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Impacts des marées vertes sur les habitats essentiels au renouvellement des ressources halieutiques des secteurs estuariens et côtiers

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Soutenue le 5 juillet 2016 devant la commission d'Examen

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Table des matières

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Résumé

Les écosystèmes côtiers et estuariens sont extrêmement riches d'un point de vue biologique et écologique et abritent des habitats essentiels au maintien et au renouvellement des ressources marines d'intérêt halieutique. Parmi les altérations subies par ces écosystèmes, les proliférations de macroalgues opportunistes sont l'un des signes les plus visibles de l'eutrophisation des secteurs côtiers et estuariens dans plusieurs régions du monde, et particulièrement dans le nord-ouest de la France. Les processus à l'origine de ces proliférations sont relativement bien identifiés tandis que leurs conséquences écologiques - notamment sur l'ichtyofaune - restent mal connues et peu étudiées. L'objectif de cette thèse est de caractériser les effets des marées vertes sur la fonction d'habitat halieutique essentiel au renouvellement de l'ichtyofaune des zones côtières et estuariennes par une approche multi-échelle.

Dans une première partie, les conséquences des marées vertes sur l'ichtyofaune ont été examinées à l'échelle de la communauté. Pour cette approche, un suivi de type BACI (Before-After Control-Impact) a été réalisé dans les deux types de systèmes intertidaux affectés par les marées vertes, les estrans sableux et les vasières estuariennes. Au sein de chacun de ces systèmes, nos résultats mettent en avant la similarité des communautés ichtyologiques entre le site contrôle et le site impacté avant les marées vertes, puis des divergences à partir du développement des macroalgues. Les réponses des communautés ichtyologiques face à ces proliférations sont modulées en fonction de la composition, de la densité et de la durée des blooms d'algues vertes. A de faibles densités et/ou pendant une courte période, les marées vertes n'affectent pas les communautés ichtyologiques. En revanche, à des densités importantes et/ou pendant une longue période, ces proliférations entrainent une diminution de la diversité et de la densité de l'ichtyofaune. La composition de la communauté s'en trouve affectée, avec un impact initial sur les poissons benthiques qui s'étend ensuite à l'ensemble de l'ichtyofaune jusqu'à la disparition locale de poissons pour des proliférations algales fortes.

Dans une seconde partie, les processus par lesquels cette perturbation affecte l'ichtyofaune ont été examinés par une approche à l'échelle de l'individu. Dans une nourricerie côtière de type estran sableux, cette étude s'est intéressée aux réponses des juvéniles à travers la sélection de l'habitat et la comparaison des performances physiologiques des individus dans un site contrôle et un site impacté. Les réponses de juvéniles de trois espèces de poisson appartenant à des guildes de distribution verticale différentes ont été considérées : le sprat (pélagique), le bar (démersal) et la plie (benthique). La perturbation de l'habitat entraine une augmentation instantanée de la capacité de défense antioxidante des individus, puis des réponses physiologiques sont mises en œuvre. Ces

réponses se traduisent par une réduction de la croissance et des réserves lipidiques des juvéniles. Si la perturbation s'intensifie, l'espèce finit par disparaitre localement du site affecté. En fonction des guildes, ces réponses sont mises en œuvre à partir d'intensités différentes de la perturbation, soulignant un gradient de sensibilité des espèces aux marées vertes, des espèces benthiques aux espèces démersales et pélagiques.

Au travers de ces deux approches, un impact des marées vertes sur la qualité des habitats essentiels au renouvellement des ressources d'intérêt halieutique a donc été mis en évidence, avec des conséquences modulées en fonction des caractéristiques des guildes fonctionnelles ainsi que de l'intensité et de la nature des blooms de macroalgues.

Abstract

Coastal and estuarine systems are highly productive areas that provide unique biological and ecological services and shelter essential habitats to numerous fisheries resources. Among the perturbations experienced by these ecosystems, proliferations of opportunistic macroalgae, commonly known as ‘green tides’, are one of the most obvious signs of eutrophication in coastal and estuarine areas, worldwide, and in Northwestern France in particular. The processes underlying macroalgal proliferations are almost identified whereas their ecological consequences - especially for ichthyofauna - remain poorly understood and understudied. The objective of this thesis is to characterise the effects of green tides on the role of coastal and estuarine habitats for ichthyofauna, on both the community and the individual scales.

In a first section, we investigated the consequences of green tides on the ichthyofauna on the community scale. For this study, we implemented a BACI (Before-After Control-Impact) approach in the two types of intertidal systems, which experience green tides, *i.e.* coastal sandy beaches and estuarine mudflats. Within each system, our results reveal that fish communities are similar across control and impacted sites before the macroalgal bloom, and then diverge from the onset of macroalgae development onwards. Responses of fish communities to green tides vary according to the macroalgal species composition, density and duration of the bloom. When intertidal systems experience short proliferations and/or weak densities, green tides do not seem to impact the fish community. However, when green macroalgae develop in large quantities and/or when the proliferation lasts for long periods, green tides lead to a significant decrease in fish species diversity and density. In this case, benthic fish species are the most impacted at first, and then consequences extend to the entire ichthyofauna. High proliferations can even lead to local disappearance of fish.

In a second part, we examined the processes which affect the ichthyofauna during green tides, on the individual scale. In a coastal sandy beach nursery, we investigated marine juvenile fish responses based on habitat selection and comparison of individual performances between a control and an impacted site. Responses of three marine juvenile fish species with different vertical distribution were considered: sprat (pelagic), sea bass (demersal) and plaice (benthic). Individual antioxidant defence capacity increases instantaneously with the species perception of habitat perturbation by green tides. Then, physiological responses induce a decrease in growth and lipid storage. If the perturbation increases, juveniles locally disappear from the impacted site, as depending on the species, individuals either migrate or die locally. According to the species, these responses are

initiated at different intensities of the perturbation, which emphasises a decreasing gradient of sensibility to green tides, from benthic to demersal and pelagic species.

Based on these two complementary approaches, we evidence the effects of green tides on the quality of essential fish habitats. They are modulated by the intensity and nature of macroalgal blooms, and they are also related to the fish species habitat use and ecology.

Introduction générale

1. Introduction générale

1.1 Intérêts des zones côtières et estuariennes

1.1.1 Des interfaces soutenant une forte productivité

Situés à l'interface entre milieux terrestres et océaniques, les écosystèmes côtiers et estuariens sont des zones de transferts dynamiques jouant un rôle fondamental d'un point de vue biologique et écologique. Ces écotones (*i.e.* zone de transition entre deux écosystèmes) sont caractérisés par la forte variabilité de leurs conditions abiotiques le long de gradients géographiques et temporels (*i.e.* salinité, température, pH et oxygène dissous; Allen et al., 2006) ainsi que par des apports importants de nutriments et de matière organique d'origine terrigène soutenant une forte production primaire et secondaire (Largier, 1993). Ces milieux très riches et hétérogènes créent des conditions et des habitats uniques assurant de nombreuses fonctions écosystémiques (Largier, 1993; Costanza et al., 1997; Schlacher et al., 2008). Par l'association de ces conditions particulières, ces milieux peu étendus par rapport à l'océan jouent un rôle primordial dans le maintien et le renouvellement de nombreuses ressources marines (Holbrook et al., 2000; Sluka et al., 2001; Stoner, 2003).

A l'échelle de l'ichtyofaune, ces milieux remplissent diverses fonctions d'habitats essentiels : fonction de nourricerie, majoritaire, mais aussi lieu de résidence, de frayère et voie de migration (Seitz et al., 2014). Ainsi, en tenant compte de l'ensemble de ces fonctions halieutiques, 44% des espèces d'intérêt halieutique faisant l'objet d'une évaluation au niveau européen présentent une dépendance côtière et/ou estuarienne à un moment de leur cycle de vie, et ces espèces représentent 77% du tonnage des débarquements (Seitz et al., 2014).

1.1.2 Des écosystèmes abritant des habitats halieutiques essentiels

La fonction de nourricerie remplie par les habitats côtiers et estuariens est primordiale pour le renouvellement d'une proportion conséquente des ressources halieutiques marines. Ces ressources, dont le succès de la phase juvénile dépend des habitats de nourriceries, regroupent un ensemble d'espèces benthiques (Krygier and Pearcy, 1986; Gibson, 1994; Yamashita et al., 2001), démersales (Claridge and Potter, 1983) et pélagiques (Munk, 1993). Bien qu'il existe des disparités entre ces espèces dites nourricerie-dépendantes (*i.e.* dans leur cycle de vie et sa saisonnalité, la durée des différentes phases, les habitats préférentiels et la distribution des cohortes), leur cycle de vie est similaire dans sa forme (Fig 1.1).

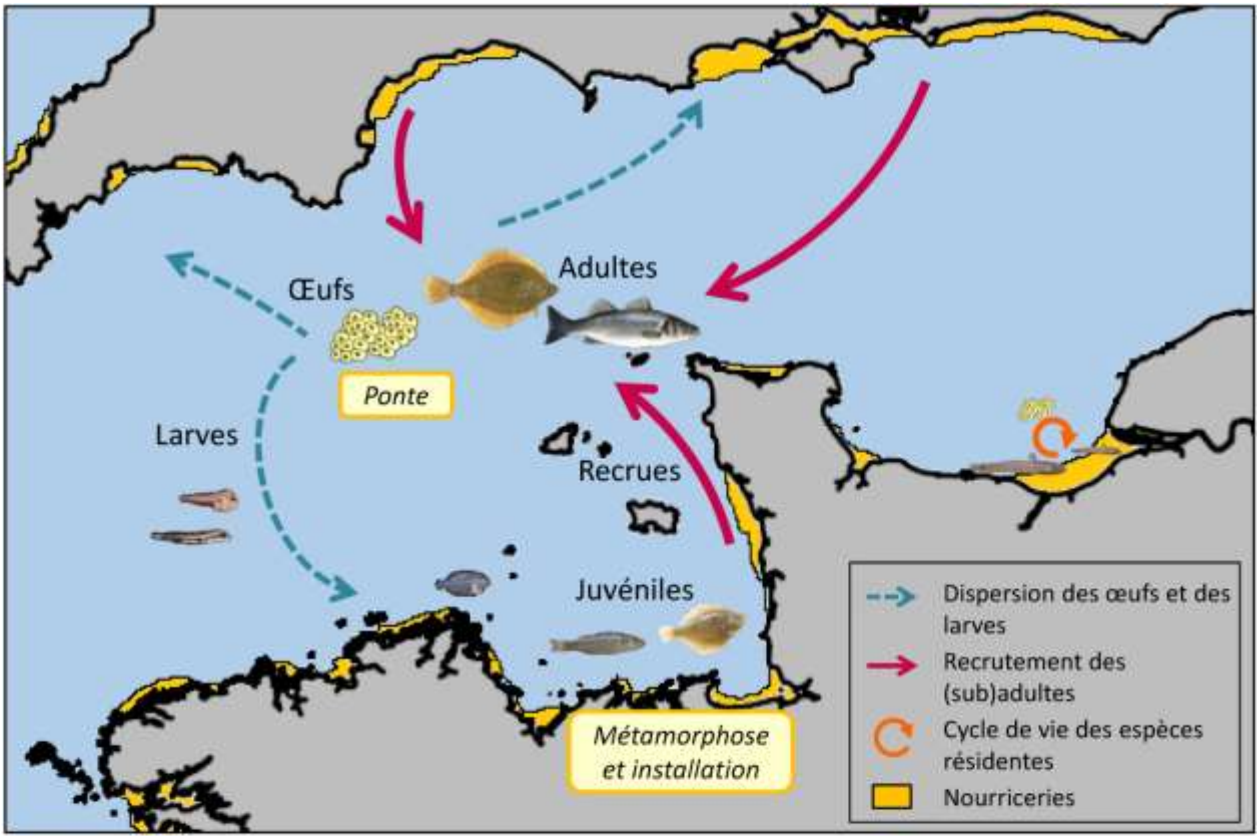

Figure 1.1 - Représentation schématique des cycles de vie d'espèces de poissons téléostéens nourricerie-dépendantes et résidentes

Les œufs pélagiques, issus de la reproduction des individus sexuellement mâtures dans les zones de frayères, sont dispersés sous l'influence de la circulation hydrodynamique (Cushing, 1995). Après l'éclosion, les larves planctoniques subissent une dérive passive dans un premier temps (van der Veer et al., 2000) puis migrent de manière active dans les derniers stades de leur développement (Rijnsdorp et al., 1985; Leis and Carson-Ewart, 2003). Les larves pélagiques ayant atteint les zones côtières et estuariennes s'établissent dans ces habitats et leur métamorphose marque le passage au stade juvénile. Suivant les espèces, et en fonction de leur durée de vie, cette phase juvénile se prolonge de quelques mois à quelques années (Beck et al., 2001; Able, 2005).

Les nourriceries côtières et estuariennes sont des habitats spécifiques aux superficies restreintes qui offrent des conditions favorables à la survie et à la croissance des juvéniles, notamment des températures estivales plus élevées que dans les eaux du large, de fortes disponibilités alimentaires et une protection accrue contre les prédateurs (Gibson, 1994; Le Pape and Bonhommeau, 2015). Les juvéniles de nombreuses espèces dépendent de ces secteurs de nourricerie et profitent de leur conditions particulières en terme d'habitat et de productivité pour se développer, puis rejoignent le stock adulte plus au large à leur maturité sexuelle (*i.e*. phase de recrutement).

Le renouvellement des ressources marines résulte donc non seulement de l'importance de la biomasse féconde du stock et de la survie des stades précoces (œufs et larves pélagiques) mais aussi de la capacité des nourriceries à produire des juvéniles (van der Veer et al., 2000; Holbrook et al., 2000; Sluka et al., 2001; Stoner, 2003). Ainsi, une diminution de la superficie et/ou de la qualité de ces habitats côtiers et estuariens peut affecter la croissance et la condition des juvéniles jusqu'à accroître la mortalité de ces jeunes stades et, par conséquent, réduire le succès de recrutement et la taille des populations (Turner and Boesch, 1987; Gibson, 1994; Piet and Rijnsdorp, 1998; Able, 1999; Peterson et al., 2000; Jones et al., 2002). La dégradation des nourriceries, habitats halieutiques essentiels peu répandus et d'équilibre fragile, est, avec la pêche, l'une des principales causes de diminution des espèces du plateau continental et du potentiel d'exploitation halieutique qu'elles représentent.

1.2 Les marées vertes : une conséquence des perturbations anthropiques de ces écosystèmes

1.2.1 Le phénomène de marées vertes

Depuis plusieurs décennies, les systèmes estuariens et côtiers sont fortement impactés par diverses pressions et activités anthropiques (Lotze et al., 2006; Halpern et al., 2008). L'eutrophisation littorale est l'une des conséquences de cette anthropisation. L'augmentation de l'occurrence, de la durée et de l'abondance de blooms de macroalgues opportunistes dans plusieurs régions du monde est l'un des signes les plus visibles de l'eutrophisation des écosystèmes estuariens et côtiers (Fletcher, 1996; Valiela et al., 1997; Raffaelli et al., 1998; Ye et al., 2011; Smetacek and Zingone, 2013; Zhou et al., 2015). Au cours des dernières décennies, l'augmentation de cette perturbation anthropique a accru l'intérêt scientifique accordé à la caractérisation, la compréhension et la prévision de ces phénomènes de marées vertes (Teichberg et al., 2010; Perrot et al., 2014).

Les proliférations de macroalgues vertes sont des phénomènes naturels régulés par des facteurs limitants (*i.e.* lumière, température et sels nutritifs, principalement la concentration en azote) (Fig 1.2). Des apports excessifs de sels nutritifs issus des bassins versants (Merceron et al., 2007) et liés aux activités anthropiques parfois d'origine urbaine (effluents de stations d'épuration), mais le plus souvent d'origine agricole (lessivage de terres cultivées excessivement enrichies en engrais organiques ou minéraux), tendent à augmenter artificiellement la production de macroalgues vertes pendant des périodes où l'activité est normalement régulée par une faible concentration en nutriments (Fig 1.2; Fletcher, 1996; Merceron et al., 2007).

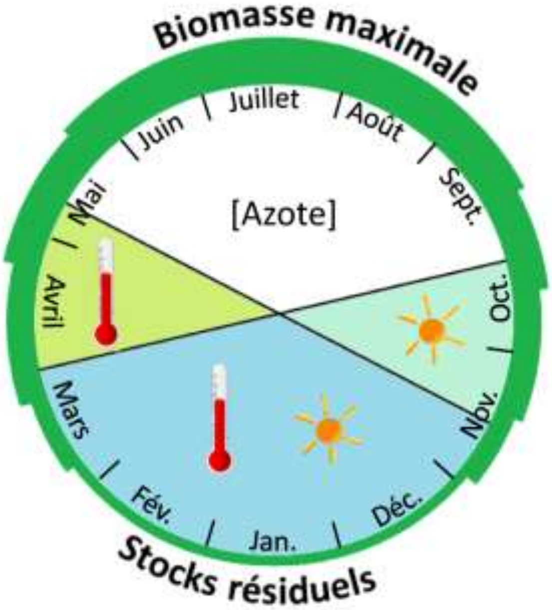

Figure 1.2 - Facteurs saisonniers limitant la prolifération des macroalgues vertes (adaptée d'après CEVA, 1998)

L'enrichissement de secteurs propices à la prolifération de macroalgues vertes tels que des zones intertidales confinées à faible pente (conditions de lumière et de température favorables à la croissance des macroalgues) avec une circulation hydrodynamique faible (permettant la rétention des sels nutritifs et/ou des macroalgues produites; Valiela et al., 1997; Raffaelli et al., 1998; Perrot et al., 2014) participe à l'augmentation du phénomène de marée verte.
La combinaison de ces facteurs nutritifs et environnementaux conduit à un développement excessif de macroalgues en zones intertidales.

Ces blooms de macroalgues vertes sont généralement dominés par des espèces opportunistes caractérisées par une forte capacité adaptative et nutritionnelle, notamment les espèces des genres *Chaetomorpha*, *Cladophora* et *Ulva* (Fletcher, 1996; Merceron et al., 2007). Ces macroalgues s'accumulent tout d'abord sur le fond et dans les premiers décimètres de la colonne d'eau puis colonisent progressivement l'ensemble de l'espace disponible au gré de l'intensification de leur prolifération (Solidoro et al., 1997).

1.2.2 Les marées vertes : des perturbations multiples de l'habitat

Le développement excessif de macroalgues vertes entraine des changements multiples au sein des écosystèmes côtiers et estuariens (Hull, 1987; Fletcher, 1996; Raffaelli et al., 1998; Raffaelli, 2000). En fonction de leur nature, ces principaux changements peuvent se regrouper en trois types de perturbations survenant de façon simultanée :

(i) Un premier type regroupe les perturbations physiques. Les macroalgues vertes prolifèrent principalement dans des habitats nus, de type vasières et estrans sableux, ce qui modifie leur complexité et leur structure (Isaksson and Pihl, 1992; Isaksson et al., 1994). Cette complexification peut s'accompagner d'une réduction de la vitesse du courant et d'une augmentation du taux de sédimentation des particules les plus fines (Hull, 1987; Fletcher, 1996), entrainant la modification de la typologie du substrat.

(ii) Le second type est relatif aux perturbations chimiques. Une partie d'entre elles est engendrée par un changement de la concentration et des amplitudes journalières en oxygène dissous résultant de l'activité photosynthétique des macroalgues. Lors de développements massifs de macroalgues, des sursaturations en oxygène sont observées pendant la phase lumineuse et des déplétions surviennent pendant la phase obscure (Johnson and Welsh, 1985). Par ailleurs, les macroalgues, fraîches et sénescentes, ainsi que leur flore bactérienne émettent diverses substances toxiques leur conférant des propriétés allélopathiques et anti-fouling (Magre, 1974; Johnson and Welsh, 1985; Nelson et al., 2003; Harder et al., 2004; Wang et al., 2011). Enfin, la décomposition des macroalgues entraine la libération d'une partie des nutriments captés (Fletcher, 1996), mais aussi de quantités importantes de sulfure d'hydrogène lorsque les macroalgues sont décomposées en conditions anaérobiques (Gamenick et al., 1996; Wetzel et al., 2002). Ces différents changements des conditions chimiques de la masse d'eau peuvent engendrer des perturbations des cycles biogéochimiques (Sfriso et al., 1992; Engström-Öst and Isaksson, 2006).

(iii) Le troisième type de perturbation résulte des modifications physiques et chimiques des conditions de l'habitat et comprend les perturbations des équilibres trophiques des écosystèmes (Hull, 1987; Andersen et al., 2005; Arroyo et al., 2012; Quillien et al., 2015, 2016).

1.2.3 Les effets des marées vertes sur les communautés

Les proliférations de macroalgues vertes en lien avec l'eutrophisation du milieu font partie des dégradations subies par les habitats côtiers et estuariens pouvant affecter les communautés, et notamment l'ichtyofaune. Les modifications physiques, chimiques et trophiques de l'habitat et leurs interactions perturbent la qualité et la capacité d'accueil de ces secteurs. Une méta-analyse des conséquences écologiques des proliférations macroalgales a permis de mettre en évidence la variabilité de leur effets en fonction de la composition, de l'intensité et de la durée des blooms (Lyons et al., 2014).

De plus, les réponses de la macrofaune apparaissent être fonction des stades de développement des espèces devant faire face aux marées vertes (Pihl and van der Veer, 1992; Wennhage and Pihl, 1994).

A de faibles densités et pour des périodes réduites, l'augmentation de la complexité de l'habitat peut faciliter le recrutement à l'échelle locale (Norkko and Bonsdorff, 1996a, 1996b; Raffaelli et al., 1998; Cardoso et al., 2004). Le bénéfice peut alors venir de l'amélioration de la capacité de refuge et de manière consécutive du taux de survie de certaines espèces (Wilson et al., 1990) notamment de la macrofaune benthique (Orr et al., 2014).

Cependant, en présence de fortes biomasses macroalgales et/ou pendant de longues périodes de proliférations, un effet négatif des mattes de macroalgues sur les communautés de la macrofaune a été démontré (Soulsby et al., 1982; Hull, 1987; Everett, 1994; Norkko and Bonsdorff, 1996a, 1996b; Norkko et al., 2000; Cardoso et al., 2004). Ces perturbations se caractérisent notamment par la modification de l'abondance et de la composition des communautés de la macrofaune benthique (Hull, 1987; Pihl et al., 2005; Andersen et al., 2005; Arroyo et al., 2012; Quillien et al., 2015, 2016). Des densités importantes de macroalgues peuvent perturber l'installation des larves, notamment d'invertébrés benthiques, en agissant comme un filtre à leur établissement sur le sédiment (Ólafsson, 1988; Bonsdorff, 1992; Bolam et al., 2000). Le déficit en oxygène (Petersen and Pihl, 1995) et la combinaison de différents types de perturbations chimiques induites par les marées vertes (*e.g.* libération de substances allélopathiques par les macroalgues et leur communauté bactérienne et de sulfure d'hydrogène lors de leur décomposition anaérobique) (Johnson and Welsh, 1985; Pihl et al., 2005; Engström-Öst and Isaksson, 2006) s'ajoutent à la complexification de l'habitat et peuvent affecter la croissance et la survie des organismes.

Ces perturbations des conditions de l'habitat peuvent avoir une incidence variable sur les organismes en lien avec leur capacité à s'échapper ou à tolérer des perturbations environnementales (Sagasti et al., 2001; MacKenzie, 2005; Wennhage and Pihl, 2007; Riedel et al., 2012).

Si un nombre conséquent de publications analyse les conséquences de blooms de macroalgues sur les invertébrés benthiques, peu d'articles s'intéressent à leurs impacts sur l'ichtyofaune (*cf.* leur faible nombre référencé dans la review de Lyons et al., 2014). Or, cette question se pose d'autant plus que les marées vertes prolifèrent du printemps à la fin de l'été en secteur tempéré (Merceron et al., 2007; Perrot et al., 2014), ce qui correspond à l'arrivée des larves et à l'établissement des juvéniles de nombreuses espèces de poissons dans les zones côtières et estuariennes (Amara, 2003; Gibson, 1994). Les effets de ces proliférations, bénéfiques ou préjudiciables, peuvent avoir des conséquences locales (Hansson and Rudstam, 1990; Jokinen et al., 2015, 2016) mais aussi à plus large échelle, en pleine mer, où la fraction adulte des populations d'espèces nourricerie-dépendantes vit et maintient les stocks de ressources halieutiques (Seitz et al., 2014). L'augmentation des phénomènes de marées vertes à l'échelle mondiale (Ye et al., 2011; Smetacek and Zingone, 2013; Zhou et al., 2015) nécessite d'accorder de l'attention à cette perturbation anthropique et à ses conséquences sur l'ichtyofaune.

1.3 Objectifs de la thèse

L'objectif général de ce travail de thèse est de caractériser les effets des marées vertes sur les habitats essentiels au maintien et au renouvellement de l'ichtyofaune des zones côtières et estuariennes.

Pour répondre à cet objectif, des approches complémentaires ont été mises en œuvre pour suivre l'intégration du stress lié à cette perturbation anthropique et ses conséquences le long de l'échelle biologique. Ces analyses ont été mises en œuvre en se focalisant sur des secteurs intertidaux du nord-ouest de la France fortement affecté par ces proliférations macroalgales.

1.3.1 Cas d'étude : les habitats côtiers et estuariens affectés par les marées vertes dans le nord-ouest de la France

Dans le nord-ouest de la France, de nombreux habitats côtiers et estuariens sont affectés par des proliférations multi-spécifiques de macroalgues vertes opportunistes (Menesguen, 2003; Charlier et al., 2007). En fonction des morphotypes des macroalgues vertes dominant la prolifération, deux types de marées vertes peuvent être distingués : (i) à macroalgues sous forme de lame étendue flottant librement dans la colonne d'eau (*e.g.* comprenant *Ulva armoricana* et *Ulva rotundata*) et (ii) à macroalgues tubulaires et filamenteuses majoritairement accrochées au substrat (*e.g.* comprenant *Ulva compressa, Ulva ramulosa, Chaetomorpha* spp. et *Cladophora* spp.). Ces proliférations peuvent s'établir de façon distincte ou conjointe dans les deux types de systèmes affectés par les marées vertes, les estrans sableux et les vasières estuariennes.

Dans cette région, plus d'une cinquantaine de systèmes de type estrans sableux et d'une trentaine de vasières estuariennes sont impactées chaque année par ces proliférations depuis les années 70 (Merceron et al., 2007; Perrot et al., 2014). Parmi l'ensemble des secteurs touchés par ces proliférations, deux zones d'étude impactées chaque année ont été sélectionnées. Chacune correspond à l'un des types d'habitats faisant face à ces proliférations : la baie de Saint-Brieuc pour les estrans sableux et la Rance pour les vasières estuariennes.

Ces deux zones d'étude sont caractérisées par des marées semi-diurnes à marnage macrotidal (d'environ 8 m), de larges estrans confinés avec une pente faible et un faible hydrodynamisme (*i.e.*

un courant résiduel faible après la suppression de l'effet cyclique de la marée; Menesguen, 2003; Menesguen and Salomon, 1988). L'association de ces caractéristiques physiques à des apports de nutriments importants, notamment en azote (Perrot et al., 2014), favorise l'installation, le développement et le maintien de macroalgues vertes dans ces zones intertidales. D'après l'indice d'évaluation de la qualité des masses d'eau de la Directive Cadre sur l'Eau (DCE) basé sur la prolifération d'algues vertes, les sites affectés sont en mauvais état écologique pour le fond de baie de Saint-Brieuc et en état moyen pour les sites impactés de l'estuaire de la Rance (Rossi, 2011).

1.3.2 Démarche adoptée

Ces travaux de thèse se sont articulés autour de deux échelles d'organisation biologique - la communauté et l'individu - afin d'appréhender et de caractériser les réponses de l'ichtyofaune intertidale face aux marées vertes dans les zones côtières et estuariennes.

Une première partie (Chapitre 2) s'est penchée sur les effets des marées vertes sur les communautés ichtyologiques en zone intertidale côtière et estuarienne. Pour ce faire, un suivi saisonnier des communautés de poissons et des proliférations de macroalgues a été réalisé à une échelle locale dans un site contrôle et un site impacté pour les deux types d'habitats affectés par les marées vertes : les estrans sableux et les vasières estuariennes. Dans ces secteurs, les caractéristiques des communautés ichtyologiques des stades larvaires d'une part et des stades juvéniles et adultes d'autre part ont été examinées par une approche de type BACI (Before-After Control-Impact) combinant la prise en compte de facteurs de variation spatiaux et temporels. Les conséquences des marées vertes sur la composition spécifique des communautés ichtyologiques installées (*i.e.* incluant les stades juvéniles et adultes) ont ensuite été analysées dans chacun des secteurs. Un suivi plus fin des effets des marées vertes sur ces communautés a finalement été réalisé au travers d'analyses des réponses de l'ichtyofaune distribuée en différentes guildes fonctionnelles présentes dans ces habitats. Dans cet objectif, les espèces ont été classées par guildes de distribution verticale (pélagique, démersale et benthique) et guildes écologiques (juvénile marine et résidente).

