (**Article 1**, figure 3). Pour *D. sargus* et *D. vulgaris*, les analyses réalisées à l'échelle de la rade de Toulon ont même montré qu'il n'existait pas différences significatives dans les taux de croissance absolus (estimés à partir de la croissance des otolithes), ou dans les indices de condition chez des juvéniles capturés à l'intérieur de ports et dans des zones naturelles adjacentes. Or, des croissances et des indices de condition élevés chez les juvéniles sont considérés comme un avantage net pour le recrutement et la contribution au stock d'adultes dans la mesure où une taille et des réserves énergétiques plus importantes à l'issue de la première année favorisent directement la survie lors du premier hiver (Sogard 1997). Un sar ayant survécu à une vie juvénile dans un port aurait ainsi, *a priori*, autant de chances de contribuer au maintien de la population adulte qu'un individu issu d'une nourricerie naturelle. La plus forte production primaire dans les ports méditerranéens par rapport aux nourriceries naturelles (e.g. Jamet et al. 2005) peut expliquer ce résultat.

A l'issue de ce travail, il semble donc clair que la contamination chimique n'est pas le facteur majeur qui limite l'utilisation des ports comme nourriceries alternatives chez les sars. Afin de vérifier si ces conclusions ne sont pas spécifiques aux espèces étudiées et si elles peuvent être généralisées à un diagnostic sur la fonctionnalité halieutique de ports (Able et al. 1999, Whitfield & Elliott 2002), ce constat mériterait néanmoins d'être validé par une approche similaire sur d'autres espèces. Gilliers et al. (2004) ont en effet démontré qu'il existe des différences de sensibilité des indicateurs de croissance des juvéniles en fonction des espèces étudiées. Il est donc possible que nos conclusions ne soient pas transposables à d'autres espèces, en particulier aux espèces de poissons plats, considérées comme particulièrement sensibles à la contamination métallique car vivant au contact du sédiment (Johnson et al. 1998, Bolton et al. 2004).

VI.1.4. Impact de la pollution sur les niveaux de contamination et la composition des otolithes des juvéniles de poissons dans les ports

Situés à l'interface terre-mer, les ports sont le lieu de nombreuses activités anthropiques et le réceptacle de multiples pollutions microbiologiques et chimiques (Darbra et al. 2004, CETMEF 2010). Ces pollutions, et en particulier la contamination chimique qu'elles engendrent, influent sur la survie des poissons sur place mais aussi plus tard, jusqu'à l'âge adulte, avec également un effet négatif sur leur capacité de reproduction future (Rowe 2003).

Au cours de notre étude, nous nous sommes focalisés sur les éléments trace métalliques (ETM), laissant de côté les autres contaminants présents en fortes concentrations dans les ports, notamment les hydrocarbures aromatiques polycycliques ou HAP (CETMEF 2010). Or, ces composés ont également des effets négatifs sur la croissance et la mortalité des juvéniles de poissons (Gilliers 2004, Kerambrun et al. 2012c). Afin d'avoir une vision plus réaliste des niveaux de contamination et de l'état de santé des poissons ayant grandi dans des ports, nos travaux devront donc être complétés à l'avenir par des analyses portant sur d'autres familles de contaminants. Néanmoins, l'existence d'une corrélation entre la concentration en HAP et celles en plomb (Dang et al. 2015) ou en vanadium (Amiard et al. 2004, Ridoux et al. 2004) permet l'utilisation de ces ETM comme proxy de l'exposition des poissons juvéniles aux hydrocarbures et nous permet d'élargir la portée de nos résultats.

