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

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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 physicochemical 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.

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1. 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

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http://dx.doi.org/10.1016/j.ecss.2016.03.031 0272-7714/© 2016 Elsevier Ltd. All rights reserved. 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) species. 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,b; Bolam and Fernandes, 2002) 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. 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. Materials and methods

2.1. 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. 1; Charlier et al., 2007; Rossi, 2011). 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. 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. 1).

2.2. Field sampling design

Sampling was performed in 2013 and 2014 during the springautumn 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 1.5-3 h 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



Fig. 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.

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. Preliminary analyses

Fish (iuvenile 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 $(kg \cdot m^{-2} \text{ in wet weight})$ and physico-chemical parameters were thus analysed per date and per site; hereafter, it is defined as the "sample unit".

2.4. Fish community analyses

2.4.1. 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 1). 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 1). The respective fish densities in these five guilds were then analysed.

2.4.2. 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.

Table 1

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

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

Table 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).

Species	Vertical distribution guild	Ecological guild	Sandy beach		Estuarine mudflat	
			SBI	SBC	EMI	EMC
Ammodytes tobianus	Demersal	Resident		+		
Atherina presbyter	Pelagic	_	Х	Х	Х	Х
Buglossidium luteum	Benthic	Juvenile	Х	Х		Х
Callionymus lyra	Demersal	Resident		+		
Chelon labrosus	Demersal	Resident	Х	Х		
Ciliata mustela	Demersal	Resident		+		
Cyclopterus lumpus	Benthic	Juvenile		+		
Dicentrarchus labrax	Demersal	Juvenile	Х	Х	Х	Х
Diplodus sargus	Demersal	Juvenile		Х		
Echiichthys vipera	Benthic	Resident	0	Х		
Gobius niger	Demersal	Resident				+
Gobius paganellus	Demersal	Resident				+
Hyperoplus immaculatus	Demersal	Juvenile		+		
Lipophrys pholis	Demersal	Resident				0
Liza aurata	Demersal	Resident	Х	Х	Х	Х
Mullus surmuletus	Demersal	Resident				+
Pegusa lascaris	Benthic	Juvenile		Х		
Pleuronectes platessa	Benthic	Juvenile	Х	Х		Х
Pomatoschistus microps	Demersal	Resident	Х	Х	Х	Х
Pomatoschistus minutus	Demersal	Resident	Х	Х		Х
Pomatoschistus pictus	Demersal	Resident	Х	Х		Х
Scophthalmus rhombus	Benthic	Juvenile	Х	Х		Х
Solea solea	Benthic	Juvenile	Х	Х		Х
Spinachia spinachia	Demersal	Resident				+
Spondyliosoma cantharus	Demersal	Juvenile		Х		Х
Sprattus sprattus	Pelagic	-	Х	Х	Х	Х
Symphodus melops	Demersal	Resident	Х	Х		Х
Trigla lucerna	Demersal	Juvenile		Х		

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 1) 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.

2.5. 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.

3. Results

3.1. Sandy beach area

3.1.1. 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 and 22 °C in 2013 and 11 °C–21 °C in 2014; Fig. 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). From mid-June to mid-July 2013, oxygen supersaturation ($\geq 10 \text{ mg} \cdot \text{L}^{-1}$) 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 $\cdot \text{L}^{-1}$ during the two studied years.

3.1.2. Macroalgal cycle

During both studied years, the development of green macroalgae was initiated when the temperature reached approximately 14 °C (Fig. 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



Fig. 2. Mean temperature (°C), mean macroalgae densities (in wet weight $kg \cdot m^{-2}$), fish larvae and fish (juvenile and adult) species richness and log-transformed densities (number $\cdot ha^{-1}$) 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.

July; Fig. 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. 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. 2a). In 2014, this species was encountered in low amounts only in September at SBI (maximum density: 0.08 kg_{wwt}·m⁻²).

3.1.3. 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). 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) 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 and Supp. Tables 1 and 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). Fish larvae densities differed between years and were higher in 2014 (Fig. 2). However, during both studied years, there was no significant difference between sites in fish larvae species richness and density (Table 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). Before the development of green macroalgae, fish communities were not different between sites in term of species composition and density (Fig. 2 and Supp. Tables 1 and 2). In 2013, during expanded blade *Ulva* spp. proliferation, fish species richness was significantly lower at SBI than at SBC (Fig. 2a and Table 3). Simultaneously, fish density did not differ significantly between sites in

Table 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

spite of null densities observed at SBI during the maximum density of expanded blade *Ulva* spp. (Fig. 2a and Table 3). In 2014, no significant difference in fish species richness and density was recorded when the factors of site and period were considered (Fig. 2b and Table 3).

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. 3a and Table 3). In 2014, no significant impact of the green tide was recorded on the densities of the functional guilds (Fig. 3b and Table 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).

3.1.4. 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. 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. 4a; p value < 0.001, R² = 0.72).

3.1.5. 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 and Supp. Table 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 **).

3.1.6. 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 1). The two-dimension MDS plot revealed dissimilarities in species composition between the control and impacted sites (Fig. 5a). At SBC, the higher species richness and density by guild were structured by many benthic and marine juvenile fish species (Fig. 5a and Table 2). Conversely, the less numerous and diverse community at SBI was structured by



Fig. 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.

resident and highly mobile fish species (*i.e.*, pelagic and demersal fish species; Fig. 5a and Table 2).

between 7 and 12 mg. L^{-1} .