Le Chapitre 3 traite ensuite de l'influence des marées vertes impactant une nourricerie côtière sur la sélection de l'habitat et les performances individuelles des juvéniles d'espèces pélagique, démersale et benthique. Ce chapitre s'est intéressé aux processus par lesquels les marées vertes affectent l'ichtyofaune, avec un focus sur la zone d'estran sableux (représentée par la baie de Saint-Brieuc) ainsi que sur la fonction de nourricerie assurée par cet habitat pour les stades juvéniles. Les réponses de trois espèces de poissons au stade juvénile ont été examinées dans un site contrôle et un site impacté. Les espèces analysées ont été choisies en fonction de leur appartenance à différentes guildes de distribution verticale afin de tester l'effet de l'utilisation de l'habitat sur leurs réponses. Le sprat européen *Sprattus sprattus* (Linnaeus, 1758) a ainsi été sélectionné pour la guilde pélagique; le bar européen *Dicentrarchus labrax* (Linnaeus, 1758) pour la guilde démersale et la plie européenne *Pleuronectes platessa* Linnaeus, 1758, pour la guilde benthique. Pour pouvoir apprécier une réponse globale des effets des marées vertes à l'échelle individuelle, une approche multi-indice a été mise en œuvre, considérant plusieurs niveaux d'intégration de la perturbation. Dans un premier temps, la sélection de l'habitat pour chacune des espèces a été examinée par l'analyse combinée de leurs densités et des signatures isotopiques spécifiques à chacun des habitats. Ensuite, les ajustements physiologiques des individus ont été considérés à travers l'analyse de réponses instantanées (capacité de défense antioxidante), ou mises en place à court terme (taux de lipides musculaires, taux de croissance journalière) et à moyen terme (indice de condition sur critères morphométriques).

Chapitre 2

Réponses des communautés ichtyologiques aux marées vertes en zone intertidale côtière et estuarienne

2. Réponses des communautés ichtyologiques aux marées vertes en zone intertidale côtière et estuarienne

Introduction du chapitre

Les écosystèmes côtiers et estuariens sont des zones extrêmement productives qui abritent des habitats essentiels au maintien et au renouvellement des ressources marines d'intérêt halieutique (Elliott and Dewailly, 1995; Beck et al., 2001; Seitz et al., 2014). Parmi les altérations subies par ces écosystèmes, les proliférations de macroalgues opportunistes sont l'un des signes les plus visibles de l'eutrophisation, particulièrement dans le nord-ouest de la France (Merceron et al., 2007; Perrot et al., 2014). Ces proliférations massives de macroalgues vertes (*i.e*. *Chaetomorpha* spp., *Cladophora* spp. et *Ulva* spp.) perturbent les conditions abiotiques et biotiques des systèmes impactés (Fletcher, 1996; Raffaelli et al., 1998). Dans les secteurs tempérés, le synchronisme de ces proliférations algales avec la colonisation des zones côtières et estuariennes par de nombreuses espèces de poissons interroge sur les répercussions de ces perturbations sur l'ichtyofaune intertidale.

Dans ce chapitre, nous proposons une analyse des conséquences des marées vertes sur les communautés ichtyologiques intertidales en s'appuyant sur un suivi saisonnier dans les deux types d'habitats affectés par les marées vertes, les estrans sableux et les vasières estuariennes. Cette analyse a été réalisée sur un site contrôle et un site impacté dans la baie de Saint-Brieuc pour les estrans sableux et la Rance au titre des vasières estuariennes.

Dans ces secteurs, les caractéristiques des communautés ichtyologiques des stades larvaires d'une part et des stades juvéniles et adultes d'autre part ont été examinées par une approche de type BACI (Before-After Control-Impact) combinant la prise en compte de facteurs de variation spatiaux et temporels. Les conséquences des marées vertes sur l'abondance, la composition spécifique et la diversité fonctionnelle des communautés ichtyologiques ont ensuite été analysées dans chacun des secteurs.

Fish community responses to green tides in shallow estuarine and coastal areas

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2.1 Abstract

All over the world, numerous bays and estuarine systems that are known to shelter essential fish habitats are experiencing proliferations of green macroalgae known as green tides. Although the processes that enhance green tides in response to nutrient enrichment are well known, their consequences for ecological communities - especially for ichthyofauna - remain poorly studied. To estimate these consequences, this analysis focused on the two types of shallow systems that are experiencing green tides: sandy beaches and estuarine mudflats. In these two systems, macroalgae proliferation and fish community were surveyed along seasonal cycles at control and impacted sites that shared similar physico-chemical parameters and sediment structure. To analyse the consequences of green tides on the fish community, a Before-After Control-Impact approach was used. This approach reveals no difference between fish communities at the control and impacted sites before the macroalgal bloom. Then, it underlines an influence of green tides on the fish community, and this influence varies according to the composition, density and duration of the macroalgal bloom. Indeed, when intertidal systems experienced short proliferation and/or weak density, green tides did not seem to impact the fish community. However, when green macroalgae proliferated in large quantities and/or when the proliferation lasted for long periods, the fish community was significantly affected. These modifications in the fish community led to a significant decrease in fish species diversity and density until fish disappeared from impacted sites at high proliferations. Furthermore, the response of fish species to green tides differed according to their functional guilds. Negative consequences for benthic and marine juvenile fish species were beginning at low proliferations, whereas for pelagic fish species they occurred only at high proliferations. Thus, green tides significantly affect fish habitat suitability because they lead to changes in the composition of the fish community and eventually to the local disappearance of fish at high proliferations.

Keywords: fish community; sandy beaches and estuarine mudflats; green tides; macroalgae; nursery

2.2 Introduction

Temperate coastal areas and estuaries are known to be highly productive systems that shelter essential habitats such as nursery grounds and feeding-breeding habitats for various fish species (Elliott and Dewailly, 1995; Beck et al., 2001). In addition to resident species, many fish gather in estuarine and coastal nurseries during their first years of life (Miller et al., 1984; Lenanton and Potter, 1987; Dorel et al., 1991); such fish include benthic (Krygier and Pearcy, 1986; Gibson, 1994; Le Pape et al., 2003), demersal (Claridge and Potter, 1983) and pelagic (Munk, 1993). The combination of high summer temperature in the coastal shelf and large food availability (Gibson, 1994; Le Pape and Bonhommeau, 2015) provides a highly suitable habitat for the settlement and growth of numerous fish species (Beck et al., 2001; Able, 2005; Trimoreau et al., 2013). The capacity of these habitats to sustain juvenile growth and other functions for ichthyofauna plays a key role in the renewal of marine fish species (Holbrook et al., 2000; Sluka et al., 2001; Stoner, 2003). However, these restricted and sensitive habitats are threatened by numerous anthropogenic pressures (Halpern et al., 2008), which could modify their quality and carrying capacity (Vasconcelos et al., 2013).

Among other anthropogenic disturbances, coastal and estuarine habitats suffer from excessive proliferations of green macroalgae. Green macroalgae proliferate in nutrient (especially nitrogen) enriched intertidal flats (Hull, 1987) and shallow sublittoral areas with a slight slope and low residual hydrodynamic conditions (*i.e.* after removing cyclic tidal circulation) (Valiela et al., 1997; Raffaelli et al., 1998; Perrot et al., 2014). These massive proliferations of green macroalgae (*i.e. Chaetomorpha* spp., *Cladophora* spp. and *Ulva* spp.), called green tides, have increased worldwide in occurrence, abundance and duration (Fletcher, 1996; Lehvo and Bäck, 2001; Ye et al., 2011; Smetacek and

Zingone, 2013; Zhou et al., 2015). In temperate latitudes, they occur during the spring-summer period (Fletcher, 1996; Merceron et al., 2007) at the same time as the settlement of many coastal and estuarine nursery dependent fish species (Amara et al., 2000; Amara, 2003). Green tides may thus affect ichthyofauna, and there are possible consequences both on the local scale (Hansson and Rudstam, 1990; Jokinen et al., 2015) and in the open sea, where the adult population of estuarine and coastal nursery-dependent fish species lives and sustains fisheries (Seitz et al., 2014). Indeed, green tides lead to major changes in habitat conditions (Fletcher, 1996; Raffaelli et al., 1998), modifying habitat structure (Isaksson et al., 1994), biogeochemical cycles (Sfriso et al., 1992), invertebrate communities (Quillien et al., 2015), trophic webs and ecosystem processes (Raffaelli et al., 1998). Furthermore, these consequences are modulated according to the composition, intensity and duration of the bloom (Lyons et al., 2014). Several studies on invertebrate species have revealed a positive influence of low patchy macroalgae development (Wilson et al., 1990; Norkko and Bonsdorff, 1996a, 1996b; Bolam et al., 2000) and a negative influence of large and/or long-term proliferations (Norkko et al., 2000; Cardoso et al., 2004; Quillien et al., 2015). However, few studies have considered fish communities (reviews in Raffaelli et al., 1998; Lyons et al., 2014). Biotic and abiotic modifications linked to macroalgal proliferation might thus affect habitat suitability and may influence (as is the case for invertebrate organisms) fish settlement potential and survival. Fish response to these habitat modifications could differ in accordance with species-specific capacity to move or to tolerate environmental pressures (Sagasti et al., 2001; MacKenzie, 2005; Wennhage and Pihl, 2007; Riedel et al., 2012).

In Northwestern France (Fig 2.1), numerous sheltered bays and estuarine systems experience multi-specific proliferations of green macroalgae (Morand and Briand, 1996; Charlier et al., 2007; Perrot et al., 2014). These blooms are composed of green macroalgae developing in free-floating expanded blade forms (*e.g. Ulva armoricana* and *Ulva rotundata*) or filamentous forms hung on the substrate (*e.g. Ulva intestinalis*, *Ulva compressa, Ulva ramulosa, Chaetomorpha* spp. and *Cladophora* spp.). Our purpose was to analyse, on a local scale, the structure of teleost fish communities in intertidal areas and their changes during green tides. This analysis was performed at control and impacted sites in the two types of ecosystems impacted by green tides: sandy beaches and estuarine mudflats. Fish communities (including larvae, juveniles and adults) were thus surveyed with respect to green tide phenological development across seasonal cycles according to temporal and spatial factors based on a Before-After Control-Impact (BACI) procedure (Parker and Wiens, 2005; Fleeger et al., 2008). Patterns in fish species composition, species richness, density and distribution by functional guilds (position in the water column and the use of intertidal and shallow areas during the life cycle; Elliott and Dewailly, 1995; Delpech et al., 2010) were thus investigated in relation to macroalgal blooms.

2.3 Materials and methods

2.3.1 Studied areas

The study was performed in Northwestern France in the Bay of Saint Brieuc and the Rance estuary. Each of these areas is representative of a type of intertidal system suffering from green tides: *i.e.* coastal sandy beaches and estuarine mudflats (Fig 2.1; Charlier et al., 2007; Rossi, 2011).

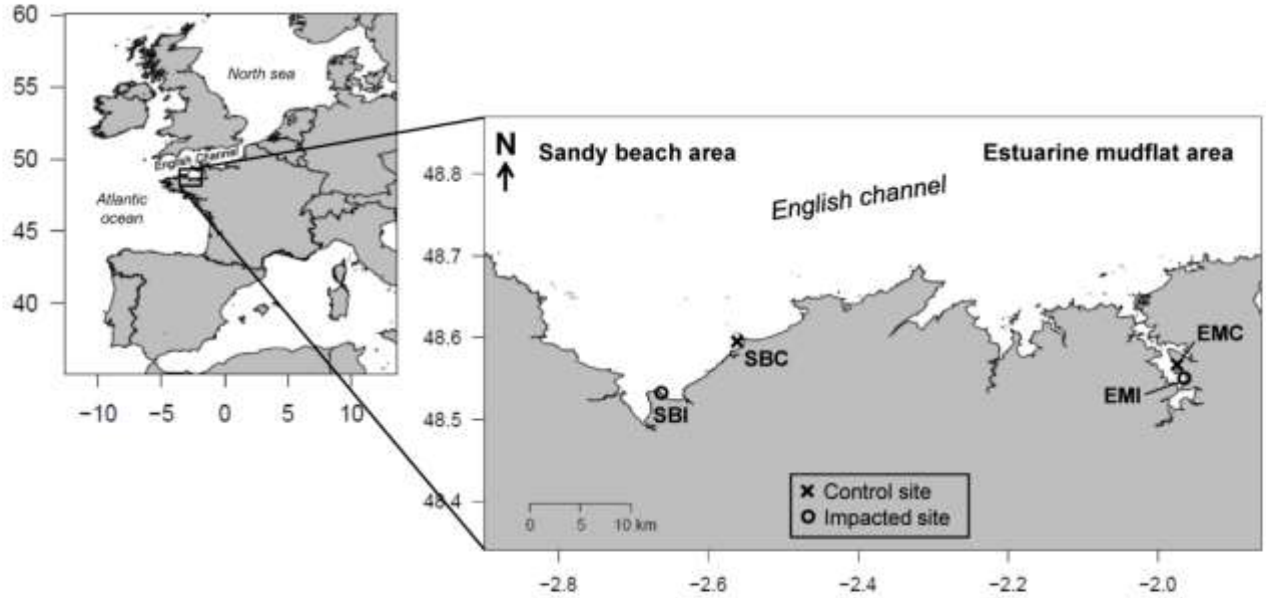

Figure 2.1- Location of the studied sites in sandy beach (SB) and estuarine mudflat (EM) areas in Northwestern France with their respective control (C) and impacted (I) sites

These areas are characterised by wide foreshores and semi-diurnal tides with a mean tidal amplitude of 8 m. Within each area, intertidal zones gather all of the conditions for proliferations of green macroalgae such as wide sheltered flats with a slight slope, low residual hydrodynamic circulation and large amounts of nutrient loadings from the watershed (Perrot et al., 2014). These zones affected by green tides are surveyed by the EU Water Framework Directive (WFD) to track the proliferation of macroalgae.

According to the macroalgae index used in that survey, the quality status of impacted zones are defined as poor in the Bay of Saint Brieuc (including sandy beaches that for decades have been the most heavily impacted in Northwestern France; Charlier et al., 2007) and moderate in the Rance estuary (Rossi, 2011).

A control and an impacted site were chosen in each area to compare spatiotemporal patterns in ichthyofauna. The control and impacted sites were selected based on their proximity (< 10 km) to enable comparison with regard to larval supply and juvenile settlement. Moreover, sites of each area have a similar sediment structure, thus enabling a comparison of fish habitat suitability, especially for demersal and benthic fish species. In the sandy beach area, the studied sites are referred to as Sandy Beach Control (SBC) and Sandy Beach Impacted (SBI) (Fig 2.1) and were surveyed during two seasonal cycles, in 2013 and 2014. The estuarine mudflat area was added to the sampling design in 2014 with Estuarine Mudflat Control (EMC) and Estuarine Mudflat Impacted (EMI) as the studied sites (Fig 2.1).

2.3.2 Field sampling design

Sampling was performed in 2013 and 2014 during the spring-autumn season from April until the end of October. This sampling period was delineated in accordance with both the proliferation cycle of green tides (Fletcher, 1996; Merceron et al., 2007) and the colonisation of shallow intertidal areas by resident and marine juvenile fish (Amara et al., 2000; Amara, 2003), which started before and ended after their maximum occurrences in coastal areas.

Within each area, the control and impacted sites were sampled one after the other twice per month during the daytime (mainly in the morning) and 1.5 to 3 hours after the high tide (*i.e.* early to mid-ebb tide) at medium tidal coefficients (between 50 and 90, *i.e.* between spring and neap tides). Six successive hauls of 25 m were performed in the shallow upper part of the intertidal zone (depth in m: [0.4-0.7]) simultaneously with two different fishing gears. Juvenile and adult fish were sampled using a trawl net of 8 m in length and 4 m in width (mesh of 8 mm), which was towed by two people (Quiniou, 1986). Simultaneously, fish larvae were sampled with a plankton net (1.25 m in length and 0.6 m in width, mesh of 1 mm), which was towed by one person. Samples were stored in coolers until further treatment at the laboratory. For each trawl sample, measures of temperature (°C), salinity, pH and dissolved oxygen concentration (mg.L^{-1}) were achieved using a multiparameter probe (Hanna HI 9828/4-02). The biomass of macroalgae (no seagrasses or other plants were present at the study sites) was measured in wet weight after at least one minute of draining for each trawl sample. The macroalgae composition was determined in the field by the estimation of the percentages of 4 groups of macroalgae (identified by either species level or general morphology): 1 - green macroalgae exclusively composed of expanded blade *Ulva* spp.; 2- filamentous green macroalgae (including filamentous *Ulva* spp., *Chaetomorpha* spp. and *Cladophora* spp.); 3- *Pylaiella littoralis*; and 4- “other macroalgae” (primarily composed of *Fucus* spp.).

Sediment structure (granulometry and distribution into sediment classes; Le Pape et al., 2003) was examined at each site in both areas during the first sampling date of the surveys using cores located at the beginning of each trawl haul.

In addition, the effects of nycthemeral and tidal cycles on physico-chemical parameters, macroalgae density and fish community were analysed based on an additional 24 h survey conducted in late spring of 2014 (5-6 June). For this additional survey, sampling was performed in the sandy beach area simultaneously at both sites at a medium density of green macroalgae. Three successive trawl hauls were performed each hour using the trawl net with the same protocol as described above.

2.3.3 Preliminary analyses

Fish (juvenile and adult from the trawl net) and fish larvae (from the plankton net) were identified at the species level and counted. The sampling distance (25 m) represented a compromise between sufficient fish catchability and the prevention of clogged trawl and plankton nets during high macroalgae proliferations. This distance led to small sampled surfaces, inducing a weak amount of catches and zero-inflated data. To offset the sparse occurrence of fish in trawl hauls and to assess a representative snapshot of the community at the sampling date, the six successive trawl hauls were pooled per date and considered as a unique sample unit for each sampling date. At each sampling date, the number of fish captured was summed per species (*i.e.* separately for fish larvae and fish) and a mean of the environmental variables was calculated. Patterns in fish larvae and fish communities as well as macroalgae densities (kg.m^{-2} in wet weight) and physico-chemical parameters were thus analysed per date and per site; hereafter, it is defined as the “sample unit”.

2.3.4 Fish community analyses

2.3.4.1 Selected indicators of the ecological status of the fish community

The total density of fish (number.ha^{-1}) was the first indicator retained to analyse fish habitat suitability (Delpech et al., 2010). Species richness was then selected as the most appropriate indicator for the analysis of fish diversity. Indeed, this index is adapted to a low number of species in sample units (Nicolas et al., 2010a; Pasquaud et al., 2015), and its value decreases with the increase in habitat degradation (Hughes et al., 1982; Gibson, 1994; Delpech et al., 2010).

In addition, the functional composition of the fish community was analysed. Fish species were classified into three classes of vertical distribution guilds - pelagic, demersal and benthic - according to their spatial occupation of the habitat (Elliott and Dewailly, 1995; Delpech et al., 2010; Nicolas et al., 2010b; Table 2.1 and Table 2.2). Next, fish species were categorised into two types of ecological guilds - marine juvenile and resident - that described their use of estuaries and enclosed bays during the life cycle (Elliott and Dewailly, 1995; Delpech et al., 2010; Nicolas et al., 2010b; Table 2.1 and Table 2.2). The respective fish densities in these five guilds were then analysed.

Table 2.1 - Ecological and vertical distribution guilds for coastal fish (adapted from Elliott and Dewailly, 1995)

Criterion	Guild	Definition
Vertical distribution	Pelagic	Species living in the water column
	Demersal	Species living in the water layer just above the bottom
	Benthic	Species living on the substratum
Ecology	Marine juvenile	Species using the shallow coastal waters and estuaries primarily as nursery ground
	Resident	Species spending their entire lives in shallow coastal waters and estuaries

Table 2.2 - Classification of the fish species into vertical distribution and ecological guilds, and their occurrence at the studied sites (O: sampled only at the larval stage; +: sampled only once; and X: sampled more than once)

			Sandy beach		Estuarine mudflat	
Species	**Vertical distribution guild**	**Ecological guild**	**SBC**	**SBI**	**EMC**	**EMI**
Ammodytes tobianus	Demersal	Resident	+			
Atherina presbyter	Pelagic	-	X	X	X	X
Buglossidium luteum	Benthic	Juvenile	X	X	X	
Callionymus lyra	Demersal	Resident	+			
Chelon labrosus	Demersal	Resident	X	X		
Ciliata mustela	Demersal	Resident	+			
Cyclopterus lumpus	Benthic	Juvenile	+			
Dicentrarchus labrax	Demersal	Juvenile	X	X	X	X
Diplodus sargus	Demersal	Juvenile	X			
Echiichthys vipera	Benthic	Resident	X	O		
Gobius niger	Demersal	Resident			+	
Gobius paganellus	Demersal	Resident			+	
Hyperoplus immaculatus	Demersal	Juvenile	+			
Lipophrys pholis	Demersal	Resident			O	
Liza aurata	Demersal	Resident	X	X	X	X
Mullus surmuletus	Demersal	Resident			+	
Pegusa lascaris	Benthic	Juvenile	X			
Pleuronectes platessa	Benthic	Juvenile	X	X	X	
Pomatoschistus microps	Demersal	Resident	X	X	X	X
Pomatoschistus minutus	Demersal	Resident	X	X	X	
Pomatoschistus pictus	Demersal	Resident	X	X	X	
Scophthalmus rhombus	Benthic	Juvenile	X	X	X	
Solea solea	Benthic	Juvenile	X	X	X	
Spinachia spinachia	Demersal	Resident			+	
Spondyliosoma cantharus	Demersal	Juvenile	X		X	
Sprattus sprattus	Pelagic	-	X	X	X	X
Symphodus melops	Demersal	Resident	X	X	X	
Trigla lucerna	Demersal	Juvenile	X			

2.3.4.2 Statistical analyses

Fish densities (total and classified into guilds) had previously been standardised using a logarithmic transformation (log10(x+1)) (Legendre and Legendre, 1998) to respect the application conditions for the further statistical analyses. Preliminary and *post hoc* analyses demonstrated that species richness and log-transformed densities could be analysed using linear models and related tests, including a BACI test, without contraindication. Their significance for statistical analyses was determined at the $\alpha = 0.05$ level, and all of the statistical analyses were performed using R version 3 (R Development Core Team, 2012).

Fish community during seasonal cycles of green tides: a Before-After Control-Impact (BACI) approach

Within each area, and for the two studied years in the sandy beach area, a Before-After Control-Impact (BACI) approach was applied to study the impacts of green tides on the fish community. We analysed differences in the communities of both fish larvae (species richness and log-transformed density) and fish (species richness and log-transformed density, both total and classified into guilds; Table 2.2) between the control and impacted sites during the seasonal cycle (*i.e.* along non-impacted and impacted successive periods). The BACI-type ANOVA is adapted to detect impacts between control and impacted sites over time because it incorporates both temporal and spatial variations (Parker and Wiens, 2005; Fleeger et al., 2008). However, a BACI analysis requires separation of the "before" and "after" periods. In this study, the "after" period was determined by the presence of green macroalgae at the impacted sites. When contrasts in proliferation were inadequately marked during the seasonal cycle (*e.g.* when the period "before" was restricted to one date), ANOVA analyses were alternatively used to compare patterns in the descriptors of the fish community between sites during the green tide.

Fish community during green tides

Fish response to an increase in green macroalgae density was analysed using fish density at SBI and combining the two years of the survey during green tides (the low contrast in green macroalgae densities at EMI prevented us from performing a similar analysis at that site). This response was assessed using a linear regression model with log-transformed fish density as the response variable and green macroalgal biomass as the explanatory variable (see the results section for *post hoc* validation of this modelling option).

In addition, the influence of tidal and daily cycles on surveyed parameters was analysed based on the 24 h survey cycle using ANOVA tests.

2.3.5 Analysis of specific composition of the fish community during green tides

The modification of fish assemblage in response to green tides was examined in each area using an unconstrained ordination method: the non-metric multi-dimensional scaling (MDS) (Clarke, 1993; Dixon and Palmer, 2003). For this analysis, we used the Bray-Curtis dissimilarity index (Bray and Curtis, 1957) to quantify contrasts between sample units in terms of fish species density (not log-transformed) during green tides. Within each area, a selection of fish species was preliminarily realised to exclude scarce species that could lead to difficulties in MDS interpretation (Manté et al., 2003). Species were thus selected for these MDS analyses when their percentage of occurrence by sample units was superior to 5% within a single area (*i.e.* combining the two years of survey in the sandy beach area). Moreover, sample units with no capture were excluded because measures of rank dissimilarity could not address data sets that included lines only composed of zeros.

2.4 Results

2.4.1 Sandy beach area

Physico-chemical parameters

According to the analysis of sediment structure, both of the sites in the intertidal sandy beach area were sandy muddy grounds. During each studied year, the seasonal cycles of salinity and pH did not vary between sites. Temperature also fluctuated similarly across sites, but its range varied between 2013 and 2014 (*i.e.* between 8 °C to 22 °C in 2013 and 11 °C to 21 °C in 2014; Fig 2.2). Low temperatures that were unfavourable for the initiation of green macroalgae development and larval settlement (*i.e.* under 14 °C) were encountered until June in 2013, two weeks later than in 2014 (Fig 2.2). From mid-June to mid-July 2013, oxygen supersaturation (≥10 mg.L^{-1}) was measured at SBI at high densities of green macroalgae. Except for this period, daytime mean dissolved oxygen concentrations were similar at both sites, with a seasonal range between 7 and 10 mg.L^{-1} during the two studied years.

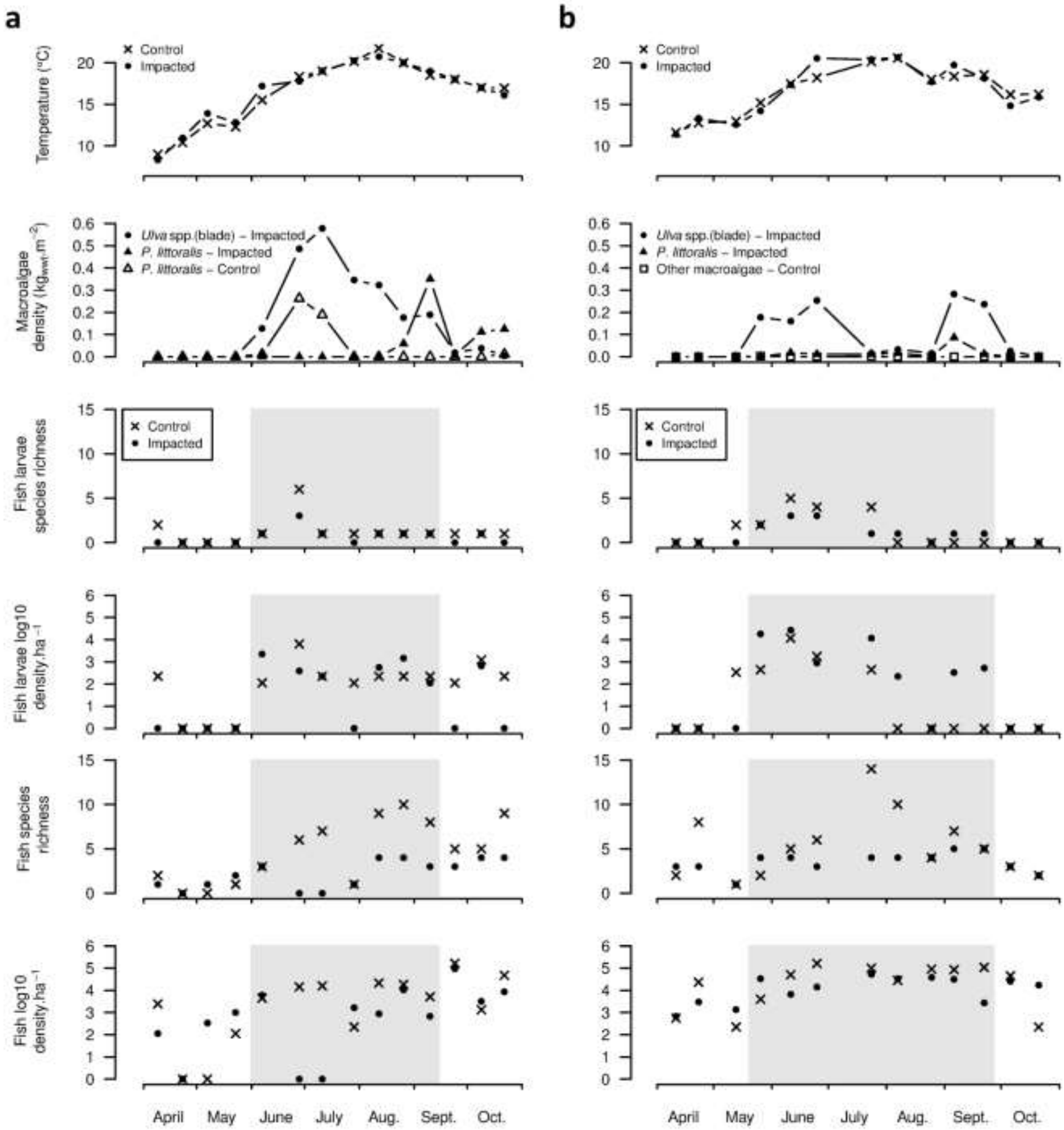

Figure 2.2 - Mean temperature (°C), mean macroalgae densities (in wet weight kg.m^{-2}), fish larvae and fish (juvenile and adult) species richness and log-transformed densities (number.ha^{-1}) from April to October in the control and impacted sites of the sandy beach area in (a) 2013 and (b) 2014. The grey area represents the period impacted by green tide

Macroalgal cycle

During both studied years, the development of green macroalgae was initiated when the temperature reached approximately 14 °C (Fig 2.2). In 2013, expanded blade *Ulva* species proliferated from June to September, with a peak of proliferation from mid-June to mid-July (average: 0.3 $kg_{wwt}.m^{-2}$; maximum: 0.6 $kg_{wwt}.m^{-2}$ in July; Fig 2.2a). In 2014, expanded blade *Ulva* spp. proliferation occurred two weeks earlier and lasted from the end of May to September. This 2014 proliferation was composed of two peaks, the first in June and the second in September, with lower levels of biomass between the two peaks (average: 0. 1 $kg_{wwt}.m^{-2}$; maximum: 0.3 $kg_{wwt}.m^{-2}$ in September; Fig 2.2b). With respect to green macroalgae proliferations in this area during recent decades, green tides could be locally characterised as late but medium in 2013 and as low in 2014 (Ballu pers. comm.).