Au cours de ce travail de thèse, nous avons mesuré, sur les mêmes individus, les concentrations musculaires en 12 éléments (Al, As, Cr, Cu, Fe, Hg, Mn, Pb, Se, Ti , V et Zn) et celles des otolithes pour 9 éléments (Ba, Cu, Mg, Mn, Pb, Sn, Sr, V et Zn). Par ailleurs, nous avons mesuré, en 2015, les concentrations en 7 éléments (Al, Cu, Cr, Cu, Fe, Mn, Pb et Zn) dans la colonne d'eau durant une période correspondant exactement à la présence de *D. vulgaris* dans les différents habitats juvéniles. Quatre ETM (Pb, Cu, Mn et Zn) ont ainsi pu être mesurés systématiquement, aux mêmes lieux et au même moment, dans les trois matrices (eau, muscle et otolithe). Pour ces éléments, aucun lien direct n'a pu être établi entre la concentration dans la colonne d'eau (**Article 2**, figure 2), celle dans les tissus musculaires (**Article 2**, figure 4 & S1) ou dans les otolithes (**Article 3,** figure 2). Par exemple, les concentrations en Cu dans les DGT au site STM (2 972 ± 997 ng.l^{-1}) sont en adéquation avec les fortes concentrations en Cu mesurées dans le muscle des *D. vulgaris* à cette station (**Article 2,** figure 3) mais n'expliquent pas l'absence de différence de concentration dans les otolithes de cette même espèce entre les sites STM et DLE (**Article 3,** figure 2). Concernant le plomb, la forte contamination mesurée dans les DGT aux sites TLN (328 ± 107 ng.l^{-1}) et STM (222 ± 47 ng.l^{-1}) par rapport aux sites DLE (86 ± 44 ng.l^{-1}) et MAG (47 ± 10 ng.l^{-1}) est partiellement en contradiction avec les mesures dans les poissons. En effet, des valeurs importantes en Pb ont été mesurées dans le muscle et les otolithes des *D. vulgaris* au site DLE (**Article 2,** figure 3 et **Article 3,** figure 2). Autre exemple, les valeurs en Mn mesurées dans les DGT au site DLE (1,5 ± 1,2 ng.l^{-1}) sont largement supérieures à celles mesurées aux sites MAG (0,50 ± 0,16 ng.l^{-1}), STM (0,67 ± 0,20 ng.l^{-1}) et TLN (0.83 ± 0,49 ng.l^{-1}). Ceci est en cohérence avec les concentrations en Mn observées dans le muscle des *D. vulgaris* (**Article 2,** figure 3) mais en désaccord avec celles dans les otolithes (**Article 3**, figure 2). Enfin, les concentrations en Zn dans les otolithes des juvéniles capturés au site DLE sont significativement supérieures à celles des deux sites portuaires (STM et TLN) alors que les concentrations dans l'eau pour ces derniers sont respectivement 2,2 et 2,1 supérieures à celle de DLE (1,47 ± 1,26 µg.l^{-1} pour DLE contre 3,27 ± 0,78 µg.l^{-1} pour STM et 3,05 ± 1,67 µg.l^{-1} pour TLN). Ainsi, même si ces données complémentaires mesurées dans les DGT confirment bien que, pour la plupart des ETM, les concentrations mesurées dans les ports sont supérieures à celles des zones naturelles, la comparaison des concentrations dans le milieu et dans les poissons (muscle et otolithe) reste difficile à interpréter. Ce constat n'est pas propre aux ports et a également été fait dans d'autres systèmes marins, en Méditerranée (e.g. Cresson et al. 2015a) et ailleurs (e.g. Nakhle et al. 2007). La voie trophique domine l'exposition et l'incorporation de ces contaminants chez les organismes supérieurs tels que les poissons (Wang 2002). Or, le transfert et le devenir des ETM du milieu vers les réseaux trophiques dépendent de leur biodisponibilité, et donc de leur spéciation (ou forme physico-chimique) dans les compartiments abiotique et biotique des écosystèmes (Nfon et al. 2009). Par exemple, la complexation du cuivre par la matière organique dissoute modifie sa biodisponibilité et ainsi sa toxicité pour les organismes (Sánchez-Marín et al. 2012, Bui et al. 2016). Par ailleurs, la bioaccumulation d'ETM chez les poissons dépend de processus endogènes, liés soit à régulation des taux d'ingestion, d'accumulation ou d'excrétion par les organismes (Newman & Heagler 1991, Phipps et al. 2002) soit à un effet de dilution chez les organismes (Newman & Heagler 1991, Campbell et al. 2005). Tous ces facteurs sont propres à chaque ETM. Enfin, le niveau d'exposition des organismes supérieurs tels les poissons aux ETM dépend de la structure et de la longueur de leurs réseaux trophiques. Il n'existe donc pas de lien direct entre les concentrations en ETM dans le milieu et leur accumulation dans les muscles et les otolithes des poissons (figure VI.1).

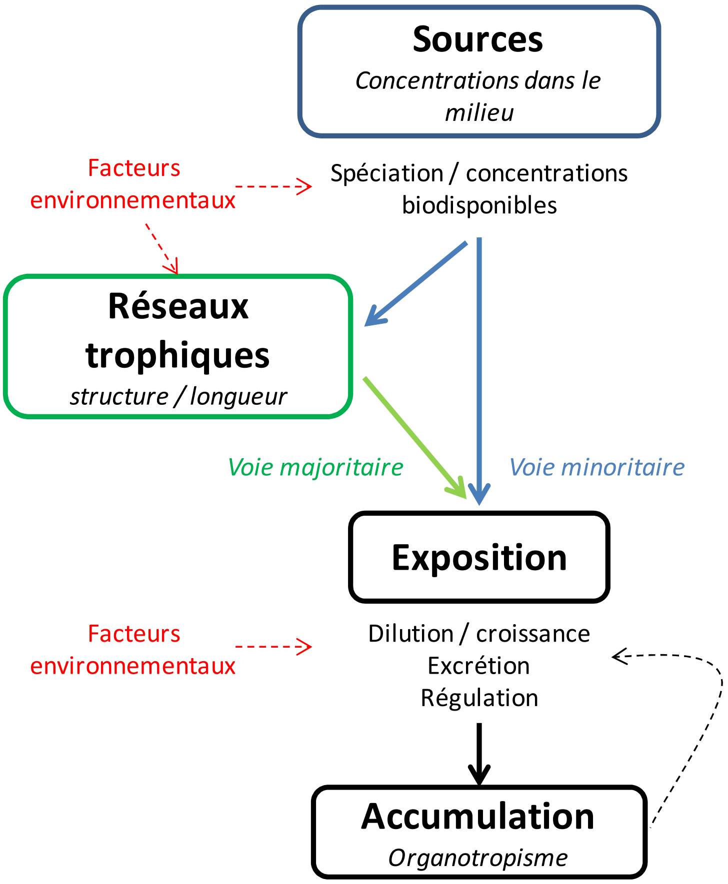


Figure VI.1 : Schéma simplifié du transfert des contaminants métalliques du milieu vers les juvéniles de poissons. Les flèches pleines représentent les transferts de contaminants. Les flèches en pointillés symbolisent l'influence des facteurs externes et internes sur ces transferts.