3.2. Estuarine mudflat area

3.2.1. Physico-chemical parameters

Both sites in the estuarine mudflat area were muddy grounds. The seasonal cycle of salinity, pH and temperature (Fig. 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

3.2.2. 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: $0.02 \text{ kg}_{wwt} \cdot \text{m}^{-2}$; maximum: $0.07 \text{ kg}_{wwt} \cdot \text{m}^{-2}$ in May) and filamentous green macroalgae hung to the substrate that dominated the macroalgae biomass (average: $0.08 \text{ kg}_{wwt} \cdot \text{m}^{-2}$; maximum: $0.2 \text{ kg}_{wwt} \cdot \text{m}^{-2}$ in October; Fig. 6). The average density of total green macroalgae species at EMI was $0.1 \text{ kg}_{wwt} \cdot \text{m}^{-2}$ during the proliferation period. Patchy filamentous green macroalgae were also encountered at EMC (average: $0.03 \text{ kg}_{wwt} \cdot \text{m}^{-2}$; Fig. 6).



Fig. 4. Fish density (number \cdot ha⁻¹) as a function of expended blade *Ulva* spp. density (in wet weight kg \cdot 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.

3.2.3. 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 4).

Fish larvae were caught from May until the beginning of July at both sites (Fig. 6). Species richness and density of fish larvae were

not significantly different between sites (Fig. 6 and Table 4).

Fish (*i.e.*, juvenile and adult) settled in April in the estuarine area (Fig. 6). Fish species richness was significantly lower at EMI, but there was no significant difference between sites with respect to fish density (Fig. 6 and Table 4). Regarding functional guilds, benthic, demersal and resident fish were significantly less abundant at EMI (Fig. 7 and Table 4).

3.2.4. 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. 6 and Supp. Table 4). The two-dimensional MDS plot confirmed the previous analysis by fish guild and revealed distinct species composition between control and impacted sites (Fig. 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. 5b and Table 2).

4. Discussion

4.1. A standardised approach to assess the effects of macroalgal proliferation

4.1.1. 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.

4.1.2. 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.



Fig. 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).



Fig. 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.

Conversely, at EMI, the green tide was dominated by filamentous green macroalgae species, although both filamentous and expanded blade green macroalgae proliferated.

4.1.3. 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)

Table 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 ***

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). 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. 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.

4.2. 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).



Fig. 7. Mean macroalgae densities (in wet weight kg·m⁻²) and log-transformed fish densities (number \cdot 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.

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.

4.3. Effects of green tides on fish communities

4.3.1. 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.

4.3.2. 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,b; 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 $kg_{wwt} \cdot m^{-2}$ 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 speciesspecific 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 (Burrows et al., 2004; 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.

4.4. 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).

4.4.1. 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 (Le Pape et al., 2004; 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).

4.4.2. 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 (Sogard and Able, 1991; Engström-Öst and Isaksson, 2006), 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).

4.5. 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; Hugues 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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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.03.031.

References

- Aarnio, K., Mattila, J., 2000. Predation by juvenile *Platichthys flesus* (L.) on shelled prey species in a bare sand and a drift algae habitat. Hydrobiologia 440, 347–355. http://dx.doi.org/10.1023/A;1004112304096.
- Able, K.W., 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuar. Coast. Shelf Sci. 64, 5–17. http://dx.doi.org/10.1016/j.ecss.2005.02.002.
- Adams, S.M., 2005. Assessing cause and effect of multiple stressors on marine systems. Mar. Pollut. Bull. 51, 649–657. http://dx.doi.org/10.1016/ j.marpolbul.2004.11.040.
- Amara, R., 2003. Seasonal ichthyodiversity and growth patterns of Juvenile flatfish on a nursery ground in the southern bight of the North Sea (France). Environ. Biol. Fishes 67, 191–201. http://dx.doi.org/10.1023/A:1025646622066.
- Amara, R., Lagardere, F., Desaunay, Y., Marchand, J., 2000. Metamorphosis and estuarine colonisation in the common sole, *Solea solea* (L.): implications for recruitment regulation. Oceanol. Acta 23, 469–484. http://dx.doi.org/10.1016/ S0399-1784(00)00134-1.
- Andersen, B.S., Carl, J.D., Grønkjær, P., Støttrup, J.G., 2005. Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and a bare sand habitat in a nutrient rich fjord. J. Fish. Biol. 66, 531–552. http://dx.doi.org/10.1111/ j.0022-1112.2005.00620.x.
- Andrades, R., Gomes, M.P., Pereira-Filho, G.H., Souza-Filho, J.F., Albuquerque, C.Q., Martins, A.S., 2014. The influence of allochthonous macroalgae on the fish

communities of tropical sandy beaches. Estuar. Coast. Shelf Sci. 144, 75-81. http://dx.doi.org/10.1016/j.ecss.2014.04.014.