A second type of macroalgae, *Pylaiella littoralis*, a filamentous brown macroalgae, was sampled in significant amounts at both sites in 2013 with a maximum density of 0.3 and 0.4 $kg_{wwt}.m^{-2}$ at SBC and SBI, respectively. At SBI, the emergence of *P. littoralis* from September onwards created a shift in the dominant macroalgae species from *Ulva* spp. to *P. littoralis* (Fig 2.2a). In 2014, this species was encountered in low amounts only in September at SBI (maximum density: 0.08 $kg_{wwt}.m^{-2}$).

Fish community: effects of the seasonal cycle and green tides

The rapid proliferation of expanded blade *Ulva* spp. enabled the identification of a shift from a state without green tide to a state with green tide at SBI (Fig 2.2). This shift enables the application of BACI tests to the two studied years. Delimitation of impacted and non-impacted periods by green tides (Fig 2.2) led to the analysis of 11 sample units per site during both studied years. Sample units were distributed into 4 “before” and 7 “after” the beginning of green tide in 2013 and into 3 “before” and 8 “after” the beginning of green tide in 2014 (Fig 2.2 and Supp. Tables 2.1 and 2.2).

Fish larvae captures were beginning in early June 2013 and mid-May 2014, with maximum density in June during both studied years (Fig 2.2). Fish larvae densities differed between years and were higher in 2014 (Fig 2.2). However, during both studied years, there was no significant difference between sites in fish larvae species richness and density (Table 2.3).

Fish (*i.e.* juvenile and adult) arrived in May during the two studied years at both the control and the impacted sites (Fig 2.2). Before the development of green macroalgae, fish communities were not different between sites in term of species composition and density (Fig 2.2 and Supp. Tables 2.1 and 2.2). In 2013, during expanded blade *Ulva* spp. proliferation, fish species richness was significantly lower at SBI than at SBC (Fig 2.2a and Table 2.3). Simultaneously, fish density did not differ significantly between sites in spite of null densities observed at SBI during the maximum density of expanded blade *Ulva* spp. (Fig 2.2a and Table 2.3). In 2014, no significant difference in fish species richness and density was recorded when the factors of site and period were considered (Fig 2.2b and Table 2.3).

Table 2.3 - BACI results (*p values*) for effects of site class, period and their interaction on species richness and log-transformed densities (D., total and classified into both vertical distribution and ecological guilds) for both fish larvae and fish in the sandy beach area in 2013 and 2014 (statistical significance: '***' <0.001; '**' <0.01; '*' <0.05)

Year	Parameter	Site class	Period	Site class: Period
2013	Fish larvae species richness	0.1317	0.1374	0.9191
	Fish larvae total D.	0.4005	0.0006***	0.5669
	Fish species richness	0.0072**	0.0172*	0.0184*
	Fish total D.	0.2505	0.0402*	0.1368
	Benthic D.	0.0019**	0.0023**	0.0245*
	Demersal D.	0.2390	0.0858	0.0079**
	Pelagic D.	0.3101	0.0495*	0.0931
	Marine juvenile D.	0.0018**	0.0023**	0.0361*
	Resident D.	0.2011	0.1300	0.0063**
2014	Fish larvae species richness	0.3156	0.2405	0.7220
	Fish larvae D.	0.0888	0.1306	0.0367*
	Fish species richness	0.0838	0.1484	0.7195
	Total fish D.	0.1602	0.0003***	0.4228
	Benthic D.	0.0287*	0.5275	0.3594
	Demersal D.	0.0555	0.0634	0.5963
	Pelagic D.	0.0084**	0.0001***	0.1365
	Marine juvenile D.	0.4316	0.1588	0.4562
	Resident D.	0.0297	0.6041	0.8471

Regarding functional guilds, except for the pelagic guild, all of the densities were significantly lower at SBI in 2013 during the green tide, especially during the maximum densities of expanded blade *Ulva* spp. (Fig 2.3a and Table 2.3). In 2014, no significant impact of the green tide was recorded on the densities of the functional guilds (Fig 2.3b and Table 2.3).

The influence of *P. littoralis* blooms on fish was evaluated with an ANOVA test at SBC in 2013 to compare fish communities before and during *P. littoralis* proliferation (its impact at SBI could not be analysed because the potential influence of the expanded blade *Ulva* spp. on the fish community could not be removed). Despite the significant proliferation in 2013, no effect of this macroalgae proliferation on the fish community has been evidenced at SBC either on fish species richness (F value = 1.05; *p value* = 0.33) or fish density (F value = 0.001; *p value* = 0.97).

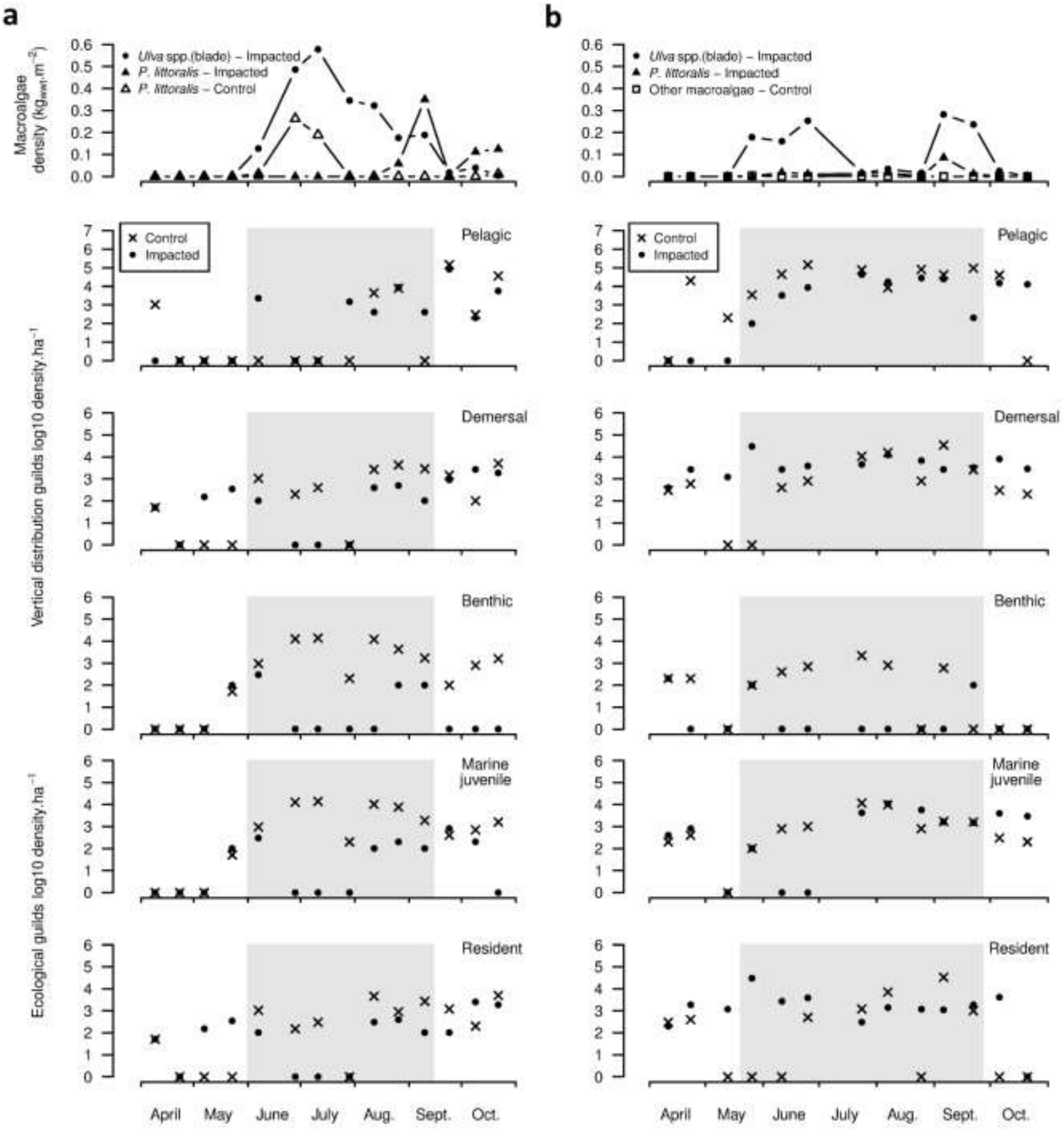

Figure 2.3 - Mean macroalgae densities (in wet weight kg.m^{-2}) and log-transformed fish densities (number.ha^{-1}) per vertical distribution (pelagic, demersal and benthic) and ecological guilds (marine juvenile and marine resident) from April to October in the control and impacted sites of the sandy beach area in (a) 2013 and (b) 2014. The grey area represents the period impacted by green tide

Fish density response to an increase in green macroalgae density

At SBI, the response of fish density to the amount of green macroalgae was analysed with a linear regression model that was applied to log-transformed fish density versus not log-transformed macroalgal density (*i.e.* the most appropriate model with respect to the distribution of the residuals; Fig 2.4b). The exponential representation of this linear regression model evidenced a significant decrease in fish density with the increase in expanded blade *Ulva* spp. density up to a density of 0.3 $kg_{wwt}.m^{-2}$, above which the mean fish density is very weak (Fig 2.4a; *p value* <0.001, $R^2 = 0.72$).

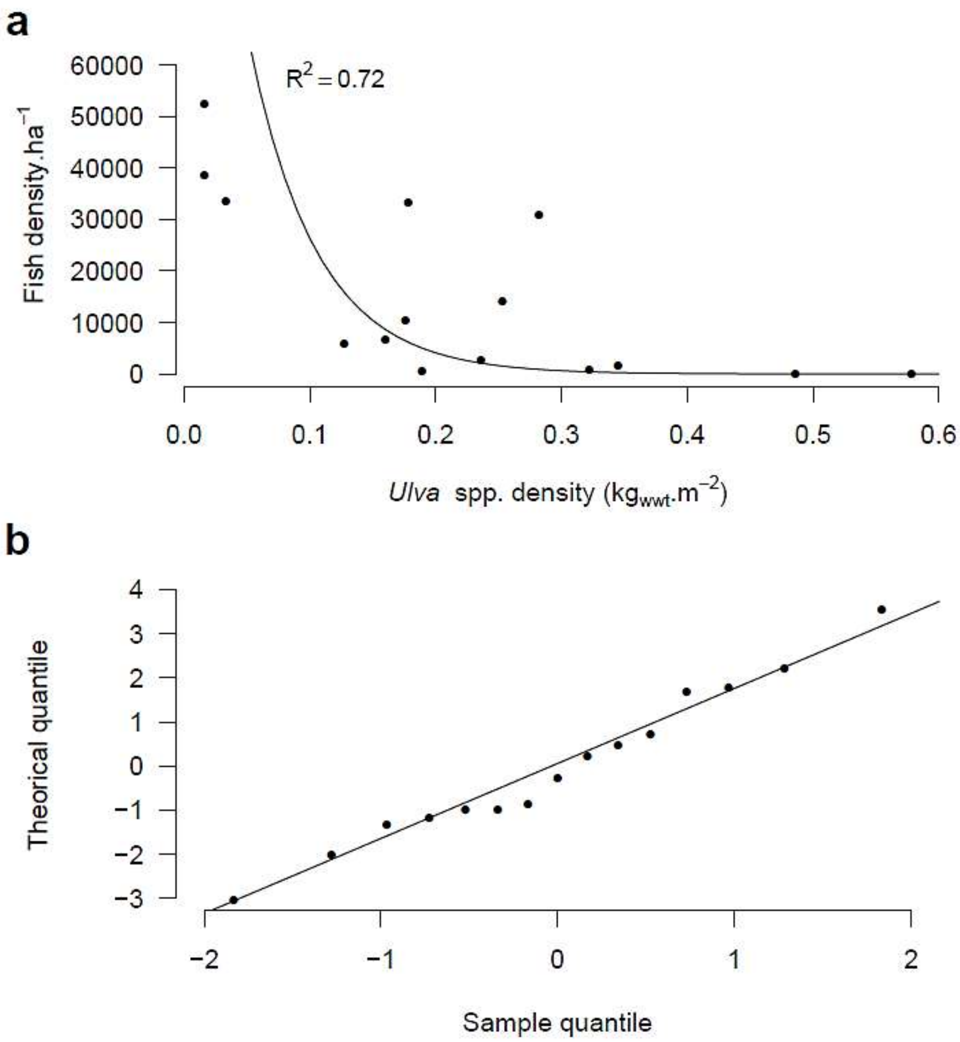

Figure 2.4 - Fish density ($number.ha^{-1}$) as a function of expended blade *Ulva* spp. density (in wet weight $kg.m^{-2}$) in the impacted site of the sandy beach area from June to September of the two studied years. (a) Plot and associated exponential representation of the linear regression model on log-transformed data, (b) quantile-quantile plot of the residuals of the linear regression against standard normal distribution

Influence of tidal and nycthemeral cycles on the fish community and environmental parameters during the green tide

The effects of tidal and nycthemeral cycles on the surveyed parameters were examined based on the 24 h additional survey realised simultaneously at both sites in early June 2014 at a medium density of green macroalgae (*Ulva* spp. density approximately 0.4 $kg_{wwt}.m^{-2}$ at SBI; Fig 2.2 and Supp. Table 2.3). The daily cycles of salinity, pH and temperature did not differ between the sites. The patterns in the daily cycle of dissolved oxygen concentration were also similar across sites; however, a wider daily range was recorded at SBI, where daily supersaturation occurred. Daily dissolved oxygen concentration ranged between 7 and 9 $mg.L^{-1}$ at SBC and between 7 and 16 $mg.L^{-1}$ at SBI at the same time. No tidal pattern was revealed for these physico-chemical parameters.

ANOVA did not evidence daily or tidal patterns either in expanded blade *Ulva* spp. density at SBI or in fish species richness and density (total and classified into guilds) at both sites. However, it did reveal a tidal pattern for benthic fish species, whose density increased during the ebb tide (F value= 10.63; *p value* = 0.00332 **).

Fish species composition during green tides

The multivariate analysis performed to investigate the influence of green tides on fish community composition was based on fish densities by species combining the two years of survey during macroalgal proliferations; the two dates when no fish were caught in 2013 were removed (Supp. Table 2.1). The two-dimension MDS plot revealed dissimilarities in species composition between the control and impacted sites (Fig 2.5a). At SBC, the higher species richness and density by guild were structured by many benthic and marine juvenile fish species (Fig 2.5a and Table 2.2). Conversely, the less numerous and diverse community at SBI was structured by resident and highly mobile fish species (*i.e*. pelagic and demersal fish species; Fig 2.5a and Table 2.2).

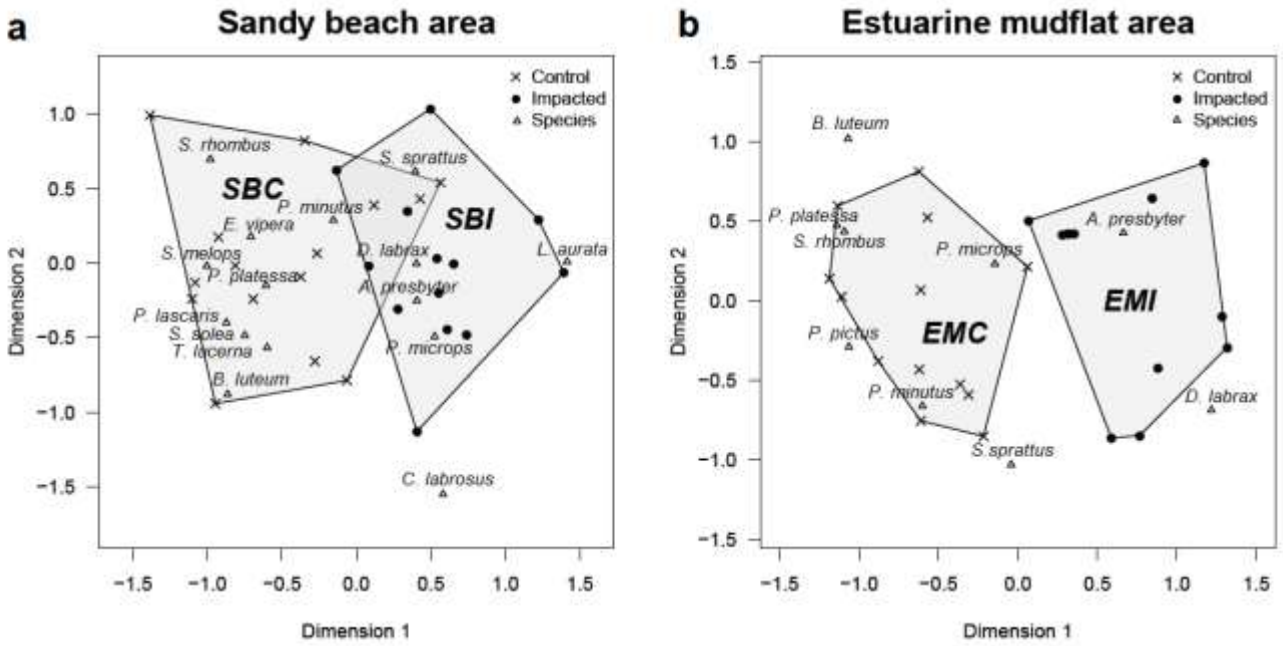

Figure 2.5 - Two-dimensional ordination of sample units during green tide proliferation from non-metric multidimensional scaling (MDS) (a) in the sandy beach area in 2013-2014 (stress = 0.18) and (b) in the estuarine mudflat area in 2014 (stress = 0.12)

2.4.2 Estuarine mudflat area

Physico-chemical parameters

Both sites in the estuarine mudflat area were muddy grounds. The seasonal cycle of salinity, pH and temperature (Fig 2.6) did not differ between sites, except for gradients of salinity in spring. From April to mid-June, average salinity was approximately 33 at EMC and approximately 31 at EMI, whereas afterwards it was approximately 34 at both sites. Daytime mean dissolved oxygen concentrations fluctuated similarly at both sites, with a seasonal range between 7 and 12 mg.L^{-1}.

Macroalgal cycle

Green macroalgae proliferation at EMI lasted from the end of April to the end of October and was composed of both expanded blade *Ulva* species (average: 0.02 kg$_{wwt}$.m^{-2}; maximum: 0.07 kg$_{wwt}$.m^{-2} in May) and filamentous green macroalgae hung to the substrate that dominated the macroalgae biomass (average: 0.08 kg$_{wwt}$.m^{-2}; maximum: 0.2 kg$_{wwt}$.m^{-2} in October; Fig 2.6). The average density of total green macroalgae species at EMI was 0.1 kg$_{wwt}$.m^{-2} during the proliferation period. Patchy filamentous green macroalgae were also encountered at EMC (average: 0.03 kg$_{wwt}$.m^{-2}; Fig 2.6).

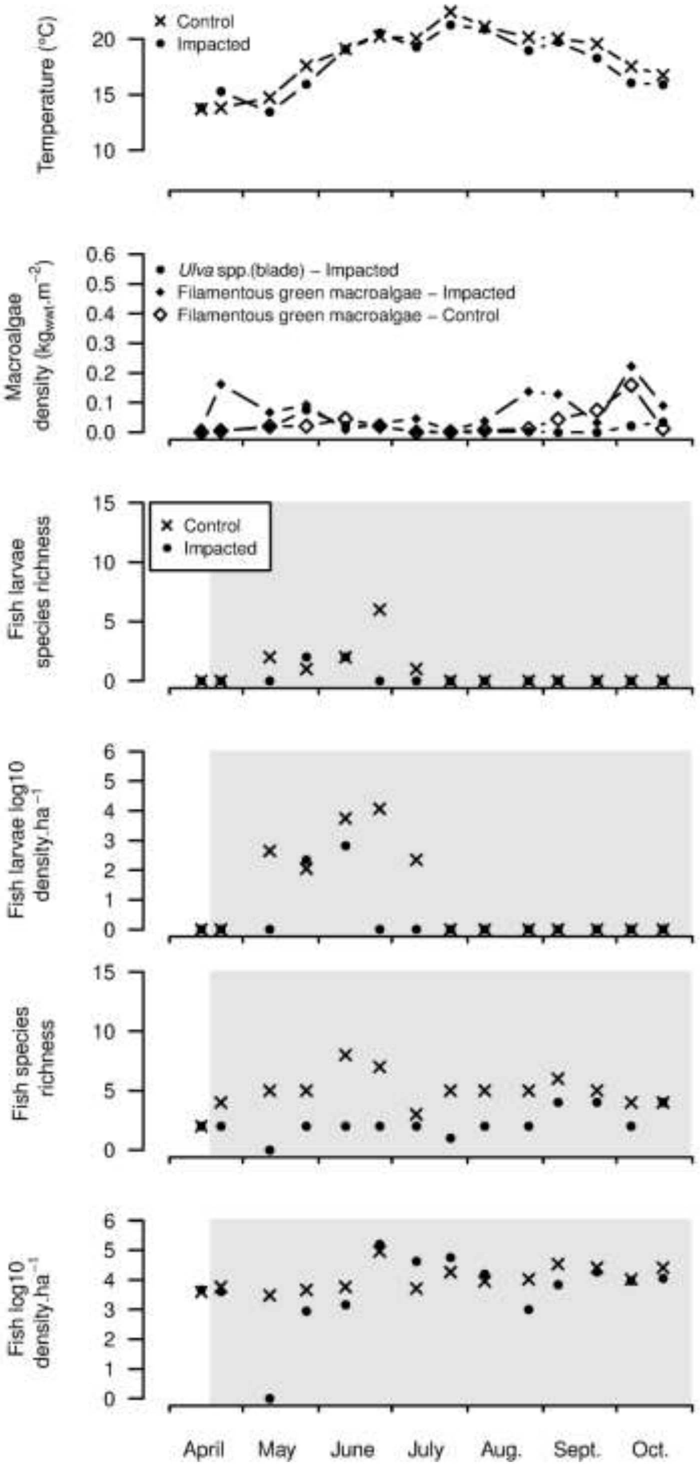

Figure 2.6 - Mean temperature (°C), mean macroalgae densities (in wet weight kg.m^{-2}), fish larvae and fish juvenile and adult) species richness and log-transformed densities (number.ha^{-1}) from April to October 2014 in the control and impacted sites of the estuarine mudflat area. The grey area represents the period impacted by green tide

Fish community: effects of the seasonal cycle and green tides

The synchronicity between green tide emergence, fish arrival in coastal zones and the beginning of the sampling survey prevented us from using BACI tests in the estuarine area (*i.e.* only one sampling date was realised before macroalgal proliferation). ANOVAs were thus alternatively used to compare fish larvae and fish communities between the control and impacted sites based on the 13 sampling units per site during the green tide (Supp. Table 2.4).

Fish larvae were caught from May until the beginning of July at both sites (Fig 2.6). Species richness and density of fish larvae were not significantly different between sites (Fig 2.6 and Table 2.4).
Fish (*i.e.* juvenile and adult) settled in April in the estuarine area (Fig 2.6). Fish species richness was significantly lower at EMI, but there was no significant difference between sites with respect to fish density (Fig 2.6 and Table 2.4). Regarding functional guilds, benthic, demersal and resident fish were significantly less abundant at EMI (Fig 2.7 and Table 2.4).

Table 2.4 - ANOVA results (impacted/control site) of species richness and log-transformed densities (D., total and classified into both vertical distribution and ecological guilds) for both fish larvae and fish in the estuarine mudflat area in 2014 (statistical significance: '***' <0.001)

Year	**Parameter**	**F value**	***p* value**
2014	Fish larvae species richness	1.4426	0.2425
	Fish larvae total D.	2.0205	0.1671
	Fish species richness	27.592	<0.001 ***
	Fish total D.	1.0794	0.3084
	Benthic D.	9.7004	<0.001 ***
	Demersal D.	24.084	<0.001 ***
	Pelagic D.	0.0067	0.9356
	Marine juvenile D.	0.5908	0.449
	Resident D.	28.942	<0.001 ***

Fish species composition during green tides

An MDS was performed on fish densities by species following the exclusion of one date when no fish was caught (Fig 2.6 and Supp. Table 2.4). The two-dimensional MDS plot confirmed the previous analysis by fish guild and revealed distinct species composition between control and impacted sites (Fig 2.5b). As in the sandy beach area, the fish community was partly structured by benthic fish species at the control site. Their scarcity at the impacted site has led to a shift in fish species composition (Fig 2.5b and Table 2.2).