A l'exception du manganèse, les concentrations maximales en ETM mesurées dans le **chapitre 4** ont été relevées dans les muscles de juvéniles prélevés dans des ports. Néanmoins, pour les ETM réglementés (i.e. Hg et Pb), ces concentrations restaient 5 à 7,5 fois inférieures aux seuils de sécurité sanitaire pour la consommation humaine. Ainsi, la dispersion de juvéniles issus de zones portuaires ne semble pas entraîner de risque pour la santé humaine. Il est bien évident qu'une certaine prudence est de mise face à une telle affirmation basée sur un seul cas d'étude et une seule famille de contaminants. Des travaux complémentaires devront être menés pour le confirmer. Par ailleurs, ce résultat ne nous informe pas sur l'impact de ces contaminants sur la fitness des poissons au stade adulte, ni sur le succès de recrutement.

Enfin, l’hypothèse de départ du **chapitre 5** était que les otolithes de juvéniles provenant de zones portuaires polluées devaient contenir des concentrations supérieures en ETM liés aux activités portuaires (comme le plomb, le cuivre, le zinc, etc.). Malgré des concentrations en ETM dans les ports supérieures à celles des zones naturelles, nous ne sommes pas parvenus à trouver ne serait-ce qu’un seul élément dont les concentrations dans les otolithes sont supérieur dans les ports (**Article 3**, figure 2). L’influence des facteurs extrinsèques et intrinsèques résumée dans la figure VI.1 en est probablement la cause. En conséquence, nous ne sommes pas en mesure d’identifier dans les otolithes de sars une signature élémentaire unique caractéristique de l’ensemble des ports de Méditerranée. Les résultats du **chapitre 5** montrent que l’étude de la contribution relative des ports aux stocks d’adultes demeure néanmoins possible mais doit passer par la caractérisation systématique de l’ensemble des zones de nourriceries potentielles.

VI.1.5. Faut-il rehabiliter une fonction de nourricerie dans les ports ou protéger les nourriceries naturelles pour conserver la biodiversité côtière ?

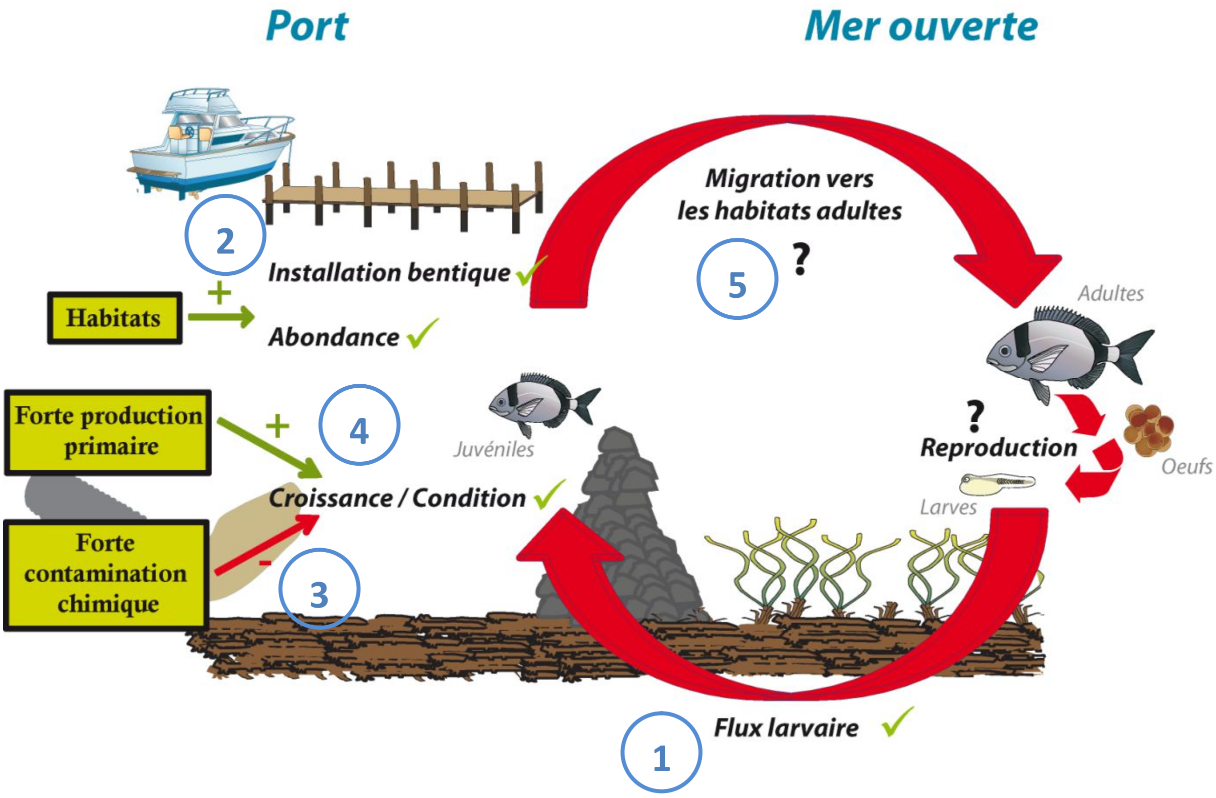
Les préoccupations quant à la conservation de la biodiversité sont relativement récentes (Rotherham 2010). En France, la gestion de la biodiversité n’a commencé à s’organiser réellement qu’après la Seconde Guerre Mondiale, notamment avec le vote de la loi sur les Parc Nationaux en 1960. Seule la protection des espaces naturels, ou du moins leur stricte réglementation, était alors envisagée pour conserver la biodiversité. Cette perception a totalement changé au début des années 90, en particulier avec la Directive habitat en 1992, et l’intervention proactive de l’Homme dans les espaces naturels dégradés est aujourd’hui considérée comme un moyen de conserver la biodiversité (Lepart & Marty 2006). Au cours des 20 dernières années, des projets de création d’habitats ou la reconnexion des habitats afin de recréer des conditions favorables dans lesquelles des espèces puissent évoluer se sont alors développés, y compris en milieu marin (Tessier 2013).