- Batiuk, R.A., Breitburg, D.L., Diaz, R.J., Cronin, T.M., Secor, D.H., Thursby, G., 2009. Derivation of habitat-specific dissolved oxygen criteria for Chesapeake Bay and its tidal tributaries. J. Exp. Mar. Biol. Ecol. 381, S204–S215. http://dx.doi.org/ 10.1016/j.jembe.2009.07.023.
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51, 633–641. http://dx.doi.org/10.1641/0006-3568(2001)051[0633:TICAMO] 2.0.CO;2.
- Bejda, A.J., Phelan, B.A., Studholme, A.L., 1992. The effect of dissolved oxygen on the growth of young-of-the-year winter flounder, *Pseudopleuronectes americanus*. Environ. Biol. Fishes 34, 321–327. http://dx.doi.org/10.1007/BF00004780.
- Beverton, R.J.H., 1995. Spatial limitation of population size; the concentration hypothesis. Neth. J. Sea Res. 34, 1–6. http://dx.doi.org/10.1016/0077-7579(95) 90010-1.
- Bolam, S.G., Fernandes, T.F., 2002. The effects of macroalgal cover on the spatial distribution of macrobenthic invertebrates: the effect of macroalgal morphology. Hydrobiologia 475/476, 437–448. http://dx.doi.org/10.1023/A: 1020307929624.
- Bolam, S.G., Fernandes, T.F., Read, P., Raffaelli, D., 2000. Effects of macroalgal mats on intertidal sandflats: an experimental study. J. Exp. Mar. Biol. Ecol. 249, 123–137. http://dx.doi.org/10.1016/S0022-0981(00)00185-4.
- Bonsdorff, E., 1992. Drifting algae and zoobenthos Effects on settling and community structure. Neth. J. Sea Res. 30, 57–62. http://dx.doi.org/10.1016/0077-7579(92)90045-G.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 27, 326–349. http://dx.doi.org/10.2307/ 1942268.
- Burrows, M.T., Gibson, R.N., Robb, L., Maclean, A., 2004. Alongshore dispersal and site fidelity of juvenile plaice from tagging and transplants. J. Fish. Biol. 65, 620–634. http://dx.doi.org/10.1111/j.0022-1112.2004.00467.x.
- Camp, E.V., Staudhammer, C.L., Pine III, W.E., Tetzlaff, J.C., Frazer, T.K., 2014. Replacement of rooted macrophytes by filamentous macroalgae: effects on small fishes and macroinvertebrates – Springer. Hydrobiologia 722, 159–170. http://dx.doi.org/10.1007/s10750-013-1694-3.
- Cardoso, P.G., Pardal, M.A., Raffaelli, D., Baeta, A., Marques, J.C., 2004. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. J. Exp. Mar. Biol. Ecol. 308, 207–220. http://dx.doi.org/ 10.1016/j.jembe.2004.02.018.
- Carl, J.D., Sparrevohn, C.R., Nicolajsen, H., Støttrup, J.G., 2008. Substratum selection by juvenile flounder *Platichthys flesus* (L.): effect of ephemeral filamentous macroalgae. J. Fish. Biol. 72, 2570–2578. http://dx.doi.org/10.1111/j.1095-8649.2008.01866.x.
- Carr, M.H., 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. 126, 59–76. http://dx.doi.org/10.1016/ 0022-0981(89)90124-X.
- Charlier, R.H., Morand, P., Finkl, C.W., Thys, A., 2007. Green Tides on the brittany coasts. Environ. Res. Eng. Manag. 41, 52–59.
- Claridge, P.N., Potter, I.C., 1983. Movements, abundance, age composition and growth of bass, *Dicentrarchus labrax*, in the Severn Estuary and inner bristol channel. J. Mar. Biol. Assoc. U. K. 63, 871–879. http://dx.doi.org/10.1017/ S0025315400071289.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x.
- Costa, M.J., Cabral, H.N., Drake, P., Economou, A.N., Fernandez-Delgado, C., Gordo, L., Marchand, J., Thiel, R., 2002. Recruitment and production of commercial species in estuaries. In: Elliott, M., Hemingway, K. (Eds.), Fishes in Estuaries. Blackwell Science Ltd, pp. 54–123.
- Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North Sea fish. Neth. J. Sea Res. 26, 343–386. http://dx.doi.org/10.1016/0077-7579(90)90096-Y.
- Delpech, C., Courrat, A., Pasquaud, S., Lobry, J., Le Pape, O., Nicolas, D., Boët, P., Girardin, M., Lepage, M., 2010. Development of a fish-based index to assess the ecological quality of transitional waters: the case of French estuaries. Mar. Pollut. Bull. 60, 908–918. http://dx.doi.org/10.1016/j.marpolbul.2010.01.001.
- De Raedemaecker, F., Brophy, D., O'Connor, I., Comerford, S., 2012. Habitat characteristics promoting high density and condition of juvenile flatfish at nursery grounds on the west coast of Ireland. J. Sea Res. 73, 7–17. http://dx.doi.org/ 10.1016/j.seares.2012.04.013.
- Deudero, S., Box, A., Vazquez-Luis, M., Arroyo, N.L., 2014. Benthic community responses to macroalgae invasions in seagrass beds: diversity, isotopic niche and food web structure at community level. Estuar. Coast. Shelf Sci. 142, 12–22.
- Dixon, P., Palmer, M.W., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930. http://dx.doi.org/10.1658/1100-9233(2003)014 [0927:VAPORF]2.0.CO;2.
- Dolbeth, M., Martinho, F., Leitão, R., Cabral, H., Pardal, M.A., 2007. Strategies of Pomatoschistus minutus and Pomatoschistus microps to cope with environmental instability. Estuar. Coast. Shelf Sci. 74, 263–273. http://dx.doi.org/10.1016/ j.ecss.2007.04.016.
- Dolbeth, M., Pardal, M.A., Lillebø, A.I., Azeiteiro, U., Marques, J.C., 2003. Short-and long-term effects of eutrophication on the secondary production of an intertidal macrobenthic community. Mar. Biol. 143, 1229–1238. http://dx.doi.org/10.1007/

