Influence of intertidal recreational fisheries and ‘bouchot’ mussel culture on bivalve recruitment

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ABSTRACT

In coastal environments, fishing and aquaculture may be important sources of disturbance to ecosystem functioning, the quantification of which must be assessed to make them more sustainable. In the Chausey Archipelago, France, recreational fishing and commercial shellfish farming are the only two evident anthropogenic activities, dominated by bivalve hand-raking and ‘bouchot’ mussel culture, respectively. This study evaluates the impact of both activities on bivalve recruitment dynamics by comparing primary recruitment intensity (short-term effect) and recruitment efficiency (medium-term effect) by sampling bivalves in reference (undisturbed) and disturbed (i.e. subjected to hand-raking or in ‘bouchot’ mussel culture areas) parcels throughout and at the end of the recruitment season, respectively. Specific hypotheses evaluated were that (H1) bivalve hand-raking negatively affects bivalve recruitment and that (H2) ‘bouchot’ mussel culture promotes bivalve recruitment.

Patterns in bivalve community structure in reference parcels (i.e. natural pattern) differed between initial and final recruitment, underlining the great importance of early post-settlement processes, particularly secondary dispersal. Primary recruitment intensity was inhibited in hand-raking parcels whereas it was promoted in ‘bouchot’ mussel culture parcels, but the effect on recruitment efficiency was muted for both activities due to post-settlement processes. Nevertheless, the importance of effects that occur during the first step of recruitment should not be ignored as they may affect bivalve communities and induce immediate consequences on the trophic web through a cascade effect. Finally, it is highlighted that hand-raking damages all life stages of the common cockle Cerastoderma edule, one of the major target species, suggesting that this activity should be managed with greater caution than is currently done.

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1. Introduction

Coastal systems provide a variety of ecosystem services, each of which has some intrinsic value. However, the degree to which each service is valued is a moving target that follows fickle societal values and the idea of limit of acceptable change is clearly a function of the social carrying capacity of an area (McKindsey et al., 2011). Growing anthropogenic pressures are of major concern for managers since all human activities (recreational and commercial) may lead to ecological disturbance, which may be defined as “any discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment” (Pickett and White, 1985). Fishing and aquaculture represent important anthropogenic disturbances in many coastal environments. Given that both activities rely on healthy ecosystems, understanding how they influence marine ecosystem functioning is not only of general importance to coastal management, but also to their sustainability (Newell, 2004; Holmer et al., 2008; Dumbauld et al., 2009; Smith et al., 2011).
Over the past few decades, littoral areas have become increasingly used for leisure activities, such as shellfish harvesting, the recent intensification of which has raised questions about its impact (Le Berre and Brigand, 2011). This activity mostly concerns harvesting infaunal bivalves, which is most often done using a garden rake. While the use of mobile bottom fishing gear can have large-scale and long-term impacts on the ecology of benthic systems (Jennings and Kaiser, 1998; Moritz et al., 2015), the negative effects of manual tools, such as hand-raking, are mostly short-lived on benthic macrofauna (Kaiser et al., 2001; MacKenzie and Pikanowski, 2004; McLaughlin et al., 2007), meiofauna (Sherman and Coull, 1980; Mistri et al., 2004), and sediment biogeochemical parameters (Falcão et al., 2003; Fiordelmondo et al., 2003). In addition, impacts due to this activity are considered to be minor as it only affects the surface layer of bottom sediments (Leitão and Gaspar, 2007), with harvesting typically causing less impacts than may storms (Carvalho et al., 2011). Recovery is often rapid, particularly in coarse sediment areas (Collier et al., 2000), with macrofauna recolonizing sediments fairly quickly (Munari et al., 2006) due to the redistribution of adults and juveniles (Hall, 1994). Nevertheless, caution is needed as community responses may vary among sites and dominant species, and with sources of disturbance (Whiteman and Bailey et al., 2010); muddiness, sand (Jennings and Kaiser, 1998; Segurado et al., 2013) and spatial extent (Kaiser et al., 2001). For example, the effect of cockle hand-raking on benthic habitat was demonstrated to last for a year, with the greatest effect being damage of under-sized cockles (Kaiser et al., 2001).