Les projets de protection et de restauration/réhabilitation d’habitats en milieu marin ayant pour but de conserver la biodiversité nécessitent des moyens techniques et financiers parfois importants. Or, confrontés à des ressources financières limitées (McCarthy et al. 2012), les gestionnaires de milieux doivent faire des choix stratégiques pour atteindre leurs objectifs (Williams et al. 2005). Bien que plusieurs interrogations demeurent, aucun des résultats obtenus dans ce travail de thèse ne s’oppose à l’hypothèse voulant que les ports puissent remplir une fonction de nourricerie pour certaines espèces. Il est donc possible, d’un point de vue théorique, d’envisager des projets d’ingénierie écologique en milieu portuaire pour contribuer au maintien de la biodiversité des poissons marins côtiers. Une question demeure cependant centrale : afin de conserver la biodiversité et les stocks des poissons marins côtiers, est-il plus efficace de protéger des habitats marins côtiers non dégradés ou de créer des habitats artificiels complexes dans les ports ?

Une position de principe de la communauté scientifique est souvent que la protection des habitats intacts doit primer à la restauration d'habitats dégradés ou à la réhabilitation de fonctions écologiques (Hobbs & Harris 2001, Williams et al. 2005, Dodds et al. 2008). Pour justifier cette position, les auteurs invoquent les coûts relatifs des deux types de mesures de gestion ainsi que les bénéfices respectifs attendus et les temps nécessaires pour les observer (Young 2000, Benayas et al. 2009). Cette position est de plus étayée par le fait que les habitats naturels intacts accueillent plus de biodiversité et assurent plus de services écosystémiques par unité de surface que des habitats restaurés / réhabilités (Possingham et al. 2015). Cependant, il est également reconnu que la protection est rarement totalement efficace, d'une part parce qu'elle n'empêche pas toute forme de dégradation (Agardy 1994, Halpern 2003) et d'autre part parce que les aires protégées ne sont pas toujours parfaitement gérées (Leverington et al. 2010) en particulier en milieu marin (Cox et al. 2017). *A contrario*, des services écosystémiques peuvent être fournis par des habitats restaurés ou réhabilités (Benayas et al. 2009), parfois rapidement après la mise en place des opérations (Jones & Schmitz 2009), tout en engendrant un bénéfice social important (Groot et al. 2013). Les coûts totaux réels des opérations de restauration / réhabilitation demeurent néanmoins souvent sous-estimés (Bayraktarov et al. 2016), ce qui rend leur comparaison avec le coût de la protection difficile.

Des travaux récents ont montré que la priorisation de la protection par rapport à la restauration / réhabilitation n'avait pas toujours de fondement scientifique et pouvait être largement remise en question selon les contextes (Possingham et al. 2015). Contre toute attente, du point de vue de la conservation de la biodiversité, les bénéfices des opérations de restauration / réhabilitation d'habitats dégradés sont même dans certains cas largement supérieurs à ceux de la protection des habitats encore intacts (Maire et al. 2015, Possingham et al. 2015). Il n'est donc pas possible d'adopter une position systématique vis-à-vis du choix entre protection et restauration / réhabilitation des habitats ce qui a conduit les directives de gestion à prôner l'utilisation des deux outils (Lammerant et al. 2013). Les deux types d'actions doivent donc être perçus comme des outils complémentaires dont le choix dépend des coûts réels respectifs des opérations, des bénéfices attendus et du temps nécessaire pour les atteindre (Possingham et al. 2015). Ces éléments doivent être évalués systématiquement pour chaque opération (Bayraktarov et al. 2016). Encore faut-il être en mesure de le faire correctement.