s00227-003-1133-5.

- Dorel, D., Koutsikopoulos, C., Desaunay, Y., Marchand, J., 1991. Seasonal distribution of young sole (*Solea solea* (L.)) in the nursery ground of the bay of Vilaine (Northern bay of Biscay). Neth. J. Sea Res. 27, 297–306. http://dx.doi.org/ 10.1016/0077-7579(91)90032-V.
- Elliott, M., Dewailly, F., 1995. The structure and components of European estuarine fish assemblages. Netherl. J. Aquat. Ecol. 29, 397–417. http://dx.doi.org/10.1007/ BF02084239.
- Engström-Öst, J., Isaksson, I., 2006. Effects of macroalgal exudates and oxygen deficiency on survival and behaviour of fish larvae. J. Exp. Mar. Biol. Ecol. 335, 227–234. http://dx.doi.org/10.1016/j.jembe.2006.03.007.
- Everett, R.A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. J. Exp. Mar. Biol. Ecol. 175, 253–274. http:// dx.doi.org/10.1016/0022-0981(94)90030-2.
- Fleeger, J.W., Johnson, D.S., Galván, K.A., Deegan, L.A., 2008. Top-down and bottomup control of infauna varies across the saltmarsh landscape. J. Exp. Mar. Biol. Ecol. 357, 20-34. http://dx.doi.org/10.1016/j.jembe.2007.12.003.
 Fletcher, R.L., 1996. The occurrence of "Green Tides"— a review. In: Schramm, D.W.,
- Fletcher, R.L., 1996. The occurrence of "Green Tides"— a review. In: Schramm, D.W., Nienhuis, P.D.P.H. (Eds.), Marine Benthic Vegetation, Ecological Studies. Springer, Berlin Heidelberg, pp. 7–43.
- Florin, A.-B., Sundblad, G., Bergström, U., 2009. Characterisation of juvenile flatfish habitats in the Baltic Sea. Estuar. Coast. Shelf Sci. 82, 294–300. http:// dx.doi.org/10.1016/j.ecss.2009.01.012.
- Fulanda, B., Ohtomi, J., 2011. Effect of tow duration on estimations of CPUE and abundance of the grenadier *Coelorinchus jordani* (Gadiformes, Macrouridae). Fish. Res, 110, 298–304. http://dx.doi.org/10.1016/j.fishres.2011.04.019.
- Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth. J. Sea Res. 32, 191–206. http://dx.doi.org/10.1016/0077-7579(94)90040-X.
- Green, L., Sutula, M., Fong, P., 2014. How much is too much? Identifying benchmarks of adverse effects of macroalgae on the macrofauna in intertidal flats. Ecol. Appl. 24, 300–314. http://dx.doi.org/10.1890/13-0524.1.
- Guelinckx, J., Maes, J., De Brabandere, L., Dehairs, F., Ollevier, F., 2006. Migration dynamics of clupeoids in the Schelde estuary: a stable isotope approach. Estuar. Coast. Shelf Sci. 66, 612–623. http://dx.doi.org/10.1016/j.ecss.2005.11.007.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952. http://dx.doi.org/10.1126/science.1149345.
- Hansson, S., Rudstam, L.G., 1990. Eutrophication and Baltic fish communities. Ambio 19, 123–125.
- Harder, T., Dobretsov, S., Qian, P., 2004. Waterborne polar macromolecules act as algal antifoulants in the seaweed Ulva reticulata. Mar. Ecol. Prog. Ser. 274, 133–141. http://dx.doi.org/10.3354/meps274133.