Extensive mussel farming may affect coastal ecosystems by modifying hydrosedimentary conditions, organic content, sediment biochemistry, biogeochemical fluxes, and infaunal and epifaunal communities (see review of McKindsey et al., 2011). Biodeposition from farmed bivalves may lead to organic enrichment (Cranford et al., 2009), although related impacts are not always observed (Crawford et al., 2003) as effects are to some degree dependent on local hydrosedimentary dynamics (Hartstein and Rowden, 2004). Bivalve farming effects also depend on the type of physical structures used for bivalve grow-out. ‘Bouchot’ mussel culture was developed in and is restricted to France and has been shown to have specific hydrodynamic effects at various spatial scales, ultimately impacting sedimentation as the grow-out structures (wooden stakes driven into the seafloor in intertidal areas – ‘bouchots’) reduce current flow, increase turbulence, and dampen wave height (Sornin, 1981). To date, only Grant et al. (2012) have examined the effects of long-established ‘bouchot’ culture in a highly dynamic intertidal system on endobenthic communities. At a meso-scale (km), finer sediments and more heterogeneous infaunal communities were present in mussel farms. At a small-scale (m), abundances of the dominant bivalve species were greater at the foot of ‘bouchots’. As may be predicted for strong hydrodynamic regimes, ‘bouchot’ culture did not appear to impact sediment organic matter, although some evidence of organic loading was observed over short time scales.

The present study evaluates how anthropogenic activities influence bivalve recruitment (population renewal) – a key benthic community ecosystem function (Menge and Sutherland, 1987) that promotes demographic resilience in marine systems (Wininemiller, 2005). The work was done in the Chausey Archipelago (Normandy, France), an highly dynamic system, 17 km from the closest coast. Intertidal soft-sediments are mainly composed of coarse sands characterized by low levels of organic matter – a relatively understudied habitat relative to muddy sandflats. Only two anthropogenic activities are evident in Chausey tidal flats: recreational fishing and commercial shellfish farming, dominated by bivalve hand-raking and ‘bouchot’ mussel culture, respectively. The present study assessed the influence of both anthropogenic activities on bivalve recruitment by performing two types of observational experiments. The first experiment was done throughout the recruitment season to evaluate the impact of both activities on recruitment intensity (short-term effect). The second was restricted to sampling at the end of the recruitment season to assess recruitment efficiency (medium-term effect). Since both activities affect the bottom surface, which is of primary importance for newly settled post-larvae, we hypothesized that (H1) bivalve hand-raking negatively affects bivalve recruitment and that (H2) ‘bouchot’ mussel culture promotes bivalve recruitment.

2. Material and methods

2.1. Study site

This study was done in the Chausey Archipelago, in the ‘Normand-Breton’ Gulf (English Channel, France; Fig. 1). This 4 500 ha archipelago is subject to an extreme tidal range (up to 14 m during spring tides) and is characterized by extensive, but very fragmented, intertidal areas, with 1 410 and 829 ha of sandflats exposed during extreme and mean low water spring tides, respectively (Godet et al., 2009). Commercial and recreational fishing, as well as shellfish farming (Fig. 1) – including mussels, oysters and Manila clams – are done in the archipelago.

The influence of the two anthropogenic activities (bivalve hand-raking and mussel ‘bouchots’ culture) on bivalve recruitment was assessed by monitoring bivalve recruitment dynamics in 2 intertidal areas, located at a similar tidal level (2.25–3 m above the zero of the chart datum), and corresponded to the most common habitat in the archipelago i.e., coarse sands dominated by Cerastoderma edule and Glycymeris glycymeris (Godet et al., 2009).

2.2. Bivalve hand-raking

Typical spring tide recreational shellfish harvests were mimicked by hand-raking several small parcels and harvesting adult bivalves each spring tide from April 9 to September 5, 2013. Experiments were done on a 0.6 ha protected (i.e., fishing is prohibited) tidal flat area between mid- to low-tide levels, where the target species (cockles and clams) are normally found (Fig. 1). Three, 9 m² experimental parcels (3 × 3 m), were disturbed during each spring tide using a 19 cm wide garden rake (ten, 6 cm long hand-raking and mussel ‘bouchots’ culture) on bivalve recruitment was assessed by monitoring bivalve recruitment dynamics in 2 intertidal areas, located at a similar tidal level (2.25–3 m above the zero of the chart datum), and corresponded to the most common habitat in the archipelago i.e., coarse sands dominated by Cerastoderma edule and Glycymeris glycymeris (Godet et al., 2009).

2.3. ‘Bouchot’ mussel culture

In contrast to long-line or raft structures (but see McKindsey et al., 2011 for more details), mussels in the Normand-Breton Gulf are traditionally cultivated on wooden stakes with ca. 3 m exposed (i.e., above the sediments) called ‘bouchots’, which are spaced by 1 m and arranged in ca. 100 m parallel paired rows separated by ca. 2 m. Experiments were done on a 37 ha tidal flat where blue mussel (Mytilus edulis) is cultivated on ‘bouchots’, in farms organized in series of paired rows, each separated from neighboring rows by ca. 25 m. Four, 12 m² disturbed parcels (3 × 4 m), were located in several farms to integrate the natural hydrosedimentary variability due, in part, to both ‘bouchot’ orientation and exposure (