Même si les capacités de migration des juvéniles des ports vers les habitats adultes et leur participation au renouvellement des générations demandent encore quelques investigations, rien ne s'oppose à l'issue de cette thèse à ce que les ports puissent servir de nourriceries alternatives pour certaines espèces de poissons marins côtiers (figure VI.2). Les projets d'ingénierie écologique dans les ports peuvent encore être reçus avec méfiance par la communauté scientifique car perçus comme des mesures compensatoires, sortes de droits à dégrader ou à détruire des écosystèmes marins déjà fragilisé. Or, bien utilisés, ces projets pourraient être bénéfiques à la conservation des stocks et contribuer au maintien de la biodiversité des poissons marins côtiers. Ils méritent donc d'être encouragés au même titre que les actions de protection et accompagnés pour être les plus efficaces possibles d'un point de vue écologique et économique.



1 – **Chapitre 3 :** la construction d'un port ne limite que peu les flux larvaires, même si ces derniers ne sont probablement pas équivalents entre les ports.

2 – **Chapitre 3 :** l'installation benthique est possible dans la majorité des ports. L'augmentation de la complexité structurale de l'habitat engendre une augmentation de l'abondance des juvéniles, notamment aux stades précoces.

3 – **Chapitres 4 & 5 :** les niveaux de contamination dans les ports sont supérieurs à ceux observés dans les nourriceries naturelles.

4 – **Chapitre 4 :** les effets négatifs des contaminants sur la croissance et la condition sont contrebalancés par les effets positifs directs et indirects de la forte production primaire en zone portuaire. Les niveaux de contamination des juvéniles sont au final faibles.

5 – **Chapitre 5 :** la contribution des juvéniles issus des ports aux stocks adultes n'a pas été étudiée à ce stade. Cette étude peut se faire par l'analyse de la composition chimique des otolithes. Il ne semble pas exister une signature élémentaire unique caractéristique des ports quelle que soit l'espèce ou l'année considérée. La signature de l'ensemble des habitats juvéniles devra donc être caractérisée.

Figure VI.2 : Schéma récapitulatif des résultats obtenus au cours de cette thèse. ✓= validé, + = effet positif, - = effet négatif, ? = reste à évaluer. Les images proviennent du site http://www.ian.umces.edu.

VI.2 Perspectives

Bien que ce travail de thèse ait permis de vérifier plusieurs hypothèses quant au rôle potentiel des ports comme nourricerie alternative pour les poissons marins côtiers, plusieurs questions subsistent et les pistes de recherche futures sont nombreuses. Nous avons choisi d'en détailler trois qui concernent l'évaluation de l'efficacité des projets d'ingénierie écologique en zone portuaire, l'étude des processus de transferts des contaminants du milieu vers les juvéniles de poissons et l'évaluation des effets de la vie juvénile en zone portuaire sur la dynamique des populations de poissons.

VI.2.1. Comment évaluer l'efficacité des projets d'ingénierie écologique en zone portuaire ?

Pour juger de l'efficacité des projets d'ingénierie écologique en zone portuaire, il est indispensable de comparer les abondances observées sur les micro-structures artificielles ajoutées à la fois à celles de zones témoin dans les ports (ouvrages nus), comme cela a été fait dans le **chapitre 3** ou dans d'autres études (Mercader et al. 2017), mais également à une référence, définie comme l'objectif final vers lequel on souhaite tendre (Aronson et al. 1993a, Aronson et al. 1993b, Le Floc'h & Aronson 1995). Dans le cas qui nous concerne, cette référence doit être une nourricerie naturelle (Lenfant et al. 2015). Cependant, ceci pose d'importants problèmes méthodologiques. En effet, quel que soit le milieu étudié, l'estimation des abondances de juvéniles de poissons nécessite un protocole standardisé dont le choix dépend de la diversité des micro-habitats rencontrés (Minello 1999, Franco et al. 2012). Or, dans les études portant sur les nourriceries de sars en Méditerranée, les abondances des juvéniles sont en général évaluées en plongée, soit le long de transects définis en longueur et en largeur (Harmelin-Vivien et al. 1995, Planes et al. 1999, Clynick 2006, Cheminee et al. 2011, Pastor et al. 2013, Ventura et al. 2014), soit en couvrant toute la surface de petites criques isolées dont les juvéniles ne peuvent théoriquement pas sortir (MacPherson 1998, Vigliola 1998, Vigliola & Harmelin-Vivien 2001). Ces méthodes sont peu adaptées aux structures verticales (quais et pontons) qui représentent la majorité des micro-habitats portuaires. Dans le **chapitre 3**, un protocole faisant appel à des comptages par points stationnaires a été proposé (Clynick 2008). Bien qu'adapté aux suivis dans les ports, ce protocole ne permet pas de comparer les abondances des juvéniles de poissons entre une nourricerie naturelle et une structure portuaire. En effet, cette comparaison pose un problème méthodologique majeur lié à l'hétérogénéité de la répartition des individus dans les habitats juvéniles (Harmelin-Vivien et al. 1995, Cheminee et al. 2011). La profondeur est un critère déterminant dans la sélection de l'habitat lors de l'installation des jeunes poissons (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995, Srinivasan 2003). L'inclinaison de la pente de l'habitat juvénile influe donc sur sa surface fonctionnelle. Or, celle-ci est fortement réduite sur les ouvrages portuaires (forte pente ou tombants verticaux) par rapport aux nourriceries naturelles (pente douce) (Bulleri & Chapman 2010). En cas de comparaison directe, sans tenir compte de la surface fonctionnelle, c'est-à-dire celle réellement utilisable par jeunes poissons, il y a un risque évident de surestimation des abondances sur les structures portuaires à forte pente par rapport aux nourriceries naturelles à faible pente. La mise en place d'un protocole adapté, tenant compte de la surface fonctionnelle pour les juvéniles de poissons dans chacun des deux systèmes, devrait permettre de faire une comparaison plus fiable et ainsi de mieux appréhender l'efficacité des projets d'ingénierie écologiques en zones portuaires actuels.