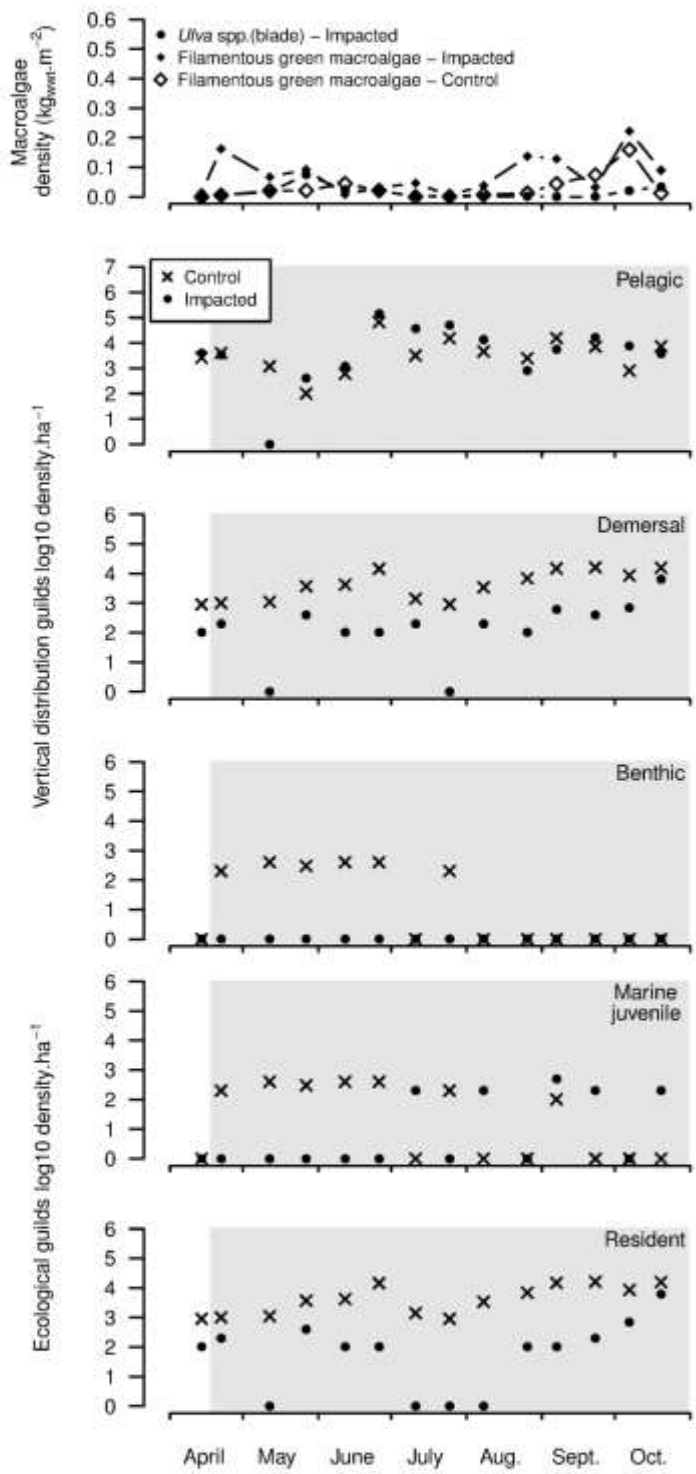

Figure 2.7 - Mean macroalgae densities (in wet weight kg.m^{-2}) and log-transformed fish densities (number.ha^{-1}) per vertical distribution (pelagic, demersal and benthic) and ecological guilds (marine juvenile and marine resident) from April to October 2014 in the control and impacted sites of the estuarine mudflat area. The grey area represents the period impacted by green tide

2.5 Discussion

2.5.1 A standardised approach to assess the effects of macroalgal proliferation

Comparable control and impacted site within each area

Within each area, the control and impacted sites were close to each other and shared similar fish-habitat conditions (*i.e.* similarity in physico-chemical parameters and sediment structure), leading to comparable fish species composition before the proliferation of macroalgae. Moreover, xenobiotics monitoring for the EU Water Framework Directive (WFD) indicated that both of the sites in each area had excellent water-chemical quality with respect to heavy metals, pesticides and industrial pollutants. Thus, noticeable differences between the impacted and control sites were primarily caused by local nutrient enrichment and lower residual hydrodynamic circulation at impacted sites, which resulted in green macroalgae proliferation and related modifications of habitat conditions.

Contrasted study areas

Within sandy beach and estuarine mudflat areas, habitat conditions have led to various types of green macroalgae species assemblages at the impacted sites. At SBI, the green tide was composed exclusively of expanded blade green macroalgae. Conversely, at EMI, the green tide was dominated by filamentous green macroalgae species, although both filamentous and expanded blade green macroalgae proliferated.

Potential biases in fish sampling design

The 24 h additional survey validated the representativeness of the sampled fish community and macroalgae under daylight in the morning or early afternoon at the beginning of the ebb tide.

The short sampling distance realised for this survey (25 m) might have decreased trawl catchability by increasing the influence of habitat disturbances related to the implementation of the sampling. However, similar sampled surfaces (*i.e.* per sample unit) have led to a representative sampling of the intertidal ichthyofauna (Orr et al., 2014) and allow us to consider this standardised sampling to be comparable.

The decrease in fish catches along with the increase in macroalgal density led us to consider a possible bias in the catchability of the trawl. Two qualitative field observations (that did not allow us to realise statistical tests) demonstrated that the gear remained efficient even if no fish was captured during important macroalgae proliferation.

(i) At SBI on 22 September 2014 at a medium density of expanded blade *Ulva* spp., we realised 3 trawl hauls of 50 m and 3 standardised trawl hauls of 25 m (Supp. Table 2.2). The two-fold longer trawl hauls have led to especially high densities of expanded blade *Ulva* spp. approximately 0.6 $kg_{wwt}.m^{-2}$ in a trawl haul (*i.e.* among the maximum densities encountered in other samples; Fig 2.4). The mean density of fish captured during these samplings was comparable to that of the standardised sampling realised on the same date. Indeed, when standardised per unit of effort, the towing distance did not significantly influence the density of captured fish (Rotherham et al., 2008; Fulanda and Ohtomi, 2011).

(ii) At high densities of green macroalgae, other mobile organisms (*Crangon crangon*) still present at SBI were caught in significant amounts.

Thus, we concede that trawl efficiency may have been reduced at significant densities of green macroalgae. However, the sampling strategy based on small trawl net distance (to avoid trawl clogging by macroalgae and to maintain its catchability) and the different qualitative field observations enable the consideration that a bias linked to macroalgae biomass in the trawl could not be the main explanatory factor of the low fish catch rates during green tides. This could neither explain fish disappearance at high densities of green macroalgae.

This standardised BACI-oriented approach thus allows the assessment of the consequences of green macroalgae proliferations on the fish community in the sandy beach and estuarine mudflat areas.

2.5.2 Contrasting effects of the proliferation of different species of macroalgae on ichthyofauna

Similar amounts of various macroalgae species can have different effects on fish diversity and abundance (Wennhage and Pihl, 1994; Camp et al., 2014; Lyons et al., 2014).

Above a mean density of 0.1 $kg_{wwt}.m^{-2}$ of green macroalgae mostly composed of filamentous species hung to the sea floor and clogging the substrate, we observed a significant negative effect on the fish community. Conversely, similar impacts on the fish community are only observed when the density of expanded blade *Ulva* species is three times higher. Furthermore, at a density level for which expanded blade *Ulva* species impacted the fish community, *P. littoralis,* a species of floating macroalgae that proliferated at both the control and impacted sandy beaches in 2013, does not seem to have any significant effect.

Thus, the specific composition of proliferating macroalgal assemblage and the related structural complexity are key driving factors of the fish community responses.

2.5.3 Effects of green tides on fish community

2.5.3.1 Synchronicity of green macroalgae proliferation and fish settlement

The responses of fish communities to green tides are linked both to the life stages impacted by macroalgae (Carr, 1989) and to the temporal overlap between their proliferation and fish life cycle (Pihl and van der Veer, 1992; Wennhage and Pihl, 1994). If macroalgal mats are already present at the arrival of fish larvae in nurseries, they may act as a filter (Pihl et al., 2005) and inhibit the settlement (Ólafsson, 1988; Bonsdorff, 1992; Bolam et al., 2000). This influence has been reported on invertebrates and has led both to a decrease in species diversity (Jones and Pinn, 2006; Scanlan et al., 2007; Quillien et al., 2015) and to changes in the composition of the benthic community (Bonsdorff, 1992; Norkko and Bonsdorff, 1996b). Conversely, if fish larvae settle in shallow waters before macroalgae development, *i.e.* if only the post-settled stage is affected, the fish might be able either to migrate out of the proliferating vegetation (Ólafsson, 1988; Wennhage and Pihl, 2007; Carl et al., 2008) or to stay at the impacted habitat.

At both impacted sites of the sandy beach and estuarine mudflat areas, fish were present before macroalgae proliferations, although in weak densities, and no influence of green tides on larval species richness and density was recorded. Consequently, fish larvae settlement could not be considered as the main driving factor of the difference in fish communities between impacted and control sites. The decrease in fish density (until the disappearance of fish) during green tides could be primarily attributed to emigration from or mortality in a non-suitable habitat (Pihl et al., 2005).

Within each area, fish settlement occurs just before macroalgal blooms and led to a weak number of informative surveys before the green tide. This constraint limited the power of the BACI test (Parker and Wiens, 2005; Fleeger et al., 2008) in the sandy beach area and even prevented its use in the estuarine area. This could have led us to underestimate the consequences of macroalgal proliferations for fish.

2.5.3.2 Effects of an increase in green macroalgae density on the fish community

In 2014, the green macroalgae proliferation at SBI was quite low and discontinuous. Patchy covers of macroalgae at low density for restricted periods of time have no noticeable negative impact on fish communities (Robertson and Lenanton, 1984; Wilson et al., 1990; Cardoso et al., 2004). Indeed, an increase in habitat complexity could even facilitate the local recruitment of various invertebrate species (Norkko and Bonsdorff, 1996a, 1996b; Holmquist, 1997; Bolam and Fernandes, 2002) by enhancing shelter capacity and survival level (Wilson et al., 1990) of the smallest fraction of the fauna (Orr et al., 2014). On the contrary, macroalgal blooms at higher density for a long period (*e.g.* such as at SBI in 2013 and at EMI in 2014) negatively impact macrofauna (*e.g*. Soulsby et al., 1982; Whitfield, 1986; Everett, 1994; Dolbeth et al., 2003; Green et al., 2014). Massive macroalgal blooms also significantly reduce both fish density and species richness (Pihl and van der Veer, 1992; Österling and Pihl, 2001; Pihl et al., 2005) and modify the composition of fish assemblage (Wennhage and Pihl, 2007). At a density of green macroalgae mostly composed of filamentous species of approximately 0.1 $kg_{wwt}.m^{-2}$ at EMI or at a density of expanded blade *Ulva* spp. of approximately 0.3 $kg_{wwt}.m^{-2}$ at SBI, both density and species richness were significantly reduced.

Furthermore, the response of ichthyofauna to green tides varies according to the vertical distribution of fish species and species-specific capacity to move and/or to tolerate environmental pressures (Sagasti et al., 2001; MacKenzie, 2005; Riedel et al., 2012). Benthic fish, mostly composed of marine juveniles, are the most sensitive guilds to green tides. Modification of the benthic habitat that is caused by the proliferation of green macroalgae affects the behaviour, distribution and growth of benthic fish species (Pihl et al., 2005; Wennhage and Pihl, 2007). Even if they could avoid vegetated or clogged substrates when alternative substrates are locally available (Wennhage and Pihl, 1994, 2007; Carl et al., 2008), the low capacity of juvenile benthic fish to migrate (Saucerman and Deegan, 1991; Le Pape and Cognez, 2016) and the weak stress tolerance of juvenile fish (Sogard, 1997) reinforce the negative influence of green tides on these species. Thus, at medium densities of green macroalgae, a local decrease in benthic marine juvenile fish species modifies the composition of the fish community. Demersal (Holden and Williams, 1974; Selleslagh and Amara, 2008) and resident species (such as the abundant *Pomatoschistus* species; Petersen and Petersen, 1990; Dolbeth et al., 2007) have a greater tolerance to environmental stress induced by green tides. Nevertheless, when proliferation either reaches high levels or lasts for several months, the density of demersal and resident fish species is lowered and these species become scarce and even disappear at high densities of green macroalgae. Pelagic fish species do not significantly respond to green tides in both the sandy beach and the estuarine mudflat areas. Even at their juvenile stage, these species are tolerant and mobile (Daan et al., 1990; Guelinckx et al., 2006) and can move into and out of the macroalgae proliferation (Potter et al., 1983). However, at high densities of green macroalgae, pelagic fish are also absent from impacted sites. High densities of green macroalgae induce hydrochemical modifications and the clogging of suitable fish habitat throughout the water column. Both of these processes are likely to force all fish species to leave shallow impacted areas. Thus, especially when macroalgae reach high densities, green tides are a limiting factor of habitat suitability for the entire fish community.

2.5.4 Processes involved in the negative consequences of green tides

On the local scale, changes in habitat conditions caused by the proliferation of macroalgae could both modify fish behaviour (Pihl et al., 1995; Nordström and Booth, 2007; Florin et al., 2009) and impact habitat selection (Nordström and Booth, 2007; Wennhage and Pihl, 2007; Carl et al., 2008). For fish present at impacted sites during green tides, the option of staying might influence their foraging success (Aarnio and Mattila, 2000; Florin et al., 2009; Orr et al., 2014) and growth (Tarpgaard et al., 2005; Carl et al., 2008; De Raedemaecker et al., 2012) as well as their survival and abundance (Pihl and van der Veer, 1992; Wennhage, 2002; Pihl et al., 2005).

2.5.4.1 A main effect via a change in habitat complexity

Modification to a habitat structure is a major factor of pressure on the fish community. Indeed, changes in habitat complexity caused by the proliferation of plants or animals affect fish abundance and distribution (Levi and Francour, 2004; Le Pape et al., 2003; Kostecki et al., 2011; Orr et al., 2014). The proliferation of green macroalgae both significantly increases the structural complexity of the habitat and modifies the invertebrate community (Hull, 1987; Quillien et al., 2015). These changes could impact fish settlement, shelter behaviour and foraging success (Aarnio and Mattila, 2000; Andersen et al., 2005; Nordström and Booth, 2007) and therefore might influence their abundance and survival (Pihl and van der Veer, 1992; Wennhage, 2002; Pihl et al., 2005). At first, an increase in habitat complexity might be profitable to fish (Sogard and Able, 1991; Andrades et al., 2014) by providing shelter (Manderson et al., 2000; Adams, 2005; Kamimura and Shoji, 2013) and food resources (Stoner et al., 2001). Above a low level of proliferation, which varies from one macroalgal species to another, the cover of the substrate and the clogging of available space from the bottom up to the water surface have negative consequences on ichthyofauna (Pihl et al., 1995; Wennhage and Pihl, 2007; Jokinen et al., 2015).

2.5.4.2 Hydrochemical modifications and toxicity

Green tides lead to major changes in water chemistry and biogeochemical cycles (Valiela et al., 1997; Jones and Pinn, 2006) both by modifying dissolved oxygen concentration and amplitude and by releasing toxic substances (Johnson and Welsh, 1985; Sogard and Able, 1991; Harder et al., 2004).

The hypoxic-to-anoxic conditions (Bejda et al., 1992; Engström-Öst and Isaksson, 2006) commonly recorded during the significant proliferation of green macroalgae (Johnson and Welsh, 1985) induce decreases in growth rate (Thetmeyer et al., 1999; Phelan et al., 2000; McNatt and Rice, 2004), predation efficiency and fish survival (Kramer, 1987; Taylor and Miller, 2001). Dissolved oxygen concentrations recorded at both of the impacted sites during the daytime and at SBI during the night-time at a medium density of green macroalgae were not detrimental to fish (negative effects on growth do not occur above oxygen concentrations of 3-5 mg.L^{-1}; Batiuk et al., 2009). Nevertheless, detrimental oxygen concentration could have occurred at night during high proliferations and when macroalgal mats decayed (Johnson and Welsh, 1985). In addition to potential hypoxic conditions, the wide daily amplitude in oxygen concentration recorded during the 24 h additional survey could have affected fish condition and fitness (Batiuk et al., 2009; Miller Neilan and Rose, 2014).

Detrimental effects may also have been induced by natural organic toxins exuded by macroalgae or their bacterial flora (Sogard and Able, 1991; Harder et al., 2004). These toxic exudates have been reported to affect neighbouring fauna (Magre, 1974; Nelson et al., 2003). The synergistic effects of low oxygen levels and/or high fluctuations in oxygen concentration, along with living or senescent macroalgae exudates, could be detrimental (Engström-Öst and Isaksson, 2006; Sogard and Able, 1991), as revealed by the direct dose-related mortality between *Ulva* spp. exudates and invertebrates at low oxygen concentration (Wang et al., 2011).

In addition to direct impacts on the fish community, these hydrochemical modifications simultaneously affect invertebrate community composition (Quillien et al., 2015) and abundance, which could decrease the number of invertebrate preys available for the fish species (Fletcher, 1996; Raffaelli et al., 1998; Lyons et al., 2014). These alterations could modify trophic cycles (Deudero et al., 2014) and might impact the capacity of coastal and estuarine habitats to host fish and fulfil their food demands (Perkins and Abbott, 1972; Bolam et al., 2000).

2.5.5 From local-scale effects to consequences for fish populations

The characteristics of macroalgae proliferations (*i.e.* species assemblage, density, coverage percentage and bloom duration) and the seasonal synchronisation of proliferations with the fish species life cycle are important factors that modulate the effects of macroalgal blooms on the fish community. At both sites of the sandy beach and estuarine mudflat areas impacted by green tides, changes in habitat conditions strongly affected fish communities. The effects of green tides on fish vary according to the fishes' functional groups and have led to a shift in species composition between the control and the impacted sites. During massive proliferations, all of the fish species are affected, and locally, they eventually disappear. These responses of fish communities to green tides have been analysed as a reaction to a global stress induced by green tides. However, attributing these responses to one or another habitat condition modification (structural, hydrochemical and trophic changes or combined effects) will require further enquiries.

Coastal areas affected by large amounts of green macroalgae constitute less suitable habitats and reduce the local amount both of settled juvenile fish (*e.g.* a 30%-40% decrease in juvenile flatfish; Pihl et al., 2005) and of resident species (Dolbeth et al., 2007). Fish population size at one life stage is the result of the carrying capacity of essential habitats during previous life stages (Costa et al., 2002; Vasconcelos et al., 2013). The effects of habitat suitability on fish survival are especially important for nursery-dependent species (Le Pape and Bonhommeau, 2015), which represent a large proportion of exploited species (*i.e.* approximately 75%; Seitz et al., 2014). The reduction of the extent and/or of the quality of nursery grounds could create a bottleneck in recruitment and thus limit the overall population size (Turner and Boesch, 1987; Beverton, 1995; Peterson et al., 2000).

The degradation of coastal and estuarine essential, sensitive and non-widespread habitats is, along with fisheries, one of the major causes of declining fish populations on the continental shelf (Gibson, 1994; Hughes et al., 2015). Because green tides are a spreading phenomenon, the potential nursery habitat capacity of a large number of fish species may have been significantly reduced.

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Supplementary Table 2.1 - Total catches of fish species (number of individuals by sample unit) and macroalgae densities (in wet weight kg.m^{-2}) in the sandy beach area in 2013 at each site (SBC: Sandy Beach Control and SBI: Sandy Beach Impacted) for each sampled date. Dates in bold correspond to the period of green tide proliferation. A star is added when the sample date was excluded from the MDS analysis (no catch during green tide proliferation)

		Fish species															**Groups of macroalgae**		
Site	**Date**	*Atherina presbyter*	*Buglossidium luteum*	*Ciliata mustela*	*Dicentrarchus labrax*	*Echiichthys vipera*	*Liza aurata*	*Pegusa lascaris*	*Pleuronectes platessa*	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Scophthalmus rhombus*	*Solea solea*	*Sprattus sprattus*	*Symphodus melops*	*Trigla lucerna*	Expanded blade *Ulva* spp.	*Pylaiella littoralis*	Other macroalgae
SBC	2013-04-09	21					1												
	2013-04-23																		
	2013-05-07																		
	2013-05-23								1										
	2013-06-07		10						9		21							0.011	
	2013-06-28		0					2	231		3	3	18			1		0.263	
	2013-07-11			1				3	128		2	5	2			1	0.014	0.189	
	2013-07-29											2							
	2013-08-12				3	22		5	85		22	4	6	44	2				
	2013-08-26		3		4	1			35		6	2	2	80	2	31			
	2013-09-10		1		3	2			12		24	2			1	1			0.012
	2013-09-24	55			3				1		12			1412					
	2013-10-09	1				1			7		1			2					0.041
	2013-10-22	18				3		1	10	11	36		2	343		3		0.011	
SBI	2013-04-09						1												
	2013-04-23																		
	2013-05-07										3								
	2013-05-23						7		2										
	2013-06-07								6	2				46			0.127		
	2013-06-28 *																0.486		
	2013-07-11 *																0.578		
	2013-07-29													15			0.345		
	2013-08-12	1			1						3			3			0.322		
	2013-08-26				1					4		1		87			0.176	0.059	
	2013-09-10								1		1			4			0.189	0.35	
	2013-09-24				8		1							820			0.018	0.006	
	2013-10-09	2			2		19				6						0.039	0.112	
	2013-10-22						7			10	2			57			0.004	0.125	0.043

Supplementary Table 2.2 - Total catches of fish species (number of individuals by sample unit) and macroalgae densities (in wet weight kg.m^{-2}) in the sandy beach area in 2014 at each site (SBC: Sandy Beach Control and SBI: Sandy Beach Impacted) for each sampled date. Dates in bold correspond to the period of green tide proliferation. Sample unit marked by a cross is those during which half of the trawl hauls were two-times longer to test for sensitivity of trawl catchability to macroalgal biomass

		Fish species																						**Groups of macroalgae**		
Site	**Date**	*Ammodytes tobianus*	*Atherina presbyter*	*Buglossidium luteum*	*Callionymus lyra*	*Chelon labrosus*	*Cyclopterus lumpus*	*Dicentrarchus labrax*	*Diplodus sargus sargus*	*Echiichthys vipera*	*Hyperoplus immaculatus*	*Liza aurata*	*Pegusa lascaris*	*Pleuronectes platessa*	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Pomatoschistus pictus*	*Scophthalmus rhombus*	*Solea lascaris*	*Solea solea*	*Spondyliosoma cantharus*	*Sprattus sprattus*	*Trigla lucerna*	Expanded blade *Ulva* spp.	*Pylaiella littoralis*	Other macroalgae
SBC	2014-04-11													2		3										
	2014-04-23	1	2			2		2						1	1			1				199				
	2014-05-13		2																							
	2014-05-26																	1				35				0.003
	2014-06-11		427	1										3								15	4			
	2014-06-25		1445										1	6	2	3			1				3			
	2014-07-24		15	2			1	88					1	12	3	8	1	5	1	1	3	759	4			0.001
	2014-08-07		68	1				79						3		71		1		3	9	15	1			
	2014-08-25		165					4	4													644				
	2014-09-06		122		1			13		2				3		332						296				
	2014-09-22		231					14	2							10						719				
	2014-10-06		120					3														284				
	2014-10-21							1			1															
SBI	2014-04-11							2						2	2											
	2014-04-23							8				6			13											
	2014-05-13											12														
	2014-05-26					296									2					1		1		0.178		
	2014-06-11		1			1						26										31		0.16	0.018	
	2014-06-25		86									39										1		0.253	0.011	
	2014-07-24		168					43							3							259		0.016	0.012	
	2014-08-07		26					110							14							152		0.033	0.016	
	2014-08-25		276					57							12							3		0.016	0.001	
	2014-09-06		47					16				7			4							205		0.282	0.086	
	2014-09-22 +		2					14				12		1	7									0.236	0.012	
	2014-10-06		147					40				41												0.025		
	2014-10-21		126					29																		

Supplementary Table 2.3 - Total catches of fish species (number of individuals by sample unit) and macroalgae densities (in wet weight kg.m^{-2}) in the sandy beach area during the 24h survey in 2014 at each site (SBC: Sandy Beach Control and SBI: Sandy Beach Impacted)

				Fish species														**Groups of macroalgae**		
Site	**Date**	**Hour**	**Height of tide**	*Anguilla anguilla*	*Atherina presbyter*	*Buglossidium luteum*	*Chelon labrosus*	*Dicentrarchus labrax*	*Liza aurata*	*Pegusa lascaris*	*Pleuronectes platessa*	*Pomatoschistus microps*	*Pomatoschistus pictus*	*Scophthalmus rhombus*	*Solea solea*	*Sprattus sprattus*	*Trigla lucerna*	Expa.nded blade *Ulva* spp.	*Pylaiella littoralis*	Other macroalgae
SBC	2014-06-05	08:00	4.4								2							0.021		0.005
		09:00	5.5															0.003		0.005
		10:00	6.9																	
		11:00	8.1					1												
		13:00	8.8															0.039		0.021
		14:00	8.3		6															
		15:00	7.4					1		1	4			1				0.002		0.006
		16:00	6.4					1	1	2	5			1	1			0.045		0.034
		17:00	5.3				2			2	4	1						0.004		0.004
	2014-06-06	02:00	8.5					6		1		5		1						
		03:00	7.7							1	1	1				1		0.06		0.024
		04:00	6.7							1	16	3		2		2	1	0.058		0.022
		05:00	5.6								4	2				2		0.007		0.003
SBI	2014-06-05	08:00	4.4			2					7	3						0.28		
		09:00	5.5			4					2							0.46		
		10:00	6.9			1	1	1				1	1		1			0.339	0.045	
		11:00	8.1	1								1				1		0.368	0.052	
		13:00	8.8					2				9						0.484	0.036	
		14:00	8.3									6						0.452	0.008	
		15:00	7.4			4						1						0.464	0.016	
		16:00	6.4			3						6						0.465	0.035	
		17:00	5.3			1	1				1	3						0.399	0.021	
	2014-06-06	02:00	8.5				2	2				20			1			0.008	0.005	
		03:00	7.7					2				20			1			0.38	0.02	
		04:00	6.7			1					1	2	1					0.465	0.035	
		05:00	5.6			2					2	4						0.47	0.03	

Supplementary Table 2.4 - Total catches of fish species (number of individuals by sample unit) and macroalgae densities (in wet weight kg.m^{-2}) in the estuarine mudflat area in 2014 at each site (EMC: Estuarine Mudflat Control and EMI: Estuarine Mudflat Impacted) for each sampled date. Dates in bold correspond to the period of green tide proliferation. A star is added when the sample date was excluded for the MDS analysis (no catch during green tide proliferation)

		Fish species																**Groups of macroalgae**		
Site	**Date**	*Atherina presbyter*	*Buglossidium luteum*	*Dicentrarchus labrax*	*Gobius niger*	*Gobius paganellus*	*Liza aurata*	*Mullus surmuletus*	*Pleuronectes platessa*	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Pomatoschistus pictus*	*Scophthalmus rhombus*	*Solea solea*	*Spinachia spinachia*	*Sprattus sprattus*	*Symphodus melops*	Expanded blade *Ulva* spp.	Filamentous green macroalgae	Other macroalgae
EMC	2014-04-14	26								9										
	2014-04-22	40			1				2	9									0.005	
	2014-05-12	12				1			4	8		2						0.002	0.02	
	2014-05-27								3	34	2	1				1			0.021	0.005
	2014-06-12	6	1						1	40		1	1	1			1	0.002	0.045	0.009
	2014-06-26	662							1	116	22	6	3		1			0.005	0.021	0.007
	2014-07-11	32								13	1									0.005
	2014-07-25	153	1						1	8	1								0.001	0.019
	2014-08-08	11								8	25	1				35			0.007	0.001
	2014-08-26	22								20	48	1				3			0.012	0.003
	2014-09-07	69		1						18	129	1				88			0.044	
	2014-09-23	58						1		32	129					13			0.074	0.001
	2014-10-07	8								26	58	2							0.159	0.051
	2014-10-20	69								9	148					5			0.012	0.02
EMI	2014-04-14	40								1									0.015	0.004
	2014-04-22	34								2								0.006	0.162	0.015
	2014-05-12 *																	0.016	0.067	0.001
	2014-05-27	4								4								0.075	0.092	
	2014-06-12	12								1								0.023	0.008	0.018
	2014-06-26	1419								1								0.018	0.031	0.02
	2014-07-11	376		2														0.004	0.046	0.019
	2014-07-25	510																	0.005	0.018
	2014-08-08	136		2														0.001	0.038	0.029
	2014-08-26	8								1								0.002	0.137	0.01
	2014-09-07	39		5						1						17			0.128	0.014
	2014-09-23	108		2						2						56			0.032	0.006
	2014-10-07	75								7								0.021	0.222	0.008
	2014-10-20	38		2			60			1								0.034	0.09	0.004

Conclusion du chapitre

L'analyse conduite dans ce chapitre visait à examiner les conséquences des marées vertes sur les communautés ichtyologiques dans les deux types d'habitats affectés par les marées vertes, les estrans sableux et les vasières estuariennes.

Dans chacun de ces secteurs, nos résultats mettent en avant des effets des proliférations de macroalgues sur les communautés ichtyologiques. Ces conséquences sont modulées en fonction de la composition spécifique, de la densité et de la durée du bloom. L'augmentation de l'intensité de la perturbation entraine une réduction progressive de la diversité et de la densité de l'ichtyofaune intertidale. Au travers d'analyses par guilde fonctionnelle, nos résultats ont permis de mettre en évidence une sensibilité variable des espèces de poissons face à cette perturbation selon leur degré de tolérance aux perturbations environnementales, leur capacité de déplacement et leur distribution dans la colonne d'eau. Ces contrastes se traduisent par une modification progressive de la composition de l'ichtyofaune, vers des espèces résidentes et des espèces mobiles, moins sensibles aux perturbations de l'habitat induites par les marées vertes. Lors de fortes proliférations, les marées vertes entrainent une disparition locale de l'ichtyofaune.

Les réponses des communautés ichtyologiques mettent donc en évidence une réduction de la qualité des habitats intertidaux affectés par les marées vertes et amènent à s'interroger sur les processus par lesquels cette perturbation affecte l'ichtyofaune à l'échelle des organismes. L'analyse de ces processus fait l'objet du second chapitre dans lequel des espèces témoins sont sélectionnées pour appréhender leurs réponses face aux proliférations algales à l'échelle de l'individu.