- Holbrook, S.J., Forrester, G.E., Schmitt, R.J., 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. Oecologia 122, 109–120. http://dx.doi.org/10.1007/PL00008826.
- Holden, M.J., Williams, T., 1974. The Biology, movements and population dynamics of bass, *Dicentrarchus labrax*, in English waters. J. Mar. Biol. Assoc. U. K. 54, 91–107. http://dx.doi.org/10.1017/S0025315400022098.
- Holmquist, J.G., 1997. Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. Mar. Ecol. Prog. Ser. 158, 121–130. http://dx.doi.org/10.3354/ meos158121.
- Hughes, R.M., Gakstatter, J.H., Shirazi, M.A., Omernik, J.M., 1982. An approach for determining biological integrity in flowing waters. In: Brann, T.B., House, L.O.I.V., Lund, H.G. (Eds.), Place Resource Inventories: Principles and Practices. Society of American Foresters, Bethesda, MD, pp. 877–888.
- Hugues, B., Levey, M., Fountain, M., Carlisle, A., Chavez, F., Gleason, M., 2015. Climate mediates hypoxic stress on fish diversity and nursery function at the land-sea interface. Proc. Natl. Acad. Sci. U. S. A. 112 (26), 8025–8030 doi: pnas.org/content/112/26/8025.
- Hull, S.C., 1987. Macroalgal mats and species abundance: a field experiment. Estuar. Coast. Shelf Sci. 25, 519–532. http://dx.doi.org/10.1016/0272-7714(87)90112-0.
- Isaksson, I., Pihl, L., van Montfrans, J., 1994. Eutrophication-related changes in macrovegetation and foraging of young cod (*Gadus morhua* L): a mesocosm experiment. J. Exp. Mar. Biol. Ecol. 177, 203–217. http://dx.doi.org/10.1016/ 0022-0981(94)90237-2.
- Johnson, D.A., Welsh, B.L., 1985. Detrimental effects of Ulva lactuca (L.) exudates and low oxygen on estuarine crab larvae. J. Exp. Mar. Biol. Ecol. 86, 73–83. http:// dx.doi.org/10.1016/0022-0981(85)90043-7.
- Jokinen, H., Wennhage, H., Ollus, V., Aro, E., Norkko, A., 2015. Juvenile flatfish in the northern Baltic Sea — long-term decline and potential links to habitat characteristics. J. Sea Res. http://dx.doi.org/10.1016/j.seares.2015.06.002.
- Jones, M., Pinn, E., 2006. The impact of a macroalgal mat on benthic biodiversity in Poole Harbour. Mar. Pollut. Bull. 53, 63–71. http://dx.doi.org/10.1016/ j.marpolbul.2005.09.018.
- Kamimura, Y., Shoji, J., 2013. Does macroalgal vegetation cover influence postsettlement survival and recruitment potential of juvenile black rockfish Sebastes cheni? Estuar. Coast. Shelf Sci. 129, 86–93. http://dx.doi.org/10.1016/ j.ecss.2013.05.028.
- Kostecki, C., Rochette, S., Girardin, R., Blanchard, M., Desroy, N., Le Pape, O., 2011. Reduction of flatfish habitat as a consequence of the proliferation of an invasive mollusc. Estuar. Coast. Shelf Sci. 92, 154–160. http://dx.doi.org/10.1016/