Cependant, même si cette comparaison d'abondances est un préalable à l'évaluation globale de l'efficacité écologique de projets de réhabilitation des fonctions de nourricerie en zone portuaire elle ne permet pas d'évaluer leur influence sur le recrutement et donc la contribution des ports concernés aux stocks d'adultes. En effet, comme nous l'avons vu tout au long de ce manuscrit, le recrutement reflète l'ensemble des processus ayant trait à la qualité de l'habitat juvénile et à l'environnement. En d'autres termes, seul un projet qui permettrait une augmentation de l'intensité globale du recrutement des juvéniles issus d'un port sans altérer celle des nourriceries naturelles adjacentes serait un projet efficace. Nous avons montré dans le **chapitre 5** que les signatures élémentaires des otolithes pouvaient être utilisées pour retracer l'origine des poissons. Cet outil devrait permettre d'évaluer la contribution relative des ports aux stocks d'adultes (e.g. Vasconcelos et al. 2008, Davoren et al. 2015, Tournois et al. 2017) et d'étudier, à terme, l'influence des projets d'ingénierie écologique sur ce paramètre. Or, nous n'avons pas mis en évidence l'existence d'une signature multi-élémentaire caractéristique de l'ensemble des zones portuaires. Par conséquent, afin d'évaluer la contribution des ports aux stocks d'adultes, la signature de tous les habitats juvéniles potentiels doit être évaluée. Au regard du temps nécessaire et des coûts liés à de telles analyses, il semble peu réaliste d'envisager de mener ce travail à l'échelle de la façade méditerranéenne. Par contre, il est possible de le poursuivre à une échelle plus restreinte comme celle de la rade de Toulon. Les travaux entrepris dans le **chapitre 5** pourraient ainsi être complétés de la manière suivante :

- Le prélèvement et l'analyse d'otolithes de juvéniles de sars capturés dans plusieurs ports de la petite rade et sur plusieurs sites de la grande rade, sur au moins trois années consécutives permettraient d'étudier la stabilité temporelle des signatures multi-élémentaires des deux types d'habitats,

- Ces signatures pourraient ensuite être comparées à celles de la partie juvénile d'otolithes d'adultes capturés dans la rade de Toulon et appartenant à des cohortes étant nées avant et après la mise en place de solutions d'ingénierie écologique dans les ports.

Grâce à une telle étude, il serait possible d'évaluer globalement l'efficacité écologique des solutions proposées et donc d'apporter des éléments concrets permettant aux gestionnaires et pouvoirs publics de juger de la pertinence de la réhabilitation écologique dans les ports.

VI.2.2. Comment les contaminants métalliques sont-ils transférés du milieu vers les juvéniles de sars ?

Les résultats du **chapitre 4** ont mis en évidence l'absence de lien direct entre les concentrations en éléments traces métalliques (ETM) dans le milieu et la contamination des *Diplodus* juvéniles. La bioaccumulation d'ETM chez les poissons dépend de mécanismes complexes et souvent encore mal appréhendés qui dépendent de la spéciation des contaminants dans le milieu, de la structure des réseaux trophiques des individus étudiés et des processus de régulation de ces contaminants dans les organismes. La compréhension du fonctionnement des réseaux trophiques en milieu portuaire est donc indispensable à la compréhension du transfert des contaminants du milieu vers les poissons. Ainsi seule une approche systémique reposant sur un couplage « chimie-biologie » permettrait d'étudier la relation entre de la spéciation des ETM dans le milieu marin, la composition chimique et biologique des premiers niveaux trophiques (plancton) et la bioaccumulation observées chez les juvéniles de sars dans les zones portuaires. Pour cela, il serait nécessaire dans un premier temps de caractériser les compartiments biologiques, en particulier du plancton, et de décrire le fonctionnement trophique des milieux portuaires. Dans un second temps, la distribution, les niveaux et la spéciation des ETM dans les différents compartiments biogéochimiques (sédiment, eau, phytoplancton et zooplancton) pourrait être étudiée.