Chapitre 3

Influence des marées vertes dans une nourricerie côtière sur la sélection de l'habitat et la performance individuelle de juvéniles de poissons

3. Influence des marées vertes dans une nourricerie côtière sur la sélection de l'habitat et la performance individuelle de juvéniles de poissons

Introduction du chapitre

Les résultats du chapitre précédent ont permis de caractériser les conséquences des marées vertes sur l'ichtyofaune à l'échelle des communautés. Des réponses à ce haut niveau d'organisation biologique transcrivent une intégration profonde de la perturbation dans les écosystèmes mais ne permettent pas de déterminer les processus par lesquels les macroalgues vertes affectent l'ichtyofaune. Les marées vertes sont des phénomènes complexes qui modifient simultanément les conditions physiques, chimiques et trophiques des habitats (Fletcher, 1996; Raffaelli et al., 1998). Ces modifications perturbent la qualité des habitats et peuvent affecter le comportement, la croissance, la condition et *in fine* la survie des organismes (Johnson and Welsh, 1985; Isaksson et al., 1994; Pihl et al., 2005), et conduire aux conséquences observées à l'échelle des communautés.

Dans ce chapitre, nous nous sommes intéressés aux effets des marées vertes au niveau de l'individu, afin d'examiner plus finement les réponses de l'ichtyofaune et de caractériser les différents mécanismes de défense mis en œuvre par les organismes. Pour cette échelle d'analyse, un focus a été fait sur la zone d'estran sableux (baie de Saint-Brieuc) ainsi que sur la fonction de nourricerie assurée par cet habitat. Les stades juvéniles représentent une proportion conséquente de l'ichtyofaune se concentrant dans les habitats côtiers intertidaux (Beck et al., 2001; Seitz et al., 2014). Une modification de leurs performances individuelles peut avoir des répercussions sur le recrutement et donc sur la taille des populations d'intérêt halieutique (Turner and Boesch, 1987; Gibson, 1994; Piet and Rijnsdorp, 1998; Able, 1999; Peterson et al., 2000; Jones et al., 2002). Cette étude s'est portée sur le sprat (pélagique), le bar (démersal) et la plie (benthique), suivis sur un site contrôle et un site impacté de la baie. Le positionnement différent de ces trois espèces dans la colonne d'eau a permis de tester un effet de l'utilisation de l'habitat sur leurs réponses face aux marées vertes. L'analyse a été menée au travers d'une approche multi-indice, considérant la sélection de l'habitat et les ajustements des performances individuelles. Dans un premier temps, la sélection de l'habitat pour chacune des espèces a été examinée par l'analyse combinée de leurs densités et de leurs signatures isotopiques spécifiques à chacun des habitats. Ensuite, les ajustements physiologiques des individus ont été considérés à travers l'analyse de réponses instantanées (capacité de défense antioxidante), ou mises en place à court terme (réserves lipidiques, taux de croissance journalière) et à moyen terme (indice de condition sur critères morphométriques).

Dans le cadre de cette partie de la thèse, deux stagiaires ont participé à la réalisation de travaux de laboratoire et d'analyses préliminaires des résultats.
Pour son stage de Master 1, Marine RANDON a réalisé les montages des photographies permettant la lecture et le comptage des stries journalières des otolithes de sprats ainsi que l'analyse préliminaire des performances individuelles de sprat (taux de croissance journalière, réserves lipidiques et condition).
Au cours d'un stage de césure de 2 mois, Clément LEBOT a aussi participé à ce travail, notamment pour l'acquisition, la lecture et le comptage des stries journalières des otolithes de bar.

Influence of Green Tides in Coastal Nursery Grounds on the Habitat Selection and Individual Performance of Juvenile Fish

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3.1 Abstract

Coastal ecosystems, which provide numerous essential ecological functions for fish, are threatened by the proliferation of green macroalgae that significantly modify habitat conditions in intertidal areas. Understanding the influence of green tides on the nursery function of these ecosystems is essential to determine their potential effects on fish recruitment success. In this study, the influence of green tides on juvenile fish was examined in an intertidal sandy beach area, the Bay of Saint-Brieuc (Northwestern France), during two seasonal cycles of green tides with varying levels of intensity. The responses of three nursery-dependent fish species, the pelagic *Sprattus sprattus* (L.), the demersal *Dicentrarchus labrax* (L.) and the benthic *Pleuronectes platessa* L., were analysed to determine the effects of green tides according to species-specific habitat niche and behaviour. The responses to this perturbation were investigated based on habitat selection and a comparison of individual performance between a control and an impacted site. Several indices on different integrative scales were examined to evaluate these responses (antioxidant defence capacity, total lipid, morphometric condition and growth). Based on these analyses, green tides affect juvenile fish differently according to macroalgal density and species-specific tolerance, which is linked to their capacity to move and to their distribution in the water column. A decreasing gradient of sensitivity was observed from benthic to demersal and pelagic fish species. At low densities of green macroalgae, the three species stayed at the impacted site and the growth of plaice was reduced. At medium macroalgal densities, plaice disappeared from the impacted site. The growth of sea bass and the total lipid content of sprat were reduced at the impacted site. Finally, when high macroalgal densities were reached, none of the studied species were captured at the impacted site. Hence, sites affected by green tides are less favourable nursery grounds for all the studied species, with species-specific effects related to macroalgal density.

Keywords: green tide, nursery grounds, habitat suitability, individual scale, multi-index analysis

3.2 Introduction

Coastal areas are productive systems that encompass essential habitats, such as nursery grounds, for various fish species (Elliott and Dewailly, 1995; Beck et al., 2001), including many economically valuable species (Seitz et al., 2014). The recruitment success of these fish species is highly dependent on the quality of coastal nurseries, which modulate the growth, condition and survival of juvenile fish (Gibson, 1994; Vasconcelos et al., 2013; Le Pape and Bonhommeau, 2015). The suitability of these sensitive habitats is threatened by numerous anthropogenic pressures (Halpern et al., 2008), including seasonal massive proliferations of free-floating green macroalgae, called green tides. This form of eutrophication has spread along many coastlines and has increased in occurrence, abundance and duration worldwide since the 1970s (Fletcher, 1996; Ye et al., 2011; Smetacek and Zingone, 2013).

The proliferation of green macroalgae leads to major changes in habitat structure (Isaksson and Pihl, 1992; Isaksson et al., 1994; Jokinen et al., 2015), water chemistry and biogeochemical cycles (Sfriso et al., 1992; Engström-Öst and Isaksson, 2006). These changes disturb ecological communities (Jokinen et al., 2015; Quillien et al., 2015) and affect both the trophic food webs and ecosystem processes (Raffaelli et al., 1998; Raffaelli, 2000; Arroyo et al., 2012). Abiotic and biotic modifications linked to green tides could thus affect the habitat suitability for coastal nursery-dependent fish species (Pihl et al., 2005; Jokinen et al., 2016, 2015; Le Luherne et al., 2016). The consequences of these changes for fish species are modulated by the composition, intensity and duration of the macroalgal bloom (Lyons et al., 2014; Le Luherne et al., 2016). Patchy or weak macroalgal proliferation could be beneficial to juvenile marine fish by providing new food resources and new shelter on unvegetated substrates, in relation to the increase in habitat complexity (Sogard and Able, 1991; Stoner et al., 2001; Kamimura and Shoji, 2013). Conversely, high and long-term proliferation could be detrimental for fish (Pihl et al., 2005; Jokinen et al., 2016) and could even lead to their total disappearance from impacted sites (Le Luherne et al., 2016). The modification of habitat conditions caused by green tides and the response of fish communities have been previously described (Pihl et al., 2005; Jokinen et al., 2015; Le Luherne et al., 2016). However, the underlying ecological processes, especially the impacts of green tides on habitat selection and individual performance, for various nursery-dependent fish species requires investigation (Lyons et al., 2014).

In Northwestern France, many shallow sandy beaches experience seasonal proliferations of green macroalgae. Among them, the Bay of Saint-Brieuc is the most heavily impacted by green tides (Charlier et al., 2007). Each year, the intertidal area of this coastal bay is covered by green macroalgae that develops in free-floating expanded blade form (mostly *Ulva armoricana* and *U. rotundata*) from spring to the end of summer (Charlier et al., 2007; Merceron et al., 2007; Perrot et al., 2014; Le Luherne et al., 2016). In temperate latitudes, this period corresponds to the settlement and growth of juvenile marine fish in shallow coastal areas (Gibson, 1994; Amara, 2003; Le Luherne et al., 2016). To analyse the impact of green tides on the nursery-dependent fish species that gather in the Bay of Saint-Brieuc, three teleost fish species with different vertical distributions, and thus potentially different responses to green tides (Le Luherne et al., 2016), were examined: a pelagic species, the European sprat *Sprattus sprattus* (Linnaeus, 1758); a demersal species, the European sea bass *Dicentrarchus labrax* (Linnaeus, 1758); and a benthic species, the European plaice *Pleuronectes platessa* Linnaeus, 1758. The effects of green tides on these three species were evaluated by comparing, for each species, behaviour and individual performance at an impacted and a control site during two annual cycles. The characterisation of species-specific fish responses was based on multi-index analysis focusing on different integrative and temporal scales (Adams, 2002). Initially, the influence of green tides on habitat selection was examined based on the combination of fish density and habitat-specific stable isotope signature in fish muscle (Vinagre et al., 2008; Quillien et al., 2016). Then, physiological adjustments were analysed for individuals who lived in coastal areas during green macroalgae proliferations. Instantaneous to mid-term physiological responses of fish to green tides were assessed using fish antioxidant defence capacity (Arts et al., 2004), muscle total lipid (Post et al., 2007; Logan et al., 2008; Svensson et al., 2014), morphometric condition (Fechhelm et al., 1995) and daily growth rate (Stevenson and Campana, 1992; Baumann et al., 2006). These responses were analysed with respect to the period and intensity of green tides and the life history of the three studied fish species.

We address several questions to improve the understanding of the green tide influence on the individual scale, in particular: (1) we investigated fish responses on different integrative scales of perturbation, from the perception of a perturbation to the implementation of behavioural responses, (2) we tested for the effect of the macroalgae density on fish responses and (3) we examined the influence of species ecological niche and behaviour on their responses.

3.3 Materials and Methods

3.3.1 Ethics statement

Permission to collect fish with a trawl net in the study areas was granted by the French Departmental Authority for Maritime Affairs "Direction Départementale des Territoires et de la Mer (DDTM) des Côtes d'Armor" (ddtm-dml@cotes-darmor.gouv.fr) after examination of the sampling protocol. Surveys in the impacted area were performed in a marine protected area, the National Nature Reserve of Saint-Brieuc. Sampling was conducted in full agreement and in collaboration with the reserve managers. In accordance with European Commission recommendation 2007/526/EC, on revised guidelines for the accommodation and care of animals used for experimental and other scientific purposes, fish sampling in the wild without experimental handling did not require an ethics agreement. Fish caught were sacrificed by hypothermia. The present field study did not involve endangered or protected species.

3.3.2. Selection of the study sites

To examine the effects of green tides on fish habitat selection and individual performance, a control (48°35.7'N, 2°33.3'W) and an impacted (48°31.9'N, 2°39.7'W) site were selected within the same water body, the Bay of Saint-Brieuc (Fig 3.1). Sites were chosen for their similarity in sediment structure and their proximity (10 km) to be comparable in terms of larval supply and habitat suitability (Le Luherne et al., 2016). Moreover, the 10 km distance was considered sufficient to prevent significant movement of juveniles of the studied fish species between sites (Hansson et al., 1997; Burrows et al., 2004; Green et al., 2012), avoiding potential mixing.

3.3.3. Field sampling

The sampling design was based on a standardised field survey performed in 2013 and 2014 from April until October to investigate the response of the fish community to green tides (Le Luherne et al., 2016). At both the control and impacted sites, sampling was conducted twice a month at the beginning of ebb tide in the shallow upper intertidal zone. At each sampling date and site, 6 successive trawl hauls of 25 m were conducted with a trawl net (mesh of 8 mm) towed by two people at a depth between 0.4 and 0.7 m. An additional sampling session was conducted over a 24 h period in late spring in 2014 (Le Luherne et al., 2016). The biomass of expanded blade *Ulva* spp. towed in each trawl haul was weighed as the wet weight after one minute of draining.

Simultaneously, seawater physico-chemical parameters (*i.e*. temperature (°C), salinity, pH and dissolved oxygen concentration (mg.L^{-1})) were measured in the middle of the water column using a multiparameter probe (Hanna HI 9828/4-02).

For the three selected species, fish were collected and stored in coolers in the field (for a one to three hour period). According to species, fish were stunned, unconscious or dead prior to be freezing and were all dead before their transport to the laboratory. At the laboratory, they were measured (total length to the nearest mm) and weighed (total mass to the nearest mg), before being individually frozen at -20 °C for further analysis. For each fish species, only sampling dates that collected at least 3 individuals at both sites after the onset of the green tide were retained for analyses on the individual scale.

In addition, to test the activation of antioxidant defence capacity in response to green tides, a specific protocol was set. Fish of each species were collected on one date during macroalgae proliferation (Supp. Table 3.1) and were deep-frozen individually in the field at -80 °C in liquid nitrogen.

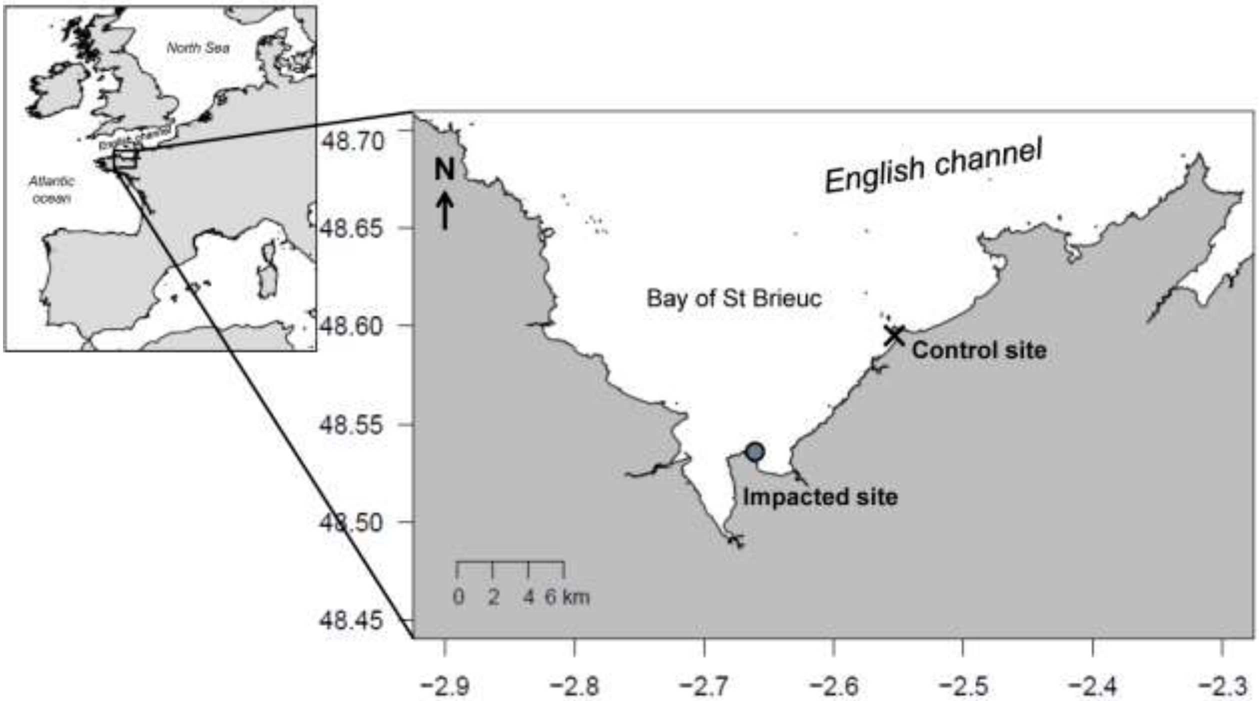

Figure 3.1 - Location of the control (C) and impacted (I) sites in the study area, Northwestern France

3.3.4. Selection of fish for analysis on the individual scale

Green tides induced a drastic decrease in fish density at species-specific levels of macroalgal density until the total disappearance of fish during the period of maximum macroalgae density (Le Luherne et al., 2016). For each species and each year, the sampling allowed the examination of fish response during green tides for a restricted number of sampling dates that differed between species (Table 3.1 and Supp. Table 3.1).

All the selected fish were used for the R relative morphometric condition analysis (Table 3.1). For the $\delta^{13}C$ signature, C:N ratio and daily growth rate (DGR) analyses, sub-samples of three to five individuals representative of the most registered size class at both sites were selected for each selected sampling date (Table 3.1). For Trolox equivalent antioxidant capacity (TEAC) analyses, all deep-frozen fish within the same length class were analysed (Table 3.1).

Table 3.1 - Number (N) of fish analysed and their total length range (TL in mm) at the control and impacted sites with the corresponding number of sampling dates (N of dates) analysed for the sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) in 2013 and 2014. For each index, “integration” refers to the range of its time of integration (or turnover rate).

Type of analysis	Integration	Species	Year	Site	N	TL (mm)	N of date
$\delta^{13}C$ signature	Month	Sprat	2013	Control	25	[35-47]	5
				Impacted	19	[33-47]	5
			2014	Control	25	[30-41]	5
				Impacted	23	[27-46]	5
		Sea bass	2014	Control	40	[28-135]	6
				Impacted	35	[26-134]	6
		Plaice	2013	Control	5	[36-52]	1
				Impacted	5	[33-45]	1
			2014	Control	11	[33-46]	1
				Impacted	6	[24-46]	1
Antioxidant defence capacity	Hour	Sprat	2013	Control	5	[36-47]	1
				Impacted	5	[33-47]	1
			2014	Control	10	[34-57]	1
				Impacted	11	[30-63]	1
		Sea bass	2014	Control	8	[109-135]	1
				Impacted	6	[86-133]	1
		Plaice	2014	Control	6	[65-78]	1
				Impacted	7	[55-71]	1
C:N ratio (lipid storage)	≤ Week	Sprat	2013	Control	15	[36-47]	3
				Impacted	12	[33-47]	3
			2014	Control	25	[30-41]	5
				Impacted	23	[27-46]	5
		Sea bass	2014	Control	26	[62-135]	3
				Impacted	19	[53-134]	3
		Plaice	2013	Control	5	[36-52]	1
				Impacted	5	[33-45]	1
			2014	Control	11	[33-46]	1
				Impacted	6	[24-46]	1

R morphometric condition	Weeks	Sprat	2013	Control	99	[35-46]	2
				Impacted	67	[32-49]	2
			2014	Control	501	[32-71]	5
				Impacted	312	[31-77]	5
		Sea bass	2014	Control	204	[25-141]	6
				Impacted	215	[23-134]	6
		Plaice	2013	Control	9	[25-73]	1
				Impacted	6	[33-45]	1
			2014	Control	32	[36-75]	1
				Impacted	7	[31-76]	1
Daily growth rate	≤ Week	Sprat	2013	Control	17	[35-41]	4
				Impacted	22	[32-44]	5
			2014	Control	23	[30-41]	5
				Impacted	22	[27-46]	5
		Sea bass	2014	Control	17	[28-75]	4
				Impacted	17	[26-56]	5
		Plaice	2013	Control	5	[36-52]	1
				Impacted	5	[33-45]	1
			2014	Control	8	[36-75]	1
				Impacted	7	[31-76]	1

3.3.5. Antioxidant defence capacity

Antioxidant defence implemented to counteract oxidative stress (Vinagre et al., 2014) involves several mechanisms with species-specific patterns of activation (Madeira et al., 2013). Fish total antioxidant defence capacity was assessed by measuring the Trolox equivalent antioxidant capacity (TEAC; mM Trolox equivalent). TEAC measurements were performed using the Antioxidant Assay Kit (AA Kit) (Sigma-Aldrich® - St Louis, USA) and following the kit procedure. Analyses were performed on a 50 mg piece of dorsal white muscle diluted in 1 mL of 1x Assay buffer. In parallel, the protein concentration (mg of soluble protein.mL^{-1}) was measured in accordance with the manufacturer's instructions using the Bicinchoninic Acid Protein Assay Kit with Bovine Serum Albumin as standard (Sigma-Aldrich® - St Louis, USA). Before measuring the protein concentration, the sample solutions used for the TEAC measurements were diluted 1 in 5 with the 1x Assay buffer of the AA Kit to be in the range of protein concentrations covered by this method of analysis. The compatibility between reagents of the two kits was ensured by Sigma-Aldrich® Company. Measurements of both TEAC and soluble proteins were performed with a spectrofluorimeter (SAFAS Flx-Xenius, Monaco).

The measured amounts of TEAC were proportional to the muscle soluble proteins released by fish muscle grinding and the TEAC results were thus expressed in mM Trolox equivalent/mg of soluble protein.

Triplicate measurements were performed for the two biochemical analyses, and antioxidant defence capacity was analysed based on the individual mean of the values.

For the antioxidant defence capacity, experimental studies have determined a turnover rate of one to a few hours for juvenile fish (Adams, 2002; Madeira et al., 2013).

3.3.6. Stable isotope analysis

Dorsal white muscle samples were freeze-dried, ground and encapsulated in tin cups to be analysed with a continuous-flow isotope-ratio mass spectrometer (Delta V Plus, Thermo Scientific) coupled to an elemental analyser (Flash 2000, Thermo Scientific). Two indices were derived from these analyses.

Firstly, the fish $\delta^{13}C$ signature was used to examine the fish habitat fidelity (Vinagre et al., 2008). The $\delta^{13}C$ signatures were expressed as isotope ratios relative to the international standard (*i.e.* VPDB: Vienna Pee Dee Belemnite; Peterson and Fry, 1987) using the following formula:

$$\delta^{13}\text{C (in ‰)} = \left[\frac{(^{13}\text{C}{:}^{12}\text{C}_{sample})}{(^{13}\text{C}{:}^{12}\text{C}_{VPDB})} - 1\right] \times 10^3$$

Three characteristics of this marker make it useful for discriminating between the impacted and control sites: (i) the $\delta^{13}C$ signature of an organism is related to the signature of its prey (DeNiro and Epstein, 1978). (ii) Terrestrial primary producers have lower $\delta^{13}C$ than marine producers (Haines and Montague, 1979; Vinagre et al., 2008), so the $\delta^{13}C$ of fish captured at the impacted site (in the same marine water mass but closer to river inputs) should be lower than those of fish at the control site (Kostecki et al., 2010). (iii) The presence of large amounts of green macroalgae influence the $\delta^{13}C$ of particulate organic matter (POM) at the base of the food web and this modification of $\delta^{13}C$ propagates along the food web, *i.e.* the invertebrate prey of juvenile fish have $\delta^{13}C$ signatures that are approximately 1‰ higher at sites impacted by green tides than at control sites (Quillien et al., 2016).

Based on these three characteristics, the spatiotemporal patterns in fish $\delta^{13}C$ could be used to trace fish habitats. The higher fish $\delta^{13}C$ signature at the impacted than at the control site reveals an inversion of the natural upstream-downstream estuarine gradient (Kostecki et al., 2010). This inverse pattern could be attributed to the impact of green tides (Quillien et al., 2016) and reveals the fidelity of fish to the restricted area impacted by green tides.

The turnover rates of the $\delta^{13}C$ signatures in the white muscle of juvenile fish, revealed by experimental and field studies, reach 3 weeks on average (Suzuki et al., 2005; Guelinckx et al., 2006, 2007; Vinagre et al., 2008) and 2 months for some species (Buchheister and Latour, 2010). Hence, as the $\delta^{13}C$ signatures represent an integration of habitat use during a time period linked to the turnover rate, changes in the kinetics of fish $\delta^{13}C$ signatures were analysed according to habitat conditions at the same date but also for 2 earlier sampling dates (*i.e*. approximately 30 days earlier).

Secondly, the C:N ratio was assessed to estimate fish muscle lipid content (DeNiro and Epstein, 1977; Post et al., 2007; Logan et al., 2008). The C:N ratios were calculated using the following formula:

$$C\colon N_{\text{ratio}} = \frac{\%\,C}{\%\,N}$$

where $\%C={}^{13}C/({}^{13}C+{}^{12}C)$ and $\%N={}^{15}N/({}^{15}N+{}^{14}N)$. C:N ratios are expressed as the mass ratio.

A preliminary delipidation was performed based on the protocol developed by (Chouvelon et al., 2014) to measure fish muscle basal signature (*i.e*. without lipid; Deudero et al., 2004). This analysis allowed us to validate the independence between fish length and fish basal signature for each species at the studied length range (Supp. Table 3.2). The fish total lipid content was analysed using the C:N ratios measured on non-delipidated muscle as a proxy.

The turnover rate of muscle total lipid for juvenile fish has been estimated to be less than a week (Gilliers et al., 2006).

3.3.7. Morphometric condition – *R relative morphometric condition*

R is a length-independent relative body condition index that examines the deviation of observed mass from predicted mass (using the log length-mass relationship). It is computed as follows (Fechhelm et al., 1995):

$$R = logW - logWc$$

where *W* is the observed total body mass and *Wc* is the computed body mass derived from the log length-mass relationships. Log length-mass relationships were established by species for each studied year based on all the individuals caught (Supp. Table 3.3).

The R morphometric condition index was preferred to the widely used K Fulton's condition index as the linear relation between fish mass and the cube of its length assumed by K Fulton's index was not systematically verified for juvenile fish (Supp. Table 3.3 and Gilliers et al., 2006; Günther et al., 2012; Peck et al., 2015).

The time of response of the morphometric conditions to environmental and food conditions has been established in a range of one to two weeks by experimental starvation of juvenile fish (Selleslagh and Amara, 2013).

3.3.8. Daily growth rates (DGRs)

Prior to the use of otolith DGRs as a proxy for fish somatic growth, their daily deposition and the relation between otolith and somatic growth rates were verified for sprat (Baumann et al., 2006), sea bass (Regner and Dulčić, 1994; Aguilera et al., 2009) and plaice (Karakiri et al., 1989; Hovenkamp, 1990).

Left sagittae were extracted, cleaned and mounted on a microscope slide with Crystal Bond® thermoplastic glue, sulcus side up for sprat and sulcus side down for sea bass and plaice. They were polished on a sagittal plane until the readability of microincrements (when necessary, for large otoliths, both sides were polished) using a polishing pad (grit 2400) with distilled water. Photographs were taken under microscope using multiple magnifications (40x and 100x) with a Zeiss Axiocam ERc 5s® digital camera and ZEN 2012 (blue edition)® software (Carl Zeiss Microscopy GmbH). Photographs were compiled and counts of daily increments were performed randomly three times each by at least two independent observers. Counts of daily increments were made from the first to the last increment deposited at the outer edge of the otolith. The coefficient of variation (CV) of the counts was calculated for each otolith to quantify inconsistencies between readers (Campana, 2001). When this CV was greater than 7%, otoliths were excluded from the analysis (Campana, 2001). According to this selection, 10 otoliths of sprat, 2 otoliths of sea bass and 1 otolith of plaice were excluded from the analysis. When the CV was less than 7%, we used the mean of the three readings as an estimation of fish age. The estimated age and the date of fish capture were then used to back-calculate the date of the first increment deposition for each individual.

For each species, individuals were grouped by cohort based on the date of deposition of the first increment (Reglero et al., 2007). This grouping was performed to identify fish that originated from the same pool of fish larvae supply (Cowen et al., 2000, 2006; Rochette et al., 2012) and that experienced comparable environmental conditions throughout their development. Each cohort pooled a minimum of 3 individuals at each site. Within the same cohort, individuals had their first increment dates within one month.

To study the juvenile phase, the age and the date of fish settlement in coastal nurseries were acquired by counts from otolith post-larval settlement marks. These marks are delineated by the initiation of the last accessory growth centre for sea bass and plaice at the end of metamorphosis (Regner and Dulčić, 1994; Modin et al., 1996) and by the peak of microincrement width for sprat (Günther et al., 2012).

For each otolith, DGRs (in µm.d^{-1}) were measured on a 5 increments interval basis (*i.e*. mean DGRs recorded over 5 days), once from the first increment and once from the settlement mark. These measurements were performed along the nucleus-post-rostrum axis for sprat and plaice and along the nucleus-dorsal axis for sea bass using ImageJ® software. Each measured DGR was associated with a fish (belonging to one cohort at one site) and with the starting date of a 5 day period.

Measurements from the first increment were plotted to visualise the DGRs of each cohort between sites from birth to capture. Then, for each of the three species, patterns of juvenile growth from the earliest date of settlement to the latest date of capture of the fish composing each cohort were statistically compared among sites. To compare intra-cohort DGRs between sites during juvenile growth, the period was split into 10-day sections, starting from the first day of the delineated juvenile period (*i.e*. the cohort settlement). This time step of 10 days fits the range of otolith integration during habitat condition modification (Baumann et al., 2005) and enables the analysis of pooled DGRs according to the intensities of green macroalgae recorded in surveys, with a 2 week time step.