j.ecss.2010.12.026.

- Kramer, D.L., 1987. Dissolved oxygen and fish behavior. Environ. Biol. Fishes 18, 81–92. http://dx.doi.org/10.1007/BF00002597.
- Krygier, E., Pearcy, W., 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. Fish. Bull. 84, 119–132. Legendre, P., Legendre, L., 1998. Numerical Ecology, Second English edition. Elsevier
- Science, Amsterdam, The Netherlands. Lehvo, A., Bäck, S., 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea. Aguat, Conserv. Mar. Freshw, Ecosyst. 11, 11–18, http://dx.doi.org/10.1002/
- aqc.428. Lenanton, R.C.J., Potter, I.C., 1987. Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. Es-
- tuaries 10, 28–35. http://dx.doi.org/10.2307/1352022.
 Le Pape, O., Bonhommeau, S., 2015. The food limitation hypothesis for juvenile marine fish. Fish Fish. 16, 373–398. http://dx.doi.org/10.1111/faf.12063.
- Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., Désaunay, Y., 2003. Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France) and the contribution of different habitats to the adult population. J. Sea Res. 50, 139–149. http://dx.doi.org/ 10.1016/S1385-1101(03)00059-5.
- Le Pape, O., Cognez, N., 2016. Which scale for the range of juvenile movements of estuarine and coastal nursery dependent flatfishes: a meta-analytical approach. J. Sea Res. 107, 43–55 doi: /S1385110115300058.
- Le Pape, O., Désaunay, Y., Guérault, D., 2004. Influence of an exotic mollusc, the American slipper limpet (*Crepidula fornicata*, L.) on habitat suitability for the juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France). Mar. Ecol. Prog. Ser. 277, 107–115 doi: meps2004/277/m277p107.pdf.
- Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queirós, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P., 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Glob. Change Biol. 20, 2712–2724. http://dx.doi.org/10.1111/ gcb.12644.
- MacKenzie, J., 2005. Removal of Sea Lettuce, Ulva spp., in estuaries to improve the environments for invertebrates, fish, wading birds, and Eelgrass, Zostera marina. Mar. Fish. Rev. 67, 1–8.
- Magre, E.J., 1974. Ulva lactuca negatively affect Balanus balanoides (Cirripedia Thoracia) in tidepools. Crustaceana 27, 231–234.
 Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator–prey relations
- Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator-prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251, 17-39. http://dx.doi.org/10.1016/S0022-0981(00)00191-X.
- Manté, C., Claudet, J., Rebzani-Zahaf, C., 2003. Fairly processing rare and common species in multivariate analysis of ecological series. Application to macrobenthic communities from Algiers harbour. Acta Biotheor. 51, 277–294.
- McNatt, R.A., Rice, J.A., 2004. Hypoxia-induced growth rate reduction in two juvenile estuary-dependent fishes. J. Exp. Mar. Biol. Ecol. 311, 147–156. http:// dx.doi.org/10.1016/j.jembe.2004.05.006.
- Merceron, M., Antoine, V., Auby, I., Morand, P., 2007. In situ growth potential of the subtidal part of green tide forming Ulva spp. stocks. Sci. Total Environ. 384, 293–305. http://dx.doi.org/10.1016/j.scitotenv.2007.05.007.
- Miller, J.M., Reed, J.P., Pietrafesa, L.J., 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and Juveniles. In: McCleave, J.D., Arnold, G.P., Dodson, J.J., Neill, W.H. (Eds.), Mechanisms of Migration in Fishes, NATO Conference Series. Springer, USA, pp. 209–225.
- Miller Neilan, R., Rose, K., 2014. Simulating the effects of fluctuating dissolved oxygen on growth, reproduction, and survival of fish and shrimp. J. Theor. Biol. 343, 54–68. http://dx.doi.org/10.1016/j.jtbi.2013.11.004.
- Morand, P., Briand, X., 1996. Excessive growth of macroalgae: a symptom of environmental disturbance. Bot. Mar. 39, 491–516. http://dx.doi.org/10.1515/ botm.1996.39.1-6.491.
- Munk, P., 1993. Differential growth of larval sprat Sprattus sprattus across a tidal front in the eastern North Sea. Mar. Ecol. – Prog. Ser. 99, 17–27.
- Nelson, T.A., Lee, D.J., Smith, B.C., 2003. Are "Green Tides" harmful algal blooms? Toxic properties of water-soluble extracts from two bloom-forming macroalgae, Ulva Fenestrata and Ulvaria Obscura (ulvophyceae). J. Phycol. 39, 874–879. http://dx.doi.org/10.1046/j.1529-8817.2003.02157.x.
- Nicolas, D., Lobry, J., Lepage, M., Sautour, B., Le Pape, O., Cabral, H., Uriarte, A., Boët, P., 2010a. Fish under influence: a macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. Estuar. Coast. Shelf Sci. 86, 137–147. http://dx.doi.org/10.1016/ i.ecss.2009.11.006.
- Nicolas, D., Lobry, J., Le Pape, O., Boët, P., 2010b. Functional diversity in European estuaries: relating the composition of fish assemblages to the abiotic environment. Estuar. Coast. Shelf Sci. 88, 329–338. http://dx.doi.org/10.1016/ j.ecss.2010.04.010.
- Nordström, M., Booth, D.M., 2007. Drift algae reduce foraging efficiency of juvenile flatfish. J. Sea Res. 58, 335–341. http://dx.doi.org/10.1016/j.seares.2007.08.001.
- Norkko, A., Bonsdorff, E., 1996a. Population responses of coastal zoobenthos to stress induced by drifting algal mats. Mar. Ecol. Prog. Ser. 140, 141–151. http:// dx.doi.org/10.3354/meps140141.
- Norkko, A., Bonsdorff, E., 1996b. Rapid zoobenthic community responses to accumulations of drifting algae. Mar. Ecol. Prog. Ser. 131, 143–157. http://dx.doi.org/ 10.3354/meps131143.
- Norkko, J., Bonsdorff, E., Norkko, A., 2000. Drifting algal mats as an alternative

habitat for benthic invertebrates: species specific responses to a transient resource. J. Exp. Mar. Biol. Ecol. 248, 79–104. http://dx.doi.org/10.1016/S0022-0981(00)00155-6.