L'analyse des isotopes stables du carbone et de l'azote a prouvé son efficacité pour retracer le transfert de la matière issue de différentes sources le long des réseaux trophiques (Pinnegar & Polunin 2000). Cette méthode analytique s'appuie sur les différences naturelles de signature isotopique en $\delta^{13}C$ et en $\delta^{15}N$ entre un consommateur et sa nourriture, l'excrétion préférentielle de l'isotope léger conduisant à un fractionnement isotopique systématique entre une proie et son consommateur. La signature isotopique en carbone varie fortement entre les producteurs primaires et fournit des informations sur l'origine de la matière organique ingérée par les organismes, avec en moyenne un coefficient de fractionnement pour la signature en $\delta^{13}C$ d'environ 1 ‰ entre chaque niveau trophique (DeNiro & Epstein 1978, Sweeting et al. 2007b). La signature isotopique de l'azote peut quant à elle être utilisée pour définir le niveau trophique des organismes avec des valeurs en $\delta^{15}N$ qui augmentent généralement de 3.4 ‰ entre une proie et son consommateur (Post 2002, Sweeting et al. 2007a). Ainsi, la combinaison de ces deux rapports isotopiques permet de reconstituer les relations trophiques au sein d'un écosystème et d'évaluer l'incorporation et le transfert des différentes sources de matière organique le long de ce réseau. Ces paramètres biologiques correspondent à des « paramètres accompagnateurs » nécessaires à une bonne interprétation des données chimiques dans les organismes vivants (e.g. Cresson et al. 2014, Cresson et al. 2015b, Cresson et al. 2016). D'autres traceurs indirects des dépendances trophiques entre les organismes, comme les profils lipidiques et les contenus stomacaux, peuvent être utilisés. La comparaison des mécanismes impliqués dans le devenir des contaminants au sein des réseaux trophiques entre les nourriceries naturelles et les zones portuaires devrait permettre de mieux comprendre les schémas de contamination des juvéniles de poissons en zone portuaire et donc d'orienter les politiques de gestion des ports.

VI.2.3. Comment mieux évaluer les effets de la vie juvénile en zone portuaire sur la dynamique des populations de poissons ?

De nombreux travaux scientifiques se sont donné pour objectif de développer des indicateurs de la qualité des habitats juvéniles des poissons à partir de bioindicateurs mesurés à différents échelons biologiques, allant de la cellule à la communauté (e.g. Adams 2002, Gilliers et al. 2006, Kerambrun et al. 2012b). Le choix des indicateurs est généralement la partie la plus délicate et la plus importante de ces études car il en oriente souvent les conclusions (Suthers 1998, Adams 2002). Dans cette thèse, la qualité des nourriceries a été évaluée sur la base d'indicateurs mesurés aux niveaux de l'individu (croissance et condition) et de la population (abondance). Or, il existe une différence de sensibilité des réponses, notamment toxiques, avec les niveaux d'organisation biologique croissants (Adams et al. 1989). Selon l'étude de référence d'Adams et al. (1989), les paramètres moléculaires ou biochimiques (biomarqueurs) sont plus spécifiques et plus sensibles à la contamination chimique que des paramètres mesurés au niveau individuel ou populationnels. En revanche, ces derniers apportent davantage d'informations sur l'état de santé des organismes et sont donc plus pertinents sur le plan écologique. Ainsi, dans l'état actuel des connaissances, les biomarqueurs renseignent essentiellement sur l'exposition des organismes à des contaminants alors que les indicateurs individuels et populationnels informent plutôt sur l'évaluation d'un risque réel pour les populations

(Lagadic & Caquet 1997). Même si la question de la signification écotoxicologique des réponses biologiques reste un champ de recherche très ouvert, les chercheurs qui travaillent sur l'utilisation d'indicateurs biologiques s'accordent à dire qu'il est nécessaire d'utiliser une approche multi-échelle pour obtenir un diagnostic abouti sur l'état de santé des organismes et de l'environnement dans lequel ils évoluent (Suthers 1998, Able et al. 1999, Adams 2002).