These 10-day sections were further considered as the factor "date" for the DGRs analysis. With regard to green tides, three situations existed for each 10-day section, *i.e*. *Before*, *During* and *After* green tides. Each "date" was thus associated with one green-tide-related situation and considered as a categorical factor.

The time of response of the daily growth rate to environmental and food conditions has been established by experimental starvation of juvenile fish to be less than a week (Selleslagh and Amara, 2013; Peck et al., 2015).

3.3.9. Statistical analyses

All the statistical analyses were performed using R version 3 (R Development Core Team, 2012), and significance was determined at the $\alpha = 0.05$ level. The normality of the data distribution and the homoscedasticity of the variance were tested using the Shapiro-Wilk and Bartlett tests, respectively. The results were non-significant, which indicated that parametric statistical tests could be performed.

TEAC, $\delta^{13}C$ signature, C:N ratio and R morphometric condition

Linear models were used to test the influence of fish length on the TEAC, $\delta^{13}C$ signature, C:N ratio and R morphometric condition. For all the studied species, fish length did not influence the indices at the selected length range. Therefore, statistical analyses were performed without preliminary correction.

For each species and each year, potential differences between the control and impacted sites at the selected sample dates were examined. We applied one-way ANOVA when indices were assessed on a single date and two-way ANOVA when several dates were used (Table 3.1).

Daily Growth Rates

For each cohort identified, each green tide period experienced throughout the juvenile stage (*i.e*. before, during and after proliferation) was considered. Potential differences in fish DGRs between the control and impacted sites were examined by one-way ANOVA when the DGR was assessed on a single date and by two-way ANOVA when several dates were assessed.

3.4. Results

3.4.2. Environmental conditions

Physico-chemical variables

During each studied year, the seasonal cycles of salinity, pH and temperature did not vary between the control and impacted sites. This similarity across sites was validated by the daily variations during the 24 h survey. However, the temperature range varied between years, *i.e*. between 8 °C and 22 °C in 2013 and 11 °C and 21 °C in 2014.

Apart from mid-June to mid-July 2013, when oxygen supersaturation (≥10 mg.L^{-1}) was measured at the impacted site under high densities of *Ulva* spp., the daytime mean dissolved oxygen concentrations did not differ between sites (seasonal range from 7 to 10 mg.L^{-1}). However, when measured throughout a 24 h cycle at a medium density of green macroalgae, the daily range had a larger amplitude at the impacted site, from 7 to 16 mg.L^{-1} (reaching oxygen supersaturation), than simultaneously recorded at the control site, 7 to 9 mg.L^{-1}.

Macroalgal cycles

At the impacted site, green tides lasted (Fig 3.2) from early June to early September in 2013 (average: 0.3 $kg_{wwt}.m^{-2}$; maximum: 0.6 $kg_{wwt}.m^{-2}$ in July) and from the end of May to the end of September in 2014 (average: 0.1 $kg_{wwt}.m^{-2}$; two maxima: 0.26 $kg_{wwt}.m^{-2}$ in June and 0.3 $kg_{wwt}.m^{-2}$ in September). The green tides could be defined as medium in 2013 and low in 2014 with respect to the *Ulva* spp. proliferation in this sandy beach area (Le Luherne et al., 2016). Other than these green macroalgae proliferations, no submerged aquatic vegetation was encountered in significant density at the impacted site nor at the control site (Le Luherne et al., 2016).

The annual cycle of green macroalgae proliferation allowed for the delineation of three periods according to the presence of *Ulva* spp. at the impacted site: *Before*, *During* and *After* proliferation (Fig 3.2). The period of maximum green macroalgae density, from mid-June to mid-July 2013, with densities greater than 0.35 $kg_{wwt}.m^{-2}$, was considered as an additional "*Max"* stage (Fig 3.2).

In the following, the densities of green macroalgae during proliferation were characterised as low: below 0.2 $kg_{wwt}.m^{-2}$, medium: between 0.2 and 0.35 $kg_{wwt}.m^{-2}$, and high: greater than 0.35 $kg_{wwt}.m^{-2}$.

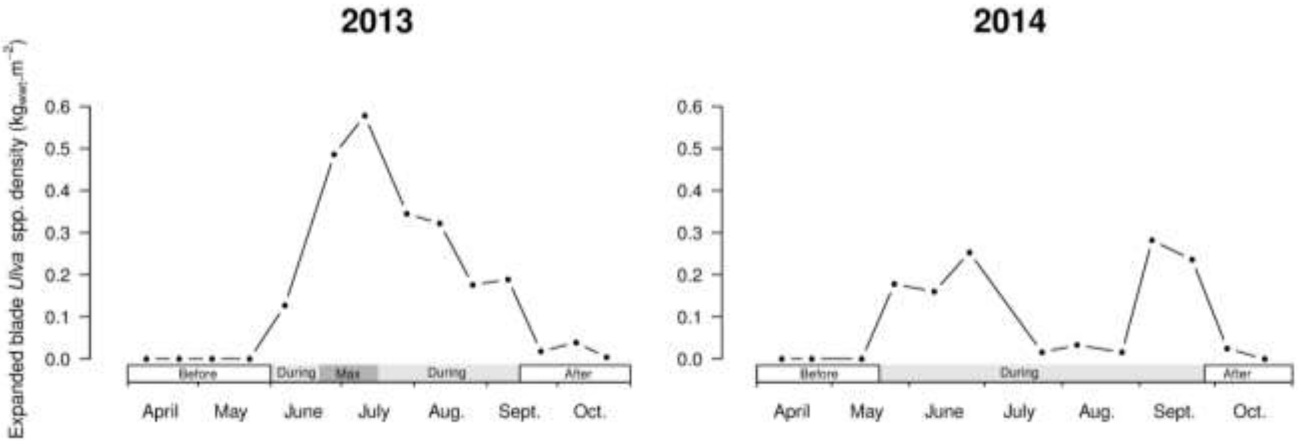

Figure 3.2 - *Ulva* spp. densities (in wet weight $kg.m^{-2}$) at the impacted site during the sampling period in 2013 and 2014. On each graph, the periods of the green tide are marked on the x-axis: *Before*, *During* and *After*. A *Max* period was added to the 2013 proliferation to underline the high peak of the green tide.

3.4.3 Habitat signature – δ^{13}C

In 2013, the δ^{13}C signatures of plaice were higher at the impacted site, but the δ^{13}C signatures of sprat were not significantly different between sites (Fig 3.3 and Table 3.2). In 2014, the δ^{13}C signatures of sprat, sea bass and plaice were significantly higher at the impacted site (Fig 3.3 and Table 3.2).

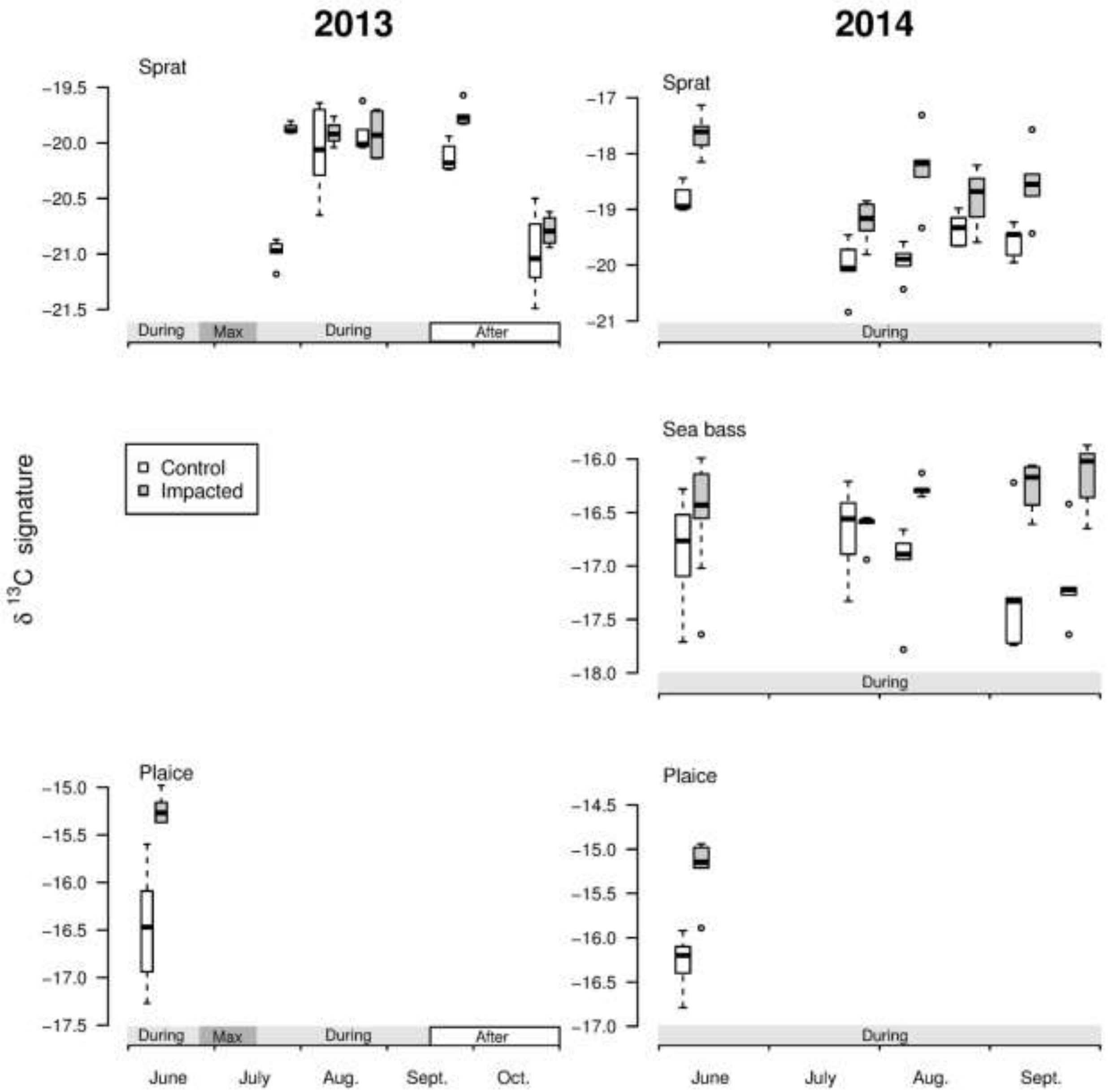

Figure 3.3 - δ^{13}C signatures (in ‰) for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) at the control and impacted sites for the selected dates in 2013 and 2014. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2).

Table 3.2 - Statistical results (*p* values: '***' <0.001; '**' <0.01; '*' <0.05) of the δ^{13}C signature, TEAC, C:N ratio and R morphometric condition analyses for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) in 2013 and 2014. ANOVA type: one-way ANOVA when indices were assessed on a single date and two-way ANOVA when several dates were analysed (factors "site", "date" and their interaction "site:date"). When an index response was significantly influenced by the factor "site", a comparison between the control (C) and impacted (I) sites was added.

Type of analysis	**Species**	**Year**	**ANOVA type**	**Site**	**Date**	**Interaction**
δ^{13}C signature	Sprat	2013	two-way	<0.001 *** C < I	<0.001 ***	<0.001 ***
		2014	two-way	**<0.001** *** C < I	<0.001 ***	0.146
	Sea bass	2014	two-way	**<0.001** *** C < I	0.885	0.121
	Plaice	2013	one-way	**0.003** ** C < I		
		2014	one-way	**<0.001** *** C < I		
TEAC	Sprat	2013	one-way	0.328		
		2014	one-way	0.508		
	Sea bass	2014	one-way	0.301		
	Plaice	2014	one-way	**0.001**** C < I		
C:N ratio	Sprat	2013	two-way	0.504	<0.001 ***	0.024 *
		2014	two-way	0.016 * C > I	0.167 *	0.337
	Sea bass	2014	two-way	0.361	0.919	0.496
	Plaice	2013	one-way	0.050		
		2014	one-way	0.448		
R morphometric condition	Sprat	2013	two-way	0.346	<0.001 ***	0.005 **
		2014	two-way	0.225	<0.001 ***	<0.001 ***
	Sea bass	2014	two-way	<0.001 *** C < I	<0.001 ***	<0.001 ***
	Plaice	2013	one-way	0.332		
		2014	one-way	**<0.001** *** C < I		

3.4.4 Fish physiological responses to green tides

Fish instantaneous response – ***Antioxidant defence capacity***

Fish TEAC was examined each year at a medium density of *Ulva* spp. on 29 July 2013 and 6 June 2014 (Fig 3.2 and Supp. Figure 3.1). For sprat and sea bass, no difference in antioxidant defence capacity was recorded between sites (Table 3.2). Conversely, on 6 June 2014, the antioxidant defence capacity of juvenile plaice at the impacted site was significantly higher than at the control site (Table 3.2 and Supp. Figure 3.1).

Short-term response – *Total lipid*

Regardless of species, muscle total lipid measured using the C:N ratios did not differ between sites, except for sprat in 2014 (Table 3.2 and Supp. Figure 3.2). In 2013, the C:N ratios of sprat increased at both sites from the end of July to the end of August, while in 2014, this increase only occurred at the control site. The C:N ratios of sprat remained stable and thus lower at the impacted site than at the control site in 2014.

Mid-term response – *Morphometric condition*

For the three species, significant inter-individual morphometric condition variability was found at both the control and impacted site during the two studied annual cycles (Supp. Figure 3.3).

Fish condition did not differ between sites in 2013. In 2014, at the beginning of the green tide, *i.e*. at a low density of green macroalgae, plaice were in better condition at the impacted site (Table 3.2 and Supp. Figure 3.3). For sprat and sea bass, a similar pattern was observed in 2014 during early green tide proliferation in spring, but it did not persist in summer (Supp. Figure 3.3). For each studied year, no significant pattern in fish condition was revealed for these two species (Table 3.2).

Response throughout the juvenile period – *Daily growth rate*

In 2013, no fish were present at the impacted site during the maximum of the green tide from mid-June to mid-July (period *Max* in Fig 3.2; Le Luherne et al., 2016). The back-calculated DGRs during this period were thus excluded from the analysis.

For sprat, three cohorts were identified in 2013 and four in 2014. These cohorts settled throughout the green macroalgae proliferation period, from June until September (Fig 3.4). The DGRs of sprat did not differ between sites in 2013 nor in 2014, except for cohort 2 in 2014. For this cohort, which settled in sandy beaches at medium densities of green macroalgae in early July (*i.e*. just after the first maximum of *Ulva* spp. density), the DGRs were significantly lower at the impacted site than at the control site (Fig 3.4 and Table 3.3).

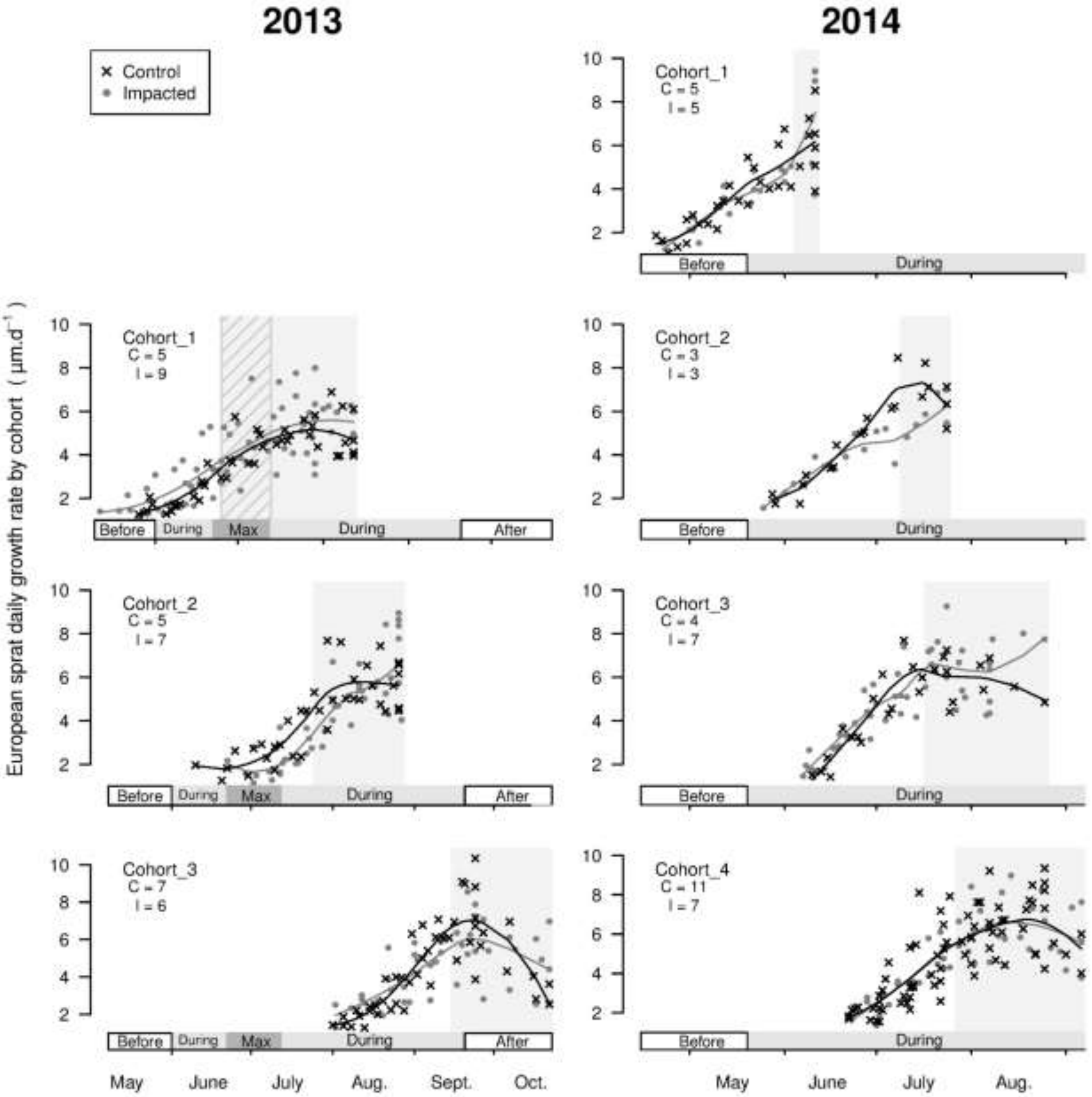

Figure 3.4 - Otolith daily growth rate (µm.d^{-1}) of juvenile sprat (*S. sprattus*) at the control and impacted sites for each cohort in 2013 and 2014, represented by a 10-day interval. Lines: associated local polynomial regression fitting (span = 0.7) of the cohort DGRs by site. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2). Grey backgrounds: the juvenile period of the cohort (*i.e.* from settlement until capture). Hatched background: period during which no fish were captured at the impacted site (DGRs of this period were excluded from the growth rate analysis). The cohort name and number of fish analysed at the control (C) and impacted (I) sites are reported on the upper left part of each graphic.

Only one cohort of sea bass was identified in 2014. The cohort settled at the end of June at medium densities of green macroalgae (*i.e*. during the first maximum of *Ulva* spp. density in 2014). The DGRs of sea bass were significantly lower at the impacted site than at the control site (Fig 3.5 and Table 3.3).

For plaice, one cohort in 2013 and two in 2014 were identified. These three cohorts settled at least one month before the beginning of the green tides (Fig 3.6), which enabled the analysis of two periods of growth for plaice: *before* and *during* green tides (Table 3.3). Before green tides, the DGRs of juvenile plaice did not differ between sites for the cohort established in 2013 nor for cohort 1 in 2014. However, cohort 2 in 2014, which settled in late April, had significantly higher DGRs at the impacted site before green tides. At the onset of macroalgal proliferation, the plaice DGRs were significantly lower at the impacted site than at the control site for the cohort in 2013 and for cohort 1 in 2014. However, the plaice DGRs of cohort 2 in 2014 were still significantly higher at the impacted site from the onset of green tides onwards (Fig 3.6 and Table 3.3).

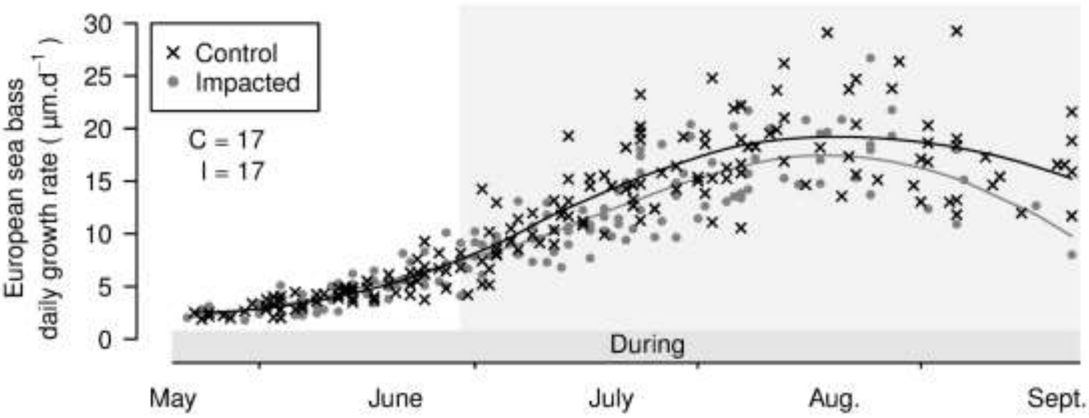

Figure 3.5 - Otolith daily growth rate (µm.d^{-1}) of juvenile sea bass (*D. labrax*) at the control and impacted sites in 2014, represented by a 10-day interval. Lines: associated local polynomial regression fitting (span = 0.7) of the cohort DGRs by site. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2). Grey backgrounds: the juvenile period of the cohort (*i.e.* from settlement until capture). The number of fish analysed at the control (C) and impacted (I) sites is reported on the upper left part of the graphic.

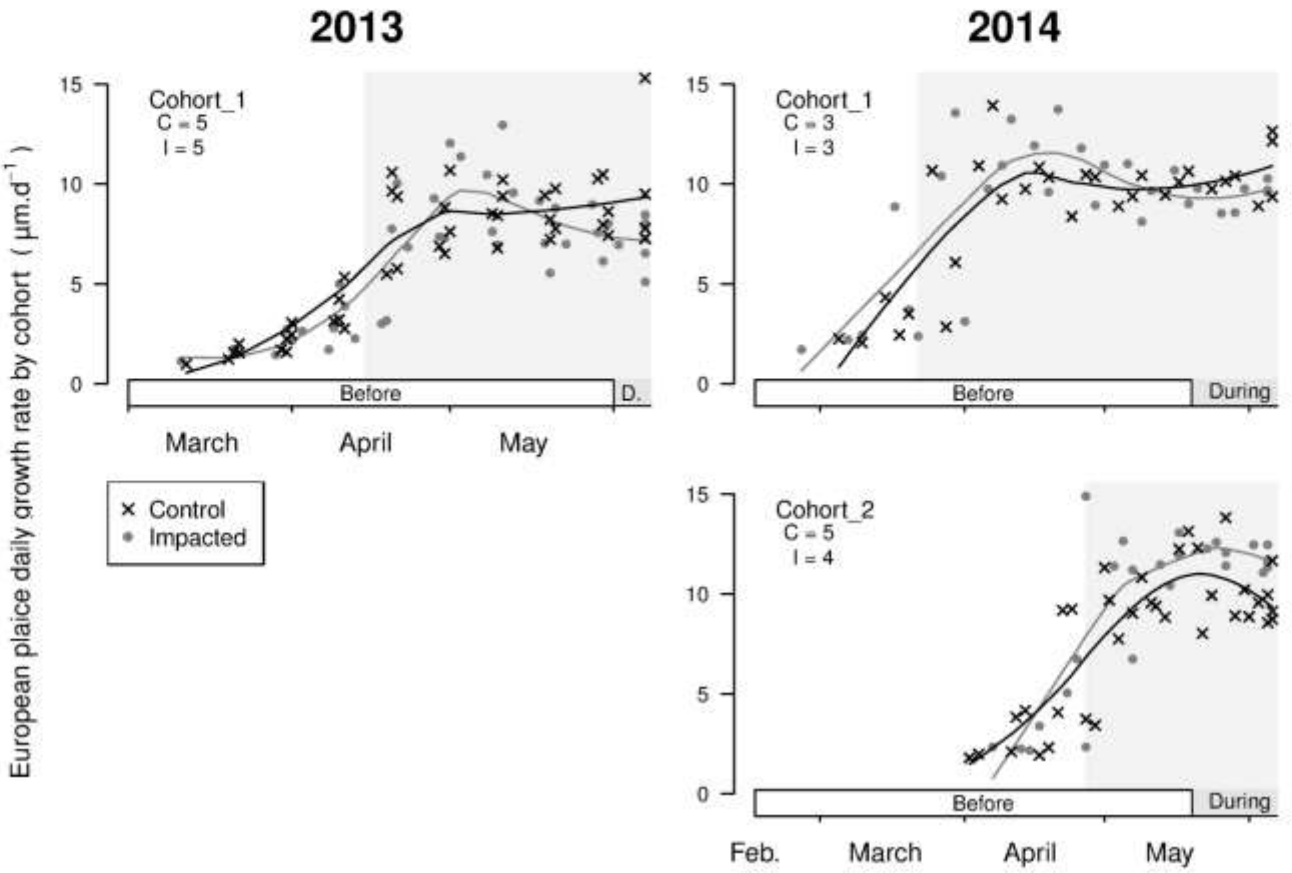

Figure 3.6 - Otolith daily growth rate (µm.d^{-1}) for juvenile plaice (*P. platessa*) at the control and impacted sites for each cohort in 2013 and 2014, represented by a 10-day interval. Lines: associated local polynomial regression fitting (span = 0.7) of the cohort DGRs by site. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2). Grey backgrounds: the juvenile period of the cohort (*i.e.* from settlement until capture). The cohort name and number of fish analysed at the control (C) and impacted (I) sites are reported on the upper left part of each graphic.

Table 3.3 - ANOVA results (*p* values: ‘***’ <0.001; ‘**’ <0.01; ‘*’ <0.05) of the juvenile daily growth rate analysis for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) in 2013 and 2014. Green tide period: period of the green tide cycle at the impacted site (see Fig 3.2). Cohorts: group of fish according to their date of first increment (see Figs 4-6). ANOVA type: one-way ANOVA when indices were assessed on a single date and two-way ANOVA when several dates were analysed (factors “site”, “date” and their interaction “site:date”). When the daily growth rate was significantly influenced by the factor “site”, a comparison between control (C) and impacted (I) sites was added.

Species	Year	Cohort	Green tide period	ANOVA type	Site	Date	Interaction
Sprat	2013	Cohort_1	*During*	two-way	0.176	0.997	0.966
		Cohort_2	*During*	two-way	0.539	0.558	0.887
		Cohort_3	*During*	two-way	0.089	0.075	0.723
			After	two-way	0.799	0.001 **	0.062
	2014	Cohort_1	*During*	one-way	0.186		
		Cohort_2	*During*	two-way	**0.010** * C > I	0. 512	0.019 *
		Cohort_3	*During*	two-way	0.160	0.119	0.052
		Cohort_4	*During*	two-way	0.520	0.017 *	0.500
Sea bass	2014	Cohort_1	*During*	two-way	**<0.001** *** C > I	<0.001 ***	0.971
Plaice	2013	Cohort_1	*Before*	two-way	0.845	0.814	0.497
			During	one-way	**0.009** ** C > I		
	2014	Cohort_1	*Before*	two-way	0.165	0.295	0.630
			During	two-way	**0.05** * C > I	0.472	0.45
		Cohort_2	*Before*	two-way	**0.006** ** C < I	0.1	0.257
			During	two-way	**0.018** * C < I	0.222	0.607

3.5 Discussion

Under stressful conditions, juvenile fish implement biochemical, physiological and behavioural coping responses. These aim to first accommodate the disturbance and maintain fish homeostasis and then to limit their exposure to perturbation when conditions become detrimental (Adams, 2002).

Here, the responses of juvenile fish to green tides have been analysed on different integrative scales on three fish species, for both control and impacted sandy beaches. Considering the responses of all the studied behavioural and physiological indices, a predominant negative influence of green tides on juvenile fish is underlined, with species-specific sensitivity to the perturbed conditions. A decreasing gradient of sensitivity to green tides is highlighted from benthic species, the first and most deeply affected, to demersal and pelagic fish species, which are less affected. Fish responses are increasingly integrative with the rise of green macroalgae density, from the implementation of an instantaneous behavioural response when environmental conditions are perceived as a perturbation, to adjustments in growth and total lipids, and finally their disappearance from the impacted site.