- Ólafsson, E.B., 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. Mar. Biol. 97, 571–574. http://dx.doi.org/10.1007/BF00391053.
- Orr, K.K., Wilding, T.A., Horstmeyer, L., Weigl, S., Heymans, J.J., 2014. Detached macroalgae: its importance to inshore sandy beach fauna. Estuar. Coast. Shelf Sci. 150 (Part A), 125–135. http://dx.doi.org/10.1016/j.ecss.2013.12.011.
- Österling, M., Pihl, L., 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. J. Exp. Mar. Biol. Ecol. 263, 159–183. http://dx.doi.org/10.1016/S0022-0981(01)00304-5.
- Parker, K.R., Wiens, J.A., 2005. Assessing recovery following environmental accidents: environmental variation, ecological assumptions and strategies. Ecol. Appl. 15, 2037–2051. http://dx.doi.org/10.1890/04-1723.
- Pasquaud, S., Vasconcelos, R., Franca, S., Henriques, S., Costa, M., Cabral, H., 2015. Worldwide patterns of fish biodiversity in estuaries: effects of global vs. local factors. Estuar. Coast. Shelf Sci. 154, 122–128. http://dx.doi.org/10.1016/ j.ecss.2014.12.050.
- Perkins, E.J., Abbott, O.J., 1972. Nutrient enrichment and sand flat fauna. Mar. Pollut. Bull. 3, 70–72. http://dx.doi.org/10.1016/0025-326X(72)90162-2.
- Perrot, T., Rossi, N., Ménesguen, A., Dumas, F., 2014. Modelling green macroalgal blooms on the coasts of Brittany, France to enhance water quality management. J. Mar. Syst. 132, 38–53. http://dx.doi.org/10.1016/j.jmarsys.2013.12.010.
- Petersen, J.K., Petersen, G.I., 1990. Tolerance, behaviour and oxygen consumption in the sand goby, *Pomatoschistus minutus* (Pallas), exposed to hypoxia. J. Fish Biol. 37, 921–933. http://dx.doi.org/10.1111/j.1095-8649.1990.tb03596.x.
- Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L., Micheli, F., Johnson, G., 2000. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bull. Mar. Sci. 66, 759–774.
- Phelan, B.A., Goldberg, R., Bejda, A.J., Pereira, J., Hagan, S., Clark, P., Studholme, A.L., Calabrese, A., Able, K.W., 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. J. Exp. Mar. Biol. Ecol. 247, 1–28. http://dx.doi.org/10.1016/S0022-0981(99)00184-7.
- Pihl, L., Isaksson, I., Wennhage, H., Moksnes, P.-O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. Netherl. J. Aquat. Ecol. 29, 349–358. http:// dx.doi.org/10.1007/BF02084234.
- Pihl, L., Modin, J., Wennhage, H., 2005. Relating plaice (*Pleuronectes platessa*) recruitment to deteriorating habitat quality: effects of macroalgal blooms in coastal nursery grounds. Can. J. Fish. Aquat. Sci. 62, 1184–1193. http:// dx.doi.org/10.1139/f05-023.
- Pihl, L, Van der Veer, H., 1992. Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L, in coastal nursery areas. Neth. J. Sea Res. 29, 145–152. http://dx.doi.org/10.1016/0077-7579(92) 90015-7.
- Potter, I.C., Loneragan, N.R., Lenanton, R.C.J., Chrystal, P.J., 1983. Blue-green algae and fish population changes in a eutrophic estuary. Mar. Pollut. Bull. 14, 228–233. http://dx.doi.org/10.1016/0025-326X(83)90257-6.
- Quillien, N., Nordström, M., Gauthier, O., Bonsdorff, E., Paulet, Y.-M., Grall, J., 2015. Effects of macroalgal accumulations on the variability in zoobenthos of highenergy macrotidal sandy beaches. Mar. Ecol. – Prog. Ser. 522, 97–114. http:// dx.doi.org/10.3354/meps11151.
- Quiniou, L., 1986. Les peuplements de poissons démersaux de la pointe de Bretagne : environnement, biologie, structure démographique, relations trophiques. Ph.D. Thesis. Université de Bretagne occidentale – Brest. http://tel. archives-ouvertes.fr/tel-00463998.
- R Development Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Available at. www. R-project.org.
- Raffaelli, D.G., Raven, J.A., Poole, LJ., 1998. Ecological impact of green macroalgal blooms. Oceanogr. Mar. Biol. Annu. Rev. 36, 97–125.
- Riedel, B., Zuschin, M., Stachowitsch, M., 2012. Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario. Mar. Ecol. Prog. Ser. 458, 39–52. http://dx.doi.org/10.3354/meps09724.
- Robertson, A.I., Lenanton, R.C.J., 1984. Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. J. Exp. Mar. Biol. Ecol. 84, 265–283. http://dx.doi.org/10.1016/0022-0981(84)90185-0.
- Rossi, N., 2011. Classement DCE des masses d'eau côtières et de transition des bassins Loire-Bretagne et Seine-Normandie. CEVA Pleubian, France. http:// envlit.ifremer.fr/content/download/81267/556723/version/1/file/DCE_ classement_blooms+opportunistes_CEVA_2012.pdf.
- Rotherham, D., Gray, C.A., Johnson, D.D., Lokys, P., 2008. Effects of diel period and tow duration on estuarine fauna sampled with a beam trawl over bare sediment: consequences for designing more reliable and efficient surveys. Estuar. Coast. Shelf Sci. 78, 179–189. http://dx.doi.org/10.1016/j.ecss.2007.11.019.
- Sagasti, A., Schaffner, L.C., Duffy, J.E., 2001. Effects of periodic hypoxia on mortality, feeding and predation in an estuarine epifaunal community. J. Exp. Mar. Biol. Ecol. 258, 257–283. http://dx.doi.org/10.1016/S0022-0981(01)00220-9.
- Scanlan, C.M., Foden, J., Wells, E., Best, M.A., 2007. The monitoring of opportunistic macroalgal blooms for the water framework directive. Mar. Pollut. Bull. 55,

162-171. http://dx.doi.org/10.1016/j.marpolbul.2006.09.017.

- Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., Ysebaert, T., 2014. Ecological value of coastal habitats for commercially and ecologically important species. ICES J. Mar. Sci. J. Cons. 71, 648–665. http://dx.doi.org/10.1093/icesjms/fst152.
- Selleslagh, J., Amara, R., 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuar. Coast. Shelf Sci. 79, 507–517. http://dx.doi.org/10.1016/ j.ecss.2008.05.006.
- Sfriso, A., Pavoni, B., Marcomini, A., Orio, A.A., 1992. Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. Estuaries 15, 517–528. http://dx.doi.org/ 10.2307/1352394.
- Sluka, R.D., Chiappone, M., Sealey, K.M.S., 2001. Influence of habitat on grouper abundance in the Florida Keys, U.S.A. J. Fish. Biol. 58, 682–700. http:// dx.doi.org/10.1111/j.1095-8649.2001.tb00522.x.
- Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. Nature 504, 84–88. http://dx.doi.org/10.1038/nature12860.
- Sogard, S.M., 1997. Size-selective mortality in the Juvenile stage of Teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.
- Sogard, S.M., Able, K.W., 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuar. Coast. Shelf Sci. 33, 501–519. http://dx.doi.org/10.1016/0272-7714(91)90087-R.
- Soulsby, P.G., Lowthion, D., Houston, M., 1982. Effects of macroalgal mats on the ecology of intertidal mudflats. Mar. Pollut. Bull. 13, 162–166. http://dx.doi.org/ 10.1016/0025-326X(82)90087-X.
- Stoner, A.W., 2003. What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. Mar. Ecol. Prog. Ser. 257, 275–289.
- Stoner, A.W., Manderson, J.P., Pessutti, J.P., 2001. Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. Mar. Ecol. Prog. Ser. 213, 253–271. http://dx.doi.org/10.3354/meps213253.
- Tarpgaard, E., Mogensen, M., Grønkjær, P., Carl, J., 2005. Using short-term growth of enclosed 0-group European flounder, *Platichthys flesus*, to assess habitat quality in a Danish bay. J. Appl. Ichthyol. 21, 53–63. http://dx.doi.org/10.1111/j.1439-0426.2004.00626.x.
- Taylor, J.C., Miller, J.M., 2001. Physiological performance of juvenile southern flounder, *Paralichthys lethostigma* (Jordan and Gilbert, 1884), in chronic and episodic hypoxia. J. Exp. Mar. Biol. Ecol. 258, 195–214. http://dx.doi.org/10.1016/ S0022-0981(01)00215-5.
- Thetmeyer, H., Waller, U., Black, K.D., Inselmann, S., Rosenthal, H., 1999. Growth of European sea bass (*Dicentrarchus labrax* L.) under hypoxic and oscillating oxygen conditions. Aquaculture 174, 355–367. http://dx.doi.org/10.1016/S0044-8486(99)00028-9.
- Trimoreau, E., Archambault, B., Brind'Amour, A., Lepage, M., Guitton, J., Le Pape, O., 2013. A quantitative estimate of the function of soft-bottom sheltered coastal areas as essential flatfish nursery habitat. Estuar. Coast. Shelf Sci. 133, 193–205. http://dx.doi.org/10.1016/j.ecss.2013.08.027.
- Turner, R.E., Boesch, D.F., 1987. Aquatic Animal Production and Wetland Relationships: Insights Gleaned Following Wetland Loss or Gain, in: the Ecology and Management of Wetlands. Springer, USA, pp. 25–39.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105–1118.
- Vasconcelos, R.P., Eggleston, D.B., Le Pape, O., Tulp, I., 2013. Patterns and processes of habitat-specific demographic variability in exploited marine species. ICES J. Mar. Sci. J. Cons. 71, 638–647. http://dx.doi.org/10.1093/icesjms/fst136.
- Wang, C., Yu, R., Zhou, M., 2011. Acute toxicity of live and decomposing green alga Ulva (Enteromorpha) prolifera to abalone Haliotis discus hannai. Chin. J. Ocean. Limn. 29, 541–546. http://dx.doi.org/10.1007/s00343-011-0126-3.
- Wennhage, H., 2002. Vulnerability of newly settled plaice (*Pleuronectes platessa* L) to predation: effects of habitat structure and predator functional response. J. Exp. Mar. Biol. Ecol. 269, 129–145. http://dx.doi.org/10.1016/S0022-0981(02) 00005-9.
- Wennhage, H., Pihl, L., 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. Neth. J. Sea Res. 32, 343–351. http://dx.doi.org/10.1016/0077-7579(94)90011-6.
- Wennhage, H., Pihl, L., 2007. From flatfish to sticklebacks: assemblage structure of epibenthic fauna in relation to macroalgal blooms. Mar. Ecol. Prog. Ser. 335, 187–198. http://dx.doi.org/10.3354/meps335187.
- Whitfield, A.K., 1986. Fish community structure response to major habitat changes within the littoral zone of an estuarine coastal lake. Environ. Biol. Fishes 17, 41–51. http://dx.doi.org/10.1007/BF00000399.
- Wilson, K.A., Able, K.W., Heck, K.L., 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Mar. Ecol. Prog. Ser. 58, 243–251.
- Ye, N., Zhang, X., Mao, Y., Liang, C., Xu, D., Zou, J., Zhuang, Z., Wang, Q., 2011. "Green tides" are overwhelming the coastline of our blue planet: taking the world's largest example. Ecol. Res. 26, 477–485. http://dx.doi.org/10.1007/s11284-011-0821-8.
- Zhou, M.-J., Liu, D.-Y., Anderson, D.M., Valiela, I., 2015. Introduction to the special issue on green tides in the Yellow Sea. Special Issue: Green Tides in the Yellow Sea Estuar. Coast. Shelf Sci. 163 (Part A), 3–8. http://dx.doi.org/10.1016/ j.ecss.2015.06.023.