Une des perspectives de ce travail de thèse pourra donc être d'utiliser une approche multi-indicateurs, en utilisant en complément des biomarqueurs à l'échelle de la cellule, du tissu ou de l'organe, afin de mieux évaluer les effets biologiques de la contamination en milieu portuaire sur les juvéniles de poissons. Parmi les biomarqueurs d'exposition aux contaminants métalliques, les concentrations en métallothionéines sont souvent utilisées. Ces protéines jouent en effet un rôle primordial dans les processus homéostasiques des métaux essentiels comme le Zn et le Cu dans la détoxification des métaux non-essentiels comme le Cd et le Hg (Roesijadi 1992, Viarengo & Nott 1993). Néanmoins, de nombreux facteurs biotiques et abiotiques influencent leur synthèse chez les organismes aquatiques, ce qui peut perturber l'interprétation des résultats (Amiard et al. 2006). D'autres biomarqueurs au niveau subcellulaire, comme par exemple la mesure de l'activité de l'éthoxyresorufin-O-dééthylase (EROD) (Goksøyr & Förlin 1992, Whyte et al. 2000) ou celles des enzymes de la famille des Glutathion-S-Transférase (Kim et al. 2010) ont montré leur efficacité à détecter de façon précoce l'exposition de juvéniles de poissons à des contaminants chimique, en particulier aux HAP (Kerambrun et al. 2012b, Kerambrun et al. 2012c). Le couplage d'une approche multi-biomarqueurs à l'étude d'indicateurs aux niveaux individuel et populationnel devrait permettre de mieux appréhender l'état de santé des individus issus des ports ainsi que les conséquences de cette vie juvénile sur leur survie et leur reproduction futures et donc sur le maintien des populations dans le temps.

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Résumé - Au cours de leur cycle de vie, la plupart des espèces de poissons marins côtiers passent par des nourriceries littorales dont la qualité influence largement le succès du recrutement et donc le maintien de l'abondance de leurs populations. Or, la construction de ports entraine irrémédiablement une perte de fonction pour les habitats côtiers impactés. Dans ce contexte, l'objectif général de cette thèse était de voir si les zones portuaires peuvent malgré tout servir de nourriceries alternatives pour les poissons marins côtiers. Pour cela, les abondances des juvéniles de quatre espèces de sars, du genre *Diplodus*, ont d'abord été suivies dans cinq ports méditerranéens. Ceci a permis de montrer que ces espèces côtières peuvent s'installer et grandir avec succès dans les ports. La complexification de la structure 3D de l'habitat augmente sensiblement les abondances de juvéniles. Dans un second temps, la croissance, la condition et les niveaux de contamination des juvéniles de deux espèces de sars (*D. sargus* et *D. vulgaris*) ont été comparés entre différents ports et habitats naturels de la rade de Toulon. Ceci a montré que la croissance et la condition des juvéniles peut être équivalente dans certains ports et dans les zones naturelles adjacentes, avec des niveaux de contamination faibles, même dans les zones les plus polluées. Enfin, la composition multi-élémentaire des otolithes des juvéniles de *D. sargus* et *D. vulgaris* a été comparée entre trois ports et deux zones naturelles de la rade de Toulon. Aucun élément chimique lié aux activités portuaires n'a été retrouvé en plus forte concentration dans les otolithes des juvéniles issus des ports. Il n'existe donc pas une signature unique caractéristique de l'ensemble des ports. La composition chimique des otolithes peut néanmoins être utilisée pour étudier la contribution relative des ports aux stocks d'adultes à condition de caractériser la signature de l'ensemble des habitats juvéniles potentiels. L'ensemble des résultats acquis indiquent que les ports peuvent être utilisés comme nourriceries alternatives par plusieurs espèces de poissons marins côtiers. Les projets d'ingénierie écologique visant à augmenter la complexité structurale des habitats portuaires sont des pistes intéressantes pour maintenir la biodiversité côtières et les stocks de poissons.

Mots clés : Zone côtière, nourricerie, habitats artificiels, restauration écologique, poissons

Abstract - During their life cycle, most of the marine coastal fish species use nursery grounds which quality influence their recruitment and then the conservation of their populations. However, the construction of ports impair irremediably fish nursery function of the coastal areas impacted. The ultimate aim of the PhD research was to assess if ports could provide suitable alternative nursery habitats for coastal fish species. Firstly, abundances of the juveniles of four *Diplodus* species were surveyed in five marinas located along the French Mediterranean coast. This showed that coastal fishes can successfully settle and grow inside these artificialized coastal areas. Moreover, increasing the complexity of port habitats can considerably enhance their suitability for juveniles, especially at the youngest stages. Secondly, body condition, growth rate and metal contamination in the juveniles of two *Diplodus* species (*D. sargus* and *D. vulgaris*) were compared between different ports and natural areas in the Bay of Toulon. Juvenile growth and condition can be equivalent between fish collected from ports and from adjacent natural areas. Contamination levels in fish were low, even in highly polluted areas. Finally, otolith composition in the juveniles of *D. sargus* and *D. vulgaris* was investigated in three ports and two natural areas in the Bay of Toulon. None of the port related had systematically higher concentrations in otoliths from *Diplodus* juveniles collected in ports. Therefore, otolith microchemistry cannot provide a unique and reliable fingerprint discriminating ports and natural areas. Nevertheless, otolith microchemistry could provide an effective natural tag to determine the contribution of ports to adult stocks provided that a library of all potential juvenile habitat fingerprints is established. All these results confirm that ports can be used as alternative nursery habitats by marine coastal fishes. Ecological engineering projects aiming at increasing structural complexity of port habitats seem promising for biodiversity and fish stock conservation.

Keywords: Coastal area, nursery, artificial habitats, ecological restoration, fish

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