3.5.1 Fish responses to green tides: Moving, dying or coping with local perturbations

3.5.1.1 Habitat selection

When changes in habitat suitability are induced by green tides, fish can (i) die, (ii) emigrate (Pihl et al., 2005), both resulting in a decrease in fish density (Le Luherne et al., 2016), or (iii) remain in the disturbed habitat. This habitat selection was examined using the fish species catch records during the standardised sampling survey (Supp. Table 3.1; Le Luherne et al., 2016) and the fish habitat signatures from $\delta^{13}C$. The habitat selection of each species is strongly influenced by the density of green macroalgae:

At low densities of green macroalgae (*i.e.* at the beginning of green tides), juveniles of the three studied species were captured at both sites. For each species, the $\delta^{13}C$ signatures supported their site fidelity (*i.e.* higher signatures at the impacted site; see the methods section). Patchy covers of macroalgae at low densities for restricted periods of time thus have no noticeable negative impact on the habitat selection of juvenile fish (Robertson and Lenanton, 1984; Le Luherne et al., 2016).

When medium densities of green macroalgae were reached, plaice disappeared from the impacted site, whereas they were still captured at the control site. Only one plaice was captured each year in September during the decrease in green macroalgae density. The disappearance of a fish species in the catches records could be considered a result of avoidance behaviour (Little, 2002) and/or local mortality at the impacted site. Even if plaice could avoid vegetated or clogged substrates when alternative substrates are locally available (Wennhage and Pihl, 1994, 2007; Carl et al., 2008), both its weak capacity to migrate (Burrows et al., 2004) and the drastic reduction of its abundance at the impacted site suggest plaice mortality within areas impacted by green tides (Pihl et al., 2005). In contrast, at medium densities of green macroalgae, sprat and sea bass were captured at each site during both years. When medium densities of green macroalgae were maintained over the seasonal proliferation, as in 2014, their habitat signatures remained different between sites throughout the surveyed period. This underlined the fidelity of these species to their site of capture and its vicinity.

When high densities of green macroalgae were reached, sprat and sea bass were not captured at the impacted site. The great mobility of sprat (Guelinckx et al., 2007) and sea bass (Leakey et al., 2009) could have allowed them to escape from the disturbed area during massive proliferations.

Furthermore, in 2013, at medium densities of green macroalgae following the high densities, the habitat signatures of sprat were similar across the control and impacted sites. This similarity indicates that juveniles of sprat were not resident at the impacted site during the maximum proliferation but immigrated recently. At the same time, sea bass were also captured at the impacted site but in too low of densities to allow the analysis of its habitat signature. This suggests that highly mobile species had returned to the impacted site after a significant decrease in green macroalgae density.

Hence, both the green macroalgae density and the fish species capacity to move and to tolerate environmental pressures are driving factors of fish species habitat selection and fidelity. Here, sprat and sea bass implemented emigration, while mortality was the most probable scenario for plaice within the bay (Wennhage and Pihl, 1994; Pihl et al., 2005).

3.5.1.2 Physiological responses of juvenile fish

Under stressful conditions, and before their disappearance from a perturbed habitat, juvenile fish implement physiological responses to accommodate the disturbance and to maintain homeostasis (Barton et al., 2002). These responses were analysed on different integrative and temporal scales for individuals living at both the control and impacted sandy beaches during green tides. The interpretation of these indices according to habitat conditions (Suthers, 1998) requires consideration of their turnover rates (see methods section; Table 3.1). All the turnover rates were lower than the sampling time step of two weeks implemented in this study. Therefore, the results of these indices were examined according to the simultaneously monitored environmental variables.

Fish instantaneous responses

TEAC analysis under a medium density of *Ulva* species at the beginning of proliferation highlighted an increase in fish antioxidant defence capacity for plaice. This increase in physiological defence reflects their perception of non-suitable conditions (Adams, 2002). The accumulation of both fresh and senescent free-floating green macroalgae on the sea bottom (Solidoro et al., 1997) modifies the conditions of the benthic habitat (Johnson and Welsh, 1985; Wetzel et al., 2002; Engström-Öst and Isaksson, 2006) as soon as *Ulva* species proliferate at medium density. This, combined with the behaviour and weak mobility of juvenile plaice (Burrows et al., 2004; Le Pape and Cognez, 2016), may explain the early impact of green tides on the benthic plaice and the lack of signal recorded for the demersal sea bass and the pelagic sprat.

Fish short-term and mid-term responses

Fish responses on a more integrative biological scale were assessed by examination of their muscle total lipid, morphometric condition and growth rate, which are widely used to assess individual fish responses to specific and multiple environmental perturbations. These physiological indices are proxies of fish nutritional and energetic status (Barton et al., 2002; Minier et al., 2015).

An increase in muscle total lipid was observed for sprat from the end of July to the end of August at both sites in 2013 and only at the control site in 2014. This pattern could be explained by the increase of structural and storage lipids in fish muscle during favourable environmental conditions in summer (Post and Parkinson, 2001; Lloret et al., 2014). In contrast, this increase in muscle total lipids was not observed for sprat at the impacted site under medium densities of green macroalgae in 2014. This difference in response of sprat between years could be attributed to its habitat fidelity to the impacted site under medium densities of green macroalgae in 2014 and not in 2013.
During periods of stress and starvation, muscle total lipid could be modified for each of the studied species (Johnston, 1981; Alliot et al., 1984; Håkanson et al., 1994). However, the main lipid storage is in the liver for plaice and sea bass and it is less important in the white muscle for these species than for sprat (Thillart et al., 2002; Lloret et al., 2014). These species differences in main lipid storage localisation are a possible cause of the absence of a response of plaice and sea bass muscle total lipid content to the perturbed habitat conditions.

Somatic fish health status was analysed using the R morphometric condition index. Compared to the control site, better body conditions were observed for all fish species at the impacted site under a low density of green macroalgae in 2014. This positive influence of low patchy green macroalgae proliferation might be explained by the local increase in new shelter and food resources (Sogard and Able, 1991; Stoner et al., 2001; Kamimura and Shoji, 2013). Later in the proliferation of green macroalgae, no clear trend of beneficial or detrimental effects of green tides on fish conditions was observed. The high inter-individual variability of each species may have hidden the differences in individual fish conditions between sites. Moreover, the disappearance of fish species from the impacted site under high densities of green macroalgae in 2013 might have occurred before the slow integration of a response to morphometric conditions, resulting in undetectable responses compared to daily growth and lipid indices.

The otoliths DGRs were examined to assess the individual history of juvenile fish. According to species-specific spawning season, the fish settled in intertidal areas at different periods of the green tide seasonal cycle. Sprat and sea bass settled at the studied sites during green tides. When settlement occurred at a medium density of green macroalgae, there was a negative influence of the green tides on the otolith growth rates of the settlers. Plaice settled at the sandy beaches before macroalgal blooms. At the beginning of the green tides, lower growth rates were recorded at the impacted site for the largest individuals but not for the smallest ones. These size-related differences in plaice response suggest a weaker influence of macroalgae on smaller individuals (Nordström and Booth, 2007). Alternatively, this differential response could arise from an estimation bias linked to differential mortality upon size in this species. A disproportionate mortality rate towards the smallest plaice caused by perturbed habitat conditions could lead to an overestimation of the growth rate of the younger individuals, selecting only faster growing individuals as survivors (Le Pape and Bonhommeau, 2015).

For the studied species, the decrease in muscle total lipid and fish growth rate in response to disturbed habitat conditions at medium density of green tides could be attributed to the reduction of both the feed intake and allocation of energy to growth and storage (Johnson and Welsh, 1985; Petersen and Pihl, 1995; Pihl et al., 2005; Wang et al., 2011; Miller Neilan and Rose, 2014).

3.5.2 Conclusion

Green tides affect fish habitat suitability through complex changes in biotic and abiotic conditions (Raffaelli et al., 1998), including (i) changes in habitat structure of both the sea bottom and the water column (Isaksson and Pihl, 1992), (ii) changes in both the concentration and the daily amplitude of dissolved oxygen and the release of toxic substances (e.g., allelopathic substances and dimethyl sulphide) by fresh and senescent macroalgae, as well as by their bacterial flora (Johnson and Welsh, 1985; Sogard and Able, 1991; Wetzel et al., 2002; Harder et al., 2004), and (iii) modifications in trophic conditions (e.g., density of available prey; (Hull, 1987; Pihl et al., 1995; Quillien et al., 2015, 2016) as a result of (i) and (ii). These changes in habitat conditions and their interactions (Johnson and Welsh, 1985; Engström-Öst and Isaksson, 2006; Nordström and Booth, 2007) affect the individual performance of juvenile fish and their habitat selection.

Fish responses to these modifications are characterised by an instantaneous response when environmental conditions are perceived as a perturbation, followed by adjustments to individual fish performance (Barton et al., 2002), especially fish lipids and growth, the two primary mechanisms of energy allocation of juvenile fish (Post and Parkinson, 2001). Under long-lasting and/or increasingly perturbed conditions, juvenile fish may implement avoidance behaviour (Little, 2002), as observed for sprat, and/or a massive local increase in mortality, as suggested for plaice.

According to species-specific tolerance, the capacity to move and the distribution in the water column, these responses are implemented at different densities of green macroalgae. These differences in response reveal a gradient of sensitivity to green tides from benthic species to demersal and pelagic fish species.

In light of fish species responses during green tides, habitats impacted by this perturbation are less suitable nursery grounds and become entirely unsuitable during massive proliferation (Le Luherne et al., 2016). This raises questions regarding the quantification of the effects of green tides on fish recruitment on the scale of their proliferation area.

3.6 Acknowledgements

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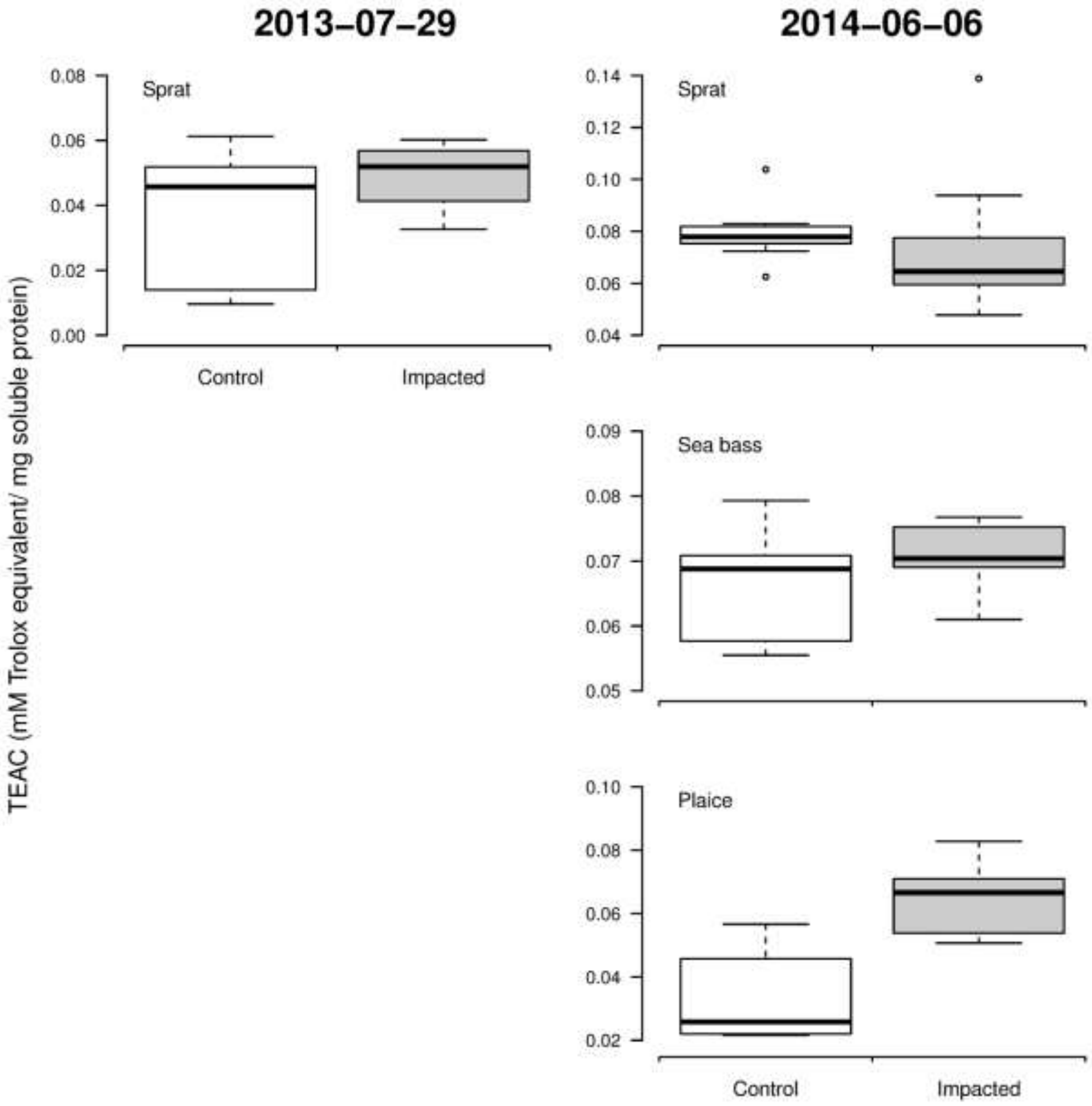
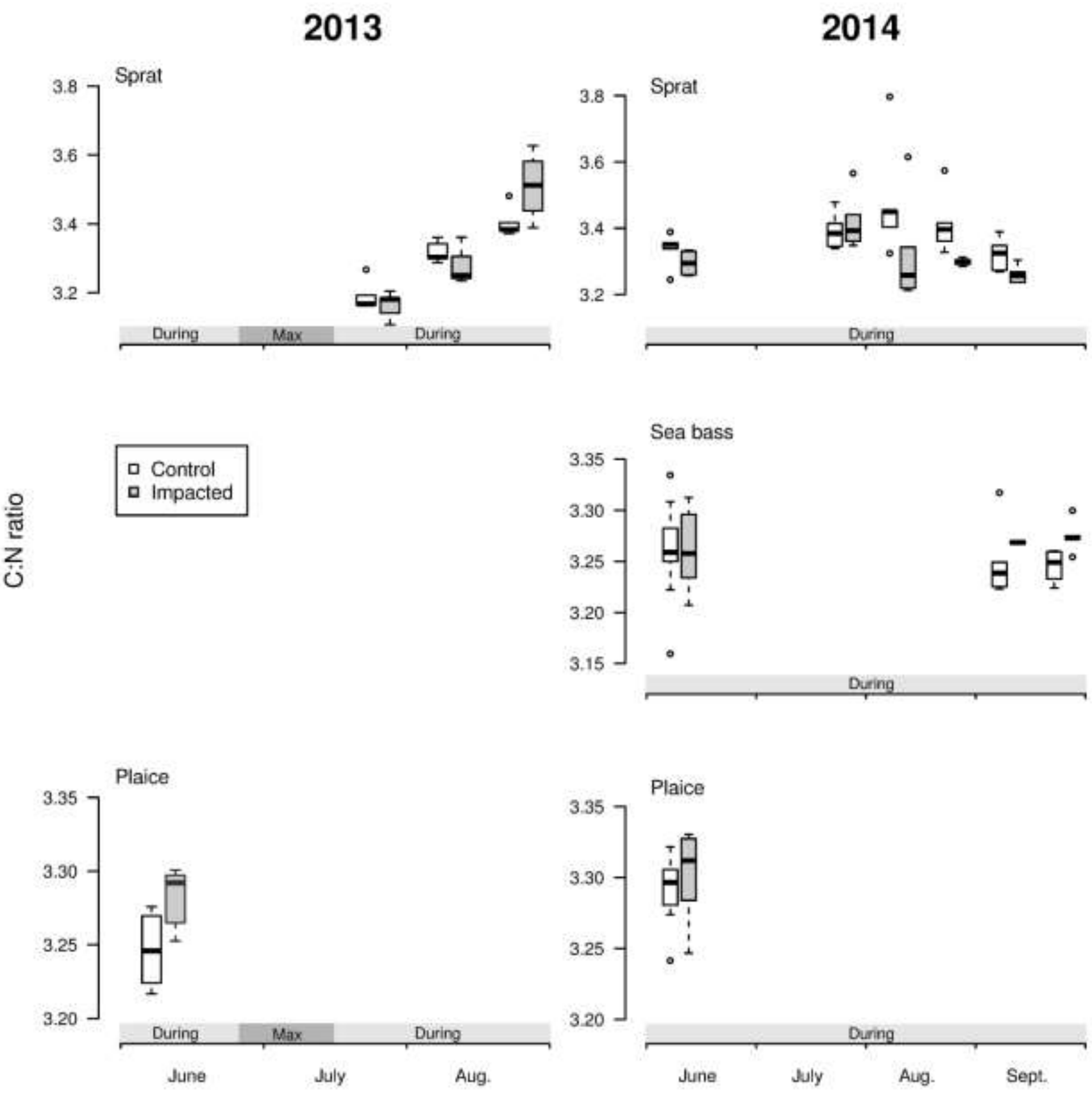
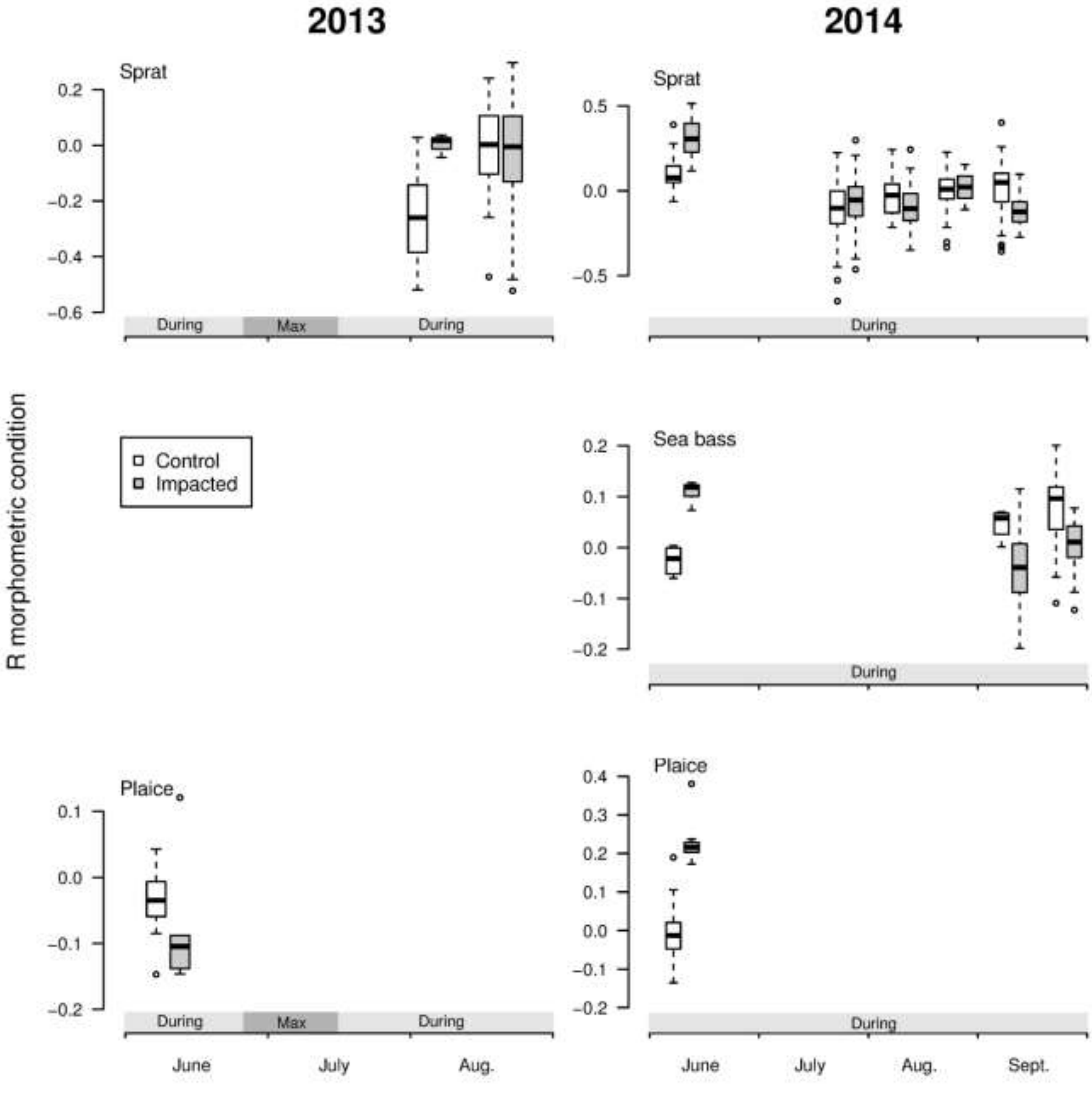
3.7 Supplementary material



Supplementary Figure 3.1 - Trolox equivalent antioxidant capacity (TEAC; in mM Trolox equivalent/mg of soluble protein) for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) at the control and impacted sites on 2013-07-29 and 2014-06-06.



Supplementary Figure 3.2 - C:N ratio for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) at the control and impacted sites for the selected dates in 2013 and 2014. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2).



Supplementary Figure 3.3 - R morphometric conditions for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) at the control and impacted sites for the selected dates in 2013 and 2014. On each graph, the periods of the green tide are marked on the x-axis (see Fig 3.2).

Supplementary Table 3.1 - Total catches (number of individuals) for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*) at the control and impacted sites in 2013 and 2014 for each sampled date during the standardised sampling survey. Dates highlighted in grey correspond to the period during green tides, and the two dates highlighted in dark grey identify the maximum of the green tide in 2013. The underlined date shows the total catches during the 24 h survey. The two dates with a star indicate the number of supplementary fish captured for the analysis of fish antioxidant defence capacity. Bold total catches refer to the dates selected for the analysis at the individual scale for each species.

		Sprat		**Sea bass**		**Plaice**	
Year	**Date**	**Control**	**Impacted**	**Control**	**Impacted**	**Control**	**Impacted**
2013	2013-04-09						
	2013-04-23						
	2013-05-07						
	2013-05-23					1	2
	2013-06-07		46			**9**	**6**
	2013-06-28					231	
	2013-07-11					128	
	2013-07-29		15				
	*2013-07-29 **	***5***	***5***				
	2013-08-12	**44**	**3**	3	1	85	
	2013-08-26	**80**	**87**	4	1	35	
	2013-09-10		4	3		12	1
	2013-09-24	**1412**	**820**	3	8	1	
	2013-10-09	2			2	7	
	2013-10-22	**343**	**57**			10	
	Total 2013	1886	1037	13	12	519	9
2014	2014-04-11				2	2	2
	2014-04-23	199		2	8	1	
	2014-05-13						
	2014-05-26	35	1				
	2014-06-06	5	1	**9**	**7**	**36**	**13**
	*2014-06-06 **	***10***	***11***	***8***	***6***	***15***	***9***
	2014-06-11	**15**	**31**			3	
	2014-06-25		1			6	
	2014-07-24	**759**	**259**	**88**	**43**	12	
	2014-08-07	**15**	**152**	**79**	**110**	3	
	2014-08-25	**644**	**3**	**4**	**57**		
	2014-09-06	**296**	**205**	**13**	**16**	3	
	2014-09-22	719		**14**	**14**		1
	2014-10-06	284		**3**	**40**		
	2014-10-21			1	29		
	Total 2014	2981	664	221	332	81	25
	Total	4867	1701	234	344	600	34

Supplementary Table 3.2 - Linear regressions (*p* values: '***'<0.001; '**'<0.01; '*'<0.05) of the C:N basal signatures according to fish size for sprat (*S. sprattus*), sea bass (*D. labrax*) and plaice (*P. platessa*).

Species	**Df**	**MS**	**F value**	***p***
Sprat	1	0.009806	0.537	0.475
Residu	15	0.018246		
Sea	1	0.0007029	1.103	0.313
Residu	13	0.0006370		
Plaice	1	0.0010118	9.249	0.0558
Residu	3	0.0001094		

Supplementary Table 3.3 - Log length-mass equations by species and by year calculated by linear regression (*p* values: '***'<0.001) and used for the R morphological condition index.

Species	**Years**	**Formula**	**r²**	***p***
Sprat	2013	Log(W)= (3.954010*log(L))-8.825545	0.8234	<0.001***
	2014	Log(W)= (3.558647*log(L))-7.279420	0.9271	<0.001***
Sea bass	2014	Log(W)= (2.998706*log(L))-4.591881	0.994	<0.001***
Plaice	2013	Log(W)= (2.993046*log(L))-4.496225	0.99	<0.001***
	2014	Log(W)= (2.916018*log(L))-4.117287	0.9909	<0.001***

Conclusion du chapitre

Ce chapitre visait à caractériser, par une approche multi-indice, les effets des marées vertes au niveau de l'individu sur trois espèces marines au positionnement différent dans la colonne d'eau et présentes en secteur intertidal au stade juvénile.

Les résultats ont mis en évidence une intégration progressive des perturbations engendrées par les marées vertes pour les trois espèces au gré de l'intensification de la perturbation.

Les réponses se sont traduites au niveau cellulaire par une augmentation de la capacité de défense antioxidante puis au niveau de l'individu par des ajustements des performances physiologiques. En fonction de l'espèce, le taux de croissance et la quantité de réserves lipidiques sont ajustés de façon conjointe ou dissociée, témoignant d'une variabilité du niveau d'intégration de la perturbation selon son intensité et selon la niche écologique occupée.

L'intensification de la perturbation conduit à terme à la disparition locale des individus. Cette disparition est le reflet d'une augmentation de la mortalité pour les espèces peu tolérantes et/ou peu mobiles (*e.g*. poissons benthiques), ou de l'émigration des individus hors de la zone affectée pour les espèces les plus mobiles (*e.g*. poissons pélagiques).

Cette succession de réponses est initiée à partir d'intensités différentes des marées vertes en fonction des caractéristiques propres aux espèces, soulignant un gradient décroissant de sensibilité de l'ichtyofaune, des espèces benthiques aux espèces démersales et pélagiques.

Discussion générale et perspectives

4. Discussion générale et perspectives

Dans un premier temps, cette discussion examine l’approche méthodologique utilisée et réalise une synthèse des différents résultats acquis au cours de ces travaux de thèse (4.1.). Elle aborde ensuite les différentes questions soulevées par nos résultats et propose des perspectives d’amélioration des protocoles d’analyse et de recherche (4.2.).

4.1 Effets des marées vertes sur l’ichtyofaune en zone intertidale – réponses de l’individu à la communauté

Les travaux engagés dans cette thèse s’inscrivent dans une démarche exploratoire de caractérisation et de compréhension des effets des marées vertes sur l’ichtyofaune dans les habitats intertidaux des secteurs côtiers et estuariens.

Dans ces secteurs, une mosaïque d’habitats assure différentes fonctions essentielles pour le maintien et le renouvellement de nombreuses espèces de poissons dont une majeure partie des ressources d’intérêt halieutique (*i.e*. fonction de nourricerie, lieu de résidence et de frayère, et voie de migration; Seitz et al., 2014). La perturbation des conditions - physiques, chimiques et trophiques - de ces habitats par la prolifération massive de macroalgues vertes modifie leur qualité et leur structure (Hull, 1987; Fletcher, 1996; Raffaelli et al., 1998; Raffaelli, 2000). L’augmentation des phénomènes de marée verte à l’échelle mondiale (Ye et al., 2011; Smetacek and Zingone, 2013; Zhou et al., 2015) nécessite d’accorder de l’attention à cette perturbation anthropique et à ses conséquences, notamment sur le compartiment ichtyologique, peu renseignées jusqu’à présent (Lyons et al., 2014; Jokinen et al., 2016).

Dans cet objectif, les effets des marées vertes sur l’ichtyofaune ont été examinés au travers d’analyses à différents niveaux d’organisation biologique pour suivre l’intégration du stress lié à la perturbation de l’habitat.

4.1.1 Intérêts d'une approche multi-échelle pour une compréhension globale des effets d'une perturbation

Face à une perturbation des conditions environnementales, un organisme peut mettre en place divers mécanismes de défense biochimiques, physiologiques et comportementaux. Ces mécanismes sont mis en œuvre par l'organisme pour s'accommoder de la perturbation en réduisant les coûts métaboliques relatifs à la gestion du stress et au maintien de l'homéostasie (*e.g.* réparation des dommages occasionnés, réallocation de l'énergie), puis pour limiter son exposition à la perturbation lorsque les conditions deviennent dommageables (*e.g.* réactions d'évitement) (Adams, 2002). Cet ensemble de réponses se reflètent au travers de différents niveaux d'organisation le long de l'échelle biologique, de la cellule à la communauté (Fig 4.1).

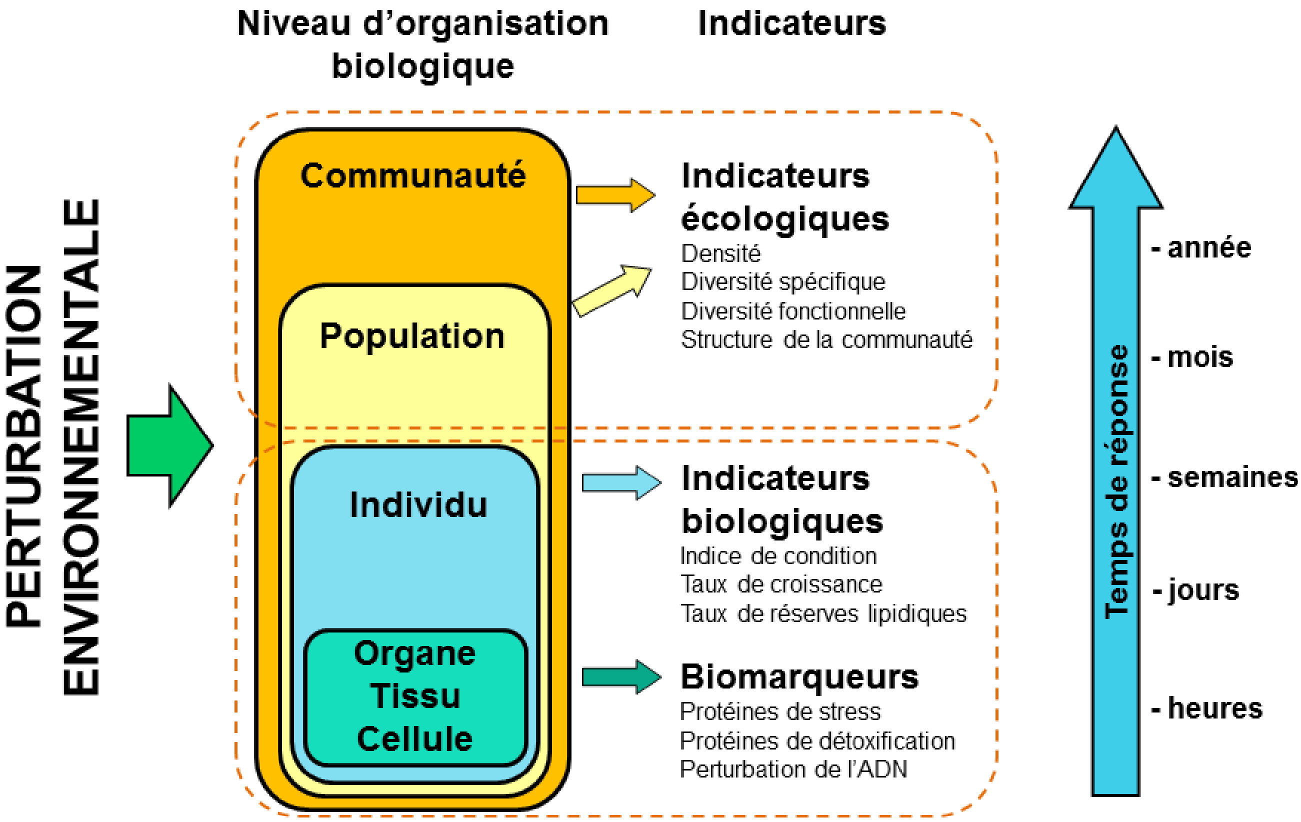


Figure 4.1 - Diagramme illustrant l'intégration d'un stress environnemental le long de l'échelle biologique et les approches correspondantes permettant son évaluation. En pointillés, les niveaux d'organisation biologique sont regroupés en fonction de leur degré d'intégration du stress (Schéma adapté d'après Adams, 2002 et Gilliers, 2004)

L'intégration du stress le long de l'échelle biologique implique que la réponse des organismes est d'autant plus intégrative - et écologiquement significative - que le niveau d'organisation biologique affecté est complexe (Fig 4.1; Adams, 2002). A l'inverse, la sensibilité à la perturbation diminue avec la complexification du niveau d'organisation biologique. Des analyses à chacun des niveaux d'organisation biologique apportent ainsi des informations différentes et complémentaires quant aux conséquences d'une perturbation sur l'ichtyofaune (Fig 4.1).

Deux principaux regroupements de niveaux d'organisation biologiques peuvent être discernés (Fig 4.1; Amara, 2011) :

(i) Un premier groupe analyse les effets des pressions environnementales du niveau cellulaire jusqu'à l'individu. Des réponses sont mises en œuvre à ces niveaux d'organisation dès la perception du stress. Elles se traduisent au niveau infra-individuel par une succession de mécanismes de défense (incluant l'activation d'hormones et d'enzymes et la production de métabolites) permettant à l'organisme de lutter contre les dommages cellulaires et tissulaire engendrés par le stress (Adams, 2002; Madeira et al., 2013; Kerambrun et al., 2014). Des réponses physiologiques, se reflétant au niveau de l'individu, sont ensuite mises en œuvre avec la persistance ou l'augmentation de la perturbation. Ces ajustements physiologiques traduisent une hausse des dépenses énergétiques de l'organisme et se manifestent au travers d'une diminution de la croissance et du stockage des réserves lipidiques (Adams, 2002; Rey et al., 2015). Pour les individus sexuellement mâtures, ces ajustements se reflètent aussi au travers d'une réduction de leurs fonctions reproductrices (Adams, 2002; Rey et al., 2015).

A ces niveaux d'organisation, les indicateurs ont des temps d'intégration rapides (*i.e.* de l'heure à quelques semaines) et sont basés sur des mesures du stress (*e.g.* protéines et enzymes de lutte contre le stress, dégradation de l'ADN) et des performances physiologiques (*e.g.* croissance, réserves lipidiques, condition corporelle) des individus. Leur analyse permet d'appréhender le seuil à partir duquel l'organisme perçoit la perturbation et les mécanismes de défense qu'il met en place pour faire face à cette perturbation (à partir des différents processus physiologiques examinés) (*e.g.* Amara et al., 2009; Kerambrun et al., 2014).

(ii) Le second groupe s'intéresse aux populations et à la communauté. Des réponses à ces niveaux d'organisation sont mises en œuvre lorsque les conditions environnementales sont trop perturbées pour que les individus (ou une partie) se maintiennent dans l'habitat. Ces réponses peuvent traduire un comportement d'évitement (Little, 2002) ou une augmentation de la mortalité locale liée à la perturbation.

A ces niveaux d'organisation biologique, les indicateurs mesurés ont des temps d'intégration important (*i.e*. du mois à l'année) et sont basés sur des mesures de densité et de diversité spécifique et fonctionnelle. Leur analyse contribue au diagnostic de la fonctionnalité et de la qualité de l'habitat (*e.g* Le Pape et al., 2003; Nicolas et al., 2010a). Des réponses à ces niveaux d'organisation biologique transcrivent une intégration profonde de la perturbation dans les écosystèmes et ont une forte signification écologique.

A chaque niveau d'organisation biologique, un panel d'indicateurs est disponible pour appréhender les différents processus mis en œuvre pour faire face à la perturbation. Cependant, la majorité des indicateurs utilisés n'a pas de spécificité de réponse à un type de perturbation (*e.g*. substances chimiques ou hypoxie). Un suivi simultané des conditions environnementales sur le site perturbé combiné à un suivi des réponses des mêmes indicateurs sur un site exempt de la perturbation est donc indispensable pour pouvoir attribuer des modifications de l'ichtyofaune à une perturbation particulière.

Par ailleurs, les réponses d'indicateurs appartenant à un même niveau d'organisation biologique peuvent être peu corrélées lorsque les indicateurs reflètent des processus physiologiques différents (Gilliers et al., 2004). Cette faible corrélation traduit la complexité des mécanismes de défense mis en œuvre par un organisme pour faire face à une perturbation (Adams, 2002). Elle souligne aussi l'intérêt d'études couplant plusieurs indicateurs pour appréhender ces liens complexes et dynamiques entre les poissons et les caractéristiques de leurs habitats.

La complexité des mécanismes de défense de l'ichtyofaune se traduit également par la variabilité des réponses des espèces face à une perturbation (Gilliers et al., 2004; Madeira et al., 2013). Pour pouvoir apprécier un diagnostic global des effets d'une perturbation sur le compartiment ichtyologique, et plus généralement sur la fonctionnalité de l'habitat, il convient d'intégrer les réponses de plusieurs espèces et d'examiner ensuite les conséquences macroécologiques à l'échelle de l'ichtyofaune.

En fonction de la perturbation examinée et des questions de recherche étudiées, différents regroupements fonctionnels peuvent être pertinents à examiner. Le regroupement d'espèces par guildes fonctionnelles consiste à rassembler des espèces ayant des caractéristiques communes, par exemple, en termes d'écologie, d'occupation des habitats ou de régime alimentaire (Delpech et al., 2010). Une étude se basant sur les réponses de guildes fonctionnelles paraît être un bon compromis entre une analyse plus fine des réponses de la communauté face à une perturbation et la complexité ainsi que la spécificité des réponses à l'échelle des populations.

L'approche méthodologique mise en œuvre pour cette thèse tient compte de l'ensemble des facteurs de variabilité des réponses de l'ichtyofaune (*i.e.* niveau d'organisation biologique, indicateur et guilde fonctionnelle/espèce) et permet de dresser un diagnostic de la qualité de l'habitat et de l'état de santé des organismes et des communautés de poissons lors de la prolifération de macroalgues vertes.

4.1.2 Synthèse des acquis

Les effets des marées vertes sur le compartiment ichtyologique ont été examinés par deux approches complémentaires, au niveau de l'(infra)individu (Chapitre 3) et des communautés (Chapitre 2).

Les conséquences des marées vertes au niveau de l'(infra)individu ont été examinées dans une nourricerie côtière à travers la sélection de l'habitat et les performances individuelles de juvéniles de trois espèces de poissons (Chapitre 3). Cette étude s'est focalisée sur des individus au stade juvénile, représentatifs d'une proportion conséquente de l'ichtyofaune se concentrant dans les habitats côtiers intertidaux (Seitz et al., 2014). Une modification de leurs performances individuelles peut avoir des répercussions sur le recrutement et donc sur la taille des populations d'intérêt halieutique (Turner and Boesch, 1987; Gibson, 1994; Piet and Rijnsdorp, 1998; Able, 1999; Peterson et al., 2000; Jones et al., 2002). Au travers de cette approche menée sur le sprat (espèce pélagique), le bar (espèce démersale) et la plie (espèce benthique), nous avons examiné la mise en œuvre de mécanismes de défense de ces espèces face aux marées vertes et exploré un effet de leur utilisation de l'habitat sur ces réponses.

La perception de conditions environnementales stressantes a été examinée par la mesure de la capacité de défense antioxidante des juvéniles. Cette réponse au niveau cellulaire a été décelée uniquement chez les juvéniles de plie en présence d'algues vertes. Cette analyse souligne une plus forte sensibilité de cette espèce aux marées vertes.

L'intégration de la perturbation au niveau de l'individu a par contre été enregistrée pour les trois espèces étudiées. Les ajustements des performances physiologiques des juvéniles se traduisent par une réduction de leur taux de croissance et de leurs réserves lipidiques. En fonction de l'espèce, ces deux principales allocations énergétiques du stade juvénile (Post and Parkinson, 2001) sont ajustées de façon conjointe ou dissociée pour s'accommoder de la perturbation. Ces différences interspécifiques témoignent d'une variabilité du niveau d'intégration de la perturbation selon son intensité et selon la niche écologique occupée.

L'intensification de la perturbation conduit ensuite à la disparition locale des individus. Cette disparition pourrait être le reflet d'une augmentation de la mortalité locale pour les espèces peu tolérantes et/ou peu mobiles (*e.g.* les espèces benthiques), ou de l'émigration des individus hors de la zone affectée pour les espèces les plus mobiles (*e.g.* les espèces pélagiques).

Pour les juvéniles de ces trois espèces, une intégration progressive du stress a été mesurée en réponse à l'augmentation de la densité de macroalgues vertes. En revanche, ces réponses sont initiées à partir d'intensités différentes de la perturbation en fonction de la distribution verticale des espèces dans l'habitat. Un gradient décroissant de sensibilité de l'ichtyofaune aux marées vertes a été souligné, des espèces benthiques aux espèces démersales et pélagiques.

Ces résultats au niveau de l'individu conduisent à s'intéresser à l'intégration des perturbations engendrées par les marées vertes à des niveaux d'organisation biologique supérieurs, *i.e.* à l'échelle de la communauté ichtyologique (Chapitre 2). A cette fin, les réponses des communautés intertidales ont été suivies sur les deux types d'habitats affectés par les marées vertes : les estrans sableux et les vasières estuariennes.

Dans la continuité des résultats obtenus à l'échelle de l'individu, une réponse progressive des communautés ichtyologiques est mise en avant en fonction de la densité et de la durée du bloom de macroalgues vertes. Une augmentation de l'intensité de la perturbation engendre une réduction progressive de la diversité et de la densité de l'ichtyofaune intertidale, jusqu'à la disparition locale de l'ichtyofaune lors de fortes densités de macroalgues vertes.

L'analyse en guildes de distribution verticale (pélagique, démersale et benthique) et en guildes écologiques (résidente et juvénile marine) a permis de compléter les résultats obtenus à l'échelle de l'individu concernant le gradient de sensibilité aux marées vertes (*i.e.* décroissant des espèces benthiques aux espèces démersales puis pélagiques) et de mettre en avant une meilleure résistance des espèces résidentes par rapport aux juvéniles d'espèces marines. Ces différentes sensibilités se traduisent par une modification progressive de la structure de la communauté ichtyologique au cours des marées vertes vers des espèces moins sensibles à cette perturbation.

La capacité des espèces à faire face aux marées vertes est influencée par leur tolérance aux pressions induites et leur capacité d'échappement. La distribution verticale des espèces dans l'habitat contraint les organismes à être plus ou moins en contact avec les perturbations de l'habitat inhérentes à la prolifération de macroalgues vertes. En zone intertidale, les macroalgues vertes s'établissent principalement sur le fond avant de coloniser l'ensemble de l'espace disponible lorsque leur densité augmente (Solidoro et al., 1997). Ce pattern de prolifération modifie tout d'abord l'habitat benthique et affecte en premier lieu les espèces vivant sur le fond.

Les conséquences des proliférations sont également modulées par la composition spécifique des assemblages de marées vertes. Les macroalgues sous forme de lame étendue flottant librement dans la colonne d'eau s'accumulent sur le fond puis colonisent l'ensemble de la masse d'eau tandis que les espèces filamenteuses attachées au substrat se développent simultanément au fond et dans la masse d'eau, complexifiant plus rapidement l'habitat. Les conséquences de ces deux types de prolifération sur l'ichtyofaune sont similaires mais surviennent pour des accumulations d'algues trois fois moindres lors de marées vertes majoritairement composées d'espèces filamenteuses.

Ainsi, les résultats de cette étude à l'échelle des communautés transcrivent une intégration des effets des marées vertes à un haut niveau d'organisation biologique dans les deux types d'habitat affectés. En gardant à l'esprit que cette étude a été réalisée à partir d'échantillonnages opérés pendant des marées vertes d'une intensité locale faible à moyenne, des effets considérables sur les populations ichtyologique d'intérêt halieutique peuvent être occasionnés par des proliférations plus intenses.

En conclusion, au travers de ces deux approches, nous avons pu mettre en évidence un impact écologiquement significatif des marées vertes sur l'ichtyofaune des habitats essentiels au renouvellement des ressources d'intérêt halieutique avec des conséquences modulées en fonction des caractéristiques des guildes fonctionnelles ainsi que de l'intensité et de la nature des blooms de macroalgues.

4.2 Limites et perspectives

4.2.1 Vers un suivi affiné des réponses de l'ichtyofaune lors des marées vertes

Augmenter l'effort d'échantillonnage lors de l'accroissement de la densité des macroalgues vertes pour préciser notre compréhension des réponses de l'ichtyofaune et améliorer la caractérisation d'un effet seuil

La stratégie d'échantillonnage mise en place pour les prélèvements de cette thèse a été établie avec un pas de temps de deux semaines. Cette fréquence d'échantillonnage est apparue adaptée pour l'analyse des réponses des communautés ichtyologiques au cours de la période de prolifération des macroalgues vertes. Cependant, elle n'a pas permis de suivre les conséquences de l'augmentation rapide de la biomasse de macroalgues vertes qui fait suite à l'initiation du bloom (*e.g.* en 2013 la densité de macroalgues vertes a été multipliée par 4 en 15 jours) et conduit, dans le même temps, à la disparition locale de l'ichtyofaune.

Un pas de temps réduit pendant cette période (*e.g.* de 2 jours) permettrait (i) d'affiner la compréhension de la réponse de l'ichtyofaune lors de l'intensification de la perturbation de l'habitat, (ii) d'analyser l'hypothèse de réponses à des échelles biologiques de niveau croissant d'intégration, et (iii) de déterminer la densité seuil de macroalgues vertes à partir de laquelle les poissons ne sont plus présents en zone intertidale.

Etudier les réponses d'une espèce résidente à l'échelle individuelle

L'étude à l'échelle de l'individu s'est focalisée sur les réponses de juvéniles d'espèces de poissons dépendantes des nourriceries côtières, dont l'intérêt halieutique est fondamental. Cependant, dans les habitats étudiés, les espèces résidentes sont présentes en forte abondance (Moore and Moore, 1976; Ntiba and Harding, 1993; Pockberger et al., 2014). Les résultats à l'échelle des communautés indiquent que ces espèces sont plus résistantes à la perturbation de l'habitat par les marées vertes que les juvéniles d'espèces marines nourriceries-dépendantes. Une analyse à l'échelle individuelle permettrait d'examiner si leurs performances physiologiques sont affectées par les marées vertes et si ces ajustements diffèrent de ceux constatés pour les espèces étudiées. Parmi les espèces résidentes et présentes en quantité suffisante au sein des zones étudiées, deux espèces de gobies prédominent et pourraient être choisies comme modèle biologique : *Pomatoschistus microps* (Krøyer, 1838) et *Pomatoschistus minutus* (Pallas, 1770).

Explorer les effets des marées vertes à une plus large échelle spatiale

L'influence des marées vertes sur l'ichtyofaune côtière a été analysée à une échelle locale (*i.e.* échelle d'une plage ou d'une vasière), adaptée à l'analyse de perturbations sur des juvéniles de poissons (Gilliers, 2004). Toutefois, une exploration à méso-échelle pourrait être entreprise afin de déterminer les effets à l'échelle de populations.

A l'échelle de la Bretagne, les échantillonnages des masses d'eau de transition réalisés dans le cadre de la Directive Cadre sur l'Eau (DCE MET - directive 2000/60/CE) procurent des informations standardisées sur les peuplements ichtyologiques dans différents estuaires avec des proliférations de macroalgues vertes contrastées. Un couplage de ces données avec la cartographie des marées vertes réalisée par le CEVA (Centre d'Etude et de Valorisation des Algues) serait un bon moyen pour une première analyse des effets des marées vertes sur l'ichtyofaune à plus large échelle.

4.2.2 Vers une meilleure compréhension des processus d'action des marées vertes sur l'ichtyofaune

Préciser les mécanismes de défense des poissons pour s'accommoder des marées vertes

L'analyse des performances individuelles a permis de réaliser des travaux mesurant les effets des marées vertes sur la sélection de l'habitat et les performances physiologiques de juvéniles de poissons. Cette analyse a porté sur différents indices de conditions reflétant l'état physiologique des poissons et sur les deux types principaux d'allocations d'énergies au stade juvénile (*i.e.* la croissance et le stockage de réserves lipidiques; Post and Parkinson, 2001). Les réponses de ces indices amènent à considérer des analyses permettant de préciser les mécanismes impliqués.

Analyse de la perception et de l'intégration du stress – L'analyse de l'intégration du stress au niveau cellulaire par l'augmentation de la capacité antioxidante a été considérée à partir de mesures de la capacité totale antioxidante à une densité de macroalgues moyenne. Les réponses mesurées pour les différentes espèces amènent à plusieurs perspectives :

(i) mesurer la capacité totale antioxidante des espèces à différentes intensités de la marée verte. Cette analyse permettrait de déterminer la densité de macroalgues à partir de laquelle les conditions sont perçues comme perturbées par les espèces. Pour une même espèce, ce type d'analyse sur des individus de tailles différentes et ayant expérimentés les mêmes conditions environnementales permettrait de tester un effet du stade de développement sur leur sensibilité aux marées vertes.

(ii) explorer une intégration du stress oxidant à l'échelle de l'ADN. La mesure d'une augmentation des capacités antioxidantes chez certaines espèces nous amène à considérer une potentielle génotoxicité des marées vertes. Pour ce faire, les dommages à l'ADN peuvent être mesurés sur des échantillons de sang à l'aide du test Comet (Akcha et al., 2003; Costa et al., 2014).

Pour ces analyses complémentaires, il conviendra de cibler des périodes clés au cours du développement des macroalgues, et notamment de réaliser un focus sur la période initiale de prolifération.

Analyse des réserves lipidiques – Dans cette thèse, nous avons choisi d'examiner les réserves lipidiques de juvéniles de poissons à travers des mesures de lipides musculaires totaux (ratio C:N). Faisant suite à cette étude standardisée sur les lipides musculaires, les différences interspécifiques de localisation des principales réserves lipidiques amènent à s'intéresser à des mesures dans différents organes (Thillart et al., 2002; Lloret et al., 2014). La principale localisation des réserves lipidiques se situe dans le foie pour certaines espèces, notamment benthiques et démersales (Thillart et al., 2002; Lloret et al., 2014). Des mesures complémentaires des réserves lipidiques hépatiques enrichiraient cette analyse et permettraient de préciser la principale réserve de lipides affectée par cette perturbation chez les espèces étudiées.

Analyse de condition nutritionnelle – La mesure de la condition nutritionnelle des poissons à partir de l'indice morphométrique de condition R a révélé une forte variabilité interindividuelle sur chacun des sites étudiés. Cette variabilité pourrait masquer des effets des marées vertes sur la condition des juvéniles de poissons. Ainsi, bien qu'aucun effet de la taille n'ait été identifié, un suivi plus précis s'intéressant à un changement de la condition des individus par cohorte au cours d'une marée verte permettrait de tester une intégration progressive de la perturbation sur la condition des juvéniles de poisson (*e.g*. Dolbeth et al., 2007).

L'exploration de l'ensemble de ces performances physiologiques a pour but de déterminer les voies d'action des perturbations environnementales engendrées par les marées vertes. La mesure de ces différents indices de performances physiologiques pour un même individu ainsi que le suivi des individus d'une cohorte au cours de la marée verte permettrait de déterminer l'intégration de la perturbation à l'échelle individuelle et d'identifier à partir de quel degré de perturbation les ajustements physiologiques successifs se mettent en place.

Appréhender les mécanismes de l'impact des marées vertes sur l'ichtyofaune

Les analyses *in situ* ont permis d'obtenir des réponses de l'ichtyofaune face aux marées vertes. Cependant, les indicateurs utilisés ne sont pas spécifiques d'une perturbation particulière et la multiplicité des perturbations des conditions de l'habitat induite par les marées vertes ne nous a pas permis de déterminer les causes et les processus de ces réponses physiologiques et comportementales. Des études expérimentales seraient très utiles pour déterminer les mécanismes d'action de cette perturbation.

Ce type d'études expérimentales a été réalisé (Johnson and Welsh, 1985; Engström-Öst and Isaksson, 2006; Nordström and Booth, 2007). Cependant, ces analyses se sont focalisées sur des espèces benthiques et aucune n'a étudié l'ensemble des conditions modifiées par les marées vertes. Des approches expérimentales seraient donc à envisager sur différentes espèces en prenant en compte l'ensemble des conditions environnementales modifiées par les marées vertes (*i.e*. modifications des conditions hydrochimiques, physiques et trophiques) ainsi que leurs interactions.

Approfondir la compréhension des réponses du compartiment biotique par des analyses des réseaux trophiques

Les analyses expérimentales pourraient être complétées par des études trophiques *in situ*. Différentes études ont été réalisées sur cette problématique à partir d'analyses de ratios isotopiques (Ouisse et al., 2011; Quillien et al., 2016). Cependant, l'unique étude prenant en compte le compartiment ichtyologique n'intègre que sa partie benthique (Quillien et al., 2016). La prise en compte d'espèces de poissons démersales et pélagiques serait à envisager pour améliorer la compréhension des effets des marées vertes sur les réseaux trophiques intertidaux (Quillien et al., 2016). Les conséquences de la modification de la composition spécifique des proies potentielles ainsi que la réduction de leur abondance et leur diversité (Quillien et al., 2015, 2016) méritent d'être analysées. Une analyse des réseaux trophiques et du comportement alimentaire d'un pool d'espèces permettrait d'examiner certaines hypothèses relatives à la réduction de la croissance et des réserves lipidiques des juvéniles de poissons. Elle permettrait, par exemple, de tester si ces réductions de performances physiologiques sont le résultat d'une diminution de la prise alimentaire et/ou des apports énergétiques des proies.

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RÉSUMÉ

Impacts des marées vertes sur les habitats essentiels au renouvellement des ressources halieutiques des secteurs estuariens et côtiers

Les écosystèmes côtiers et estuariens sont extrêmement riches d'un point de vue biologique et écologique et abritent des habitats essentiels au maintien et au renouvellement des ressources marines d'intérêt halieutique. Parmi les altérations subies par ces écosystèmes, les proliférations de macroalgues opportunistes sont l'un des signes les plus visibles de l'eutrophisation dans plusieurs régions du monde, et particulièrement dans le nord-ouest de la France. Les processus à l'origine de ces proliférations sont relativement bien identifiés tandis que leurs conséquences écologiques - notamment sur l'ichtyofaune - restent mal connues et peu étudiées. L'objectif de cette thèse est de caractériser les effets des marées vertes sur la fonction d'habitat halieutique essentiel au renouvellement de l'ichtyofaune des zones côtières et estuariennes par une approche multi-échelle.
Les conséquences des marées vertes sur l'ichtyofaune ont tout d'abord été examinées à l'échelle de la communauté. Ensuite, les processus par lesquels cette perturbation affecte l'ichtyofaune ont été étudiés par une approche à l'échelle de l'individu. Cette étude s'est intéressée aux réponses des juvéniles à travers la sélection de l'habitat et la comparaison de leurs performances physiologiques entre un site contrôle et un site impacté. Au travers de ces deux approches, un impact négatif écologiquement significatif des marées vertes sur la qualité des habitats essentiels au renouvellement des ressources d'intérêt halieutique a été mis en évidence. Les conséquences des marées vertes sur l'ichtyofaune sont modulées en fonction de l'intensité et de la nature des blooms de macroalgues ainsi que des caractéristiques des guildes fonctionnelles. Un gradient de sensibilité des espèces aux marées vertes a été souligné, des espèces benthiques aux espèces démersales et pélagiques.

Mots clés : marées vertes ; zones côtières et estuariennes ; nourriceries ; communauté de poissons ; performances individuelles

ABSTRACT

Impacts of green tides on essential habitats for the renewal of fisheries resources in coastal and estuarine systems

Coastal and estuarine systems are highly productive areas that provide unique biological and ecological services and shelter essential habitats to numerous fisheries resources. Among the perturbations experienced by these ecosystems, proliferations of opportunistic macroalgae, commonly known as 'green tides', are one of the most obvious signs of eutrophication in coastal and estuarine areas, worldwide, and in Northwestern France in particular. The processes underlying macroalgal proliferations are almost identified whereas their ecological consequences – especially for ichthyofauna – remain poorly understood and understudied. The objective of this thesis is to characterise the effects of green tides on the role of coastal and estuarine habitats for ichthyofauna, on both the community and the individual scales.
First, we investigated the consequences of green tides on ichthyofauna on the community scale. Then, we examined the processes which affect the ichthyofauna during green tides, on the individual scale. Marine juvenile fish responses were investigated based on habitat selection and comparison of individual performances between a control and an impacted site. Based on these two complementary approaches, we evidence ecological significant negative effects of green tides on the quality of essential fish habitats. The effects of green tides on ichthyofauna are modulated by the intensity and nature of macroalgal blooms, and are related to the fish habitat use and ecology. A decreasing gradient of sensibility to green tides is emphasised, from benthic to demersal and pelagic species.

Keywords: *Green tides; coastal and estuarine areas; nursery grounds; fish community; individual performances*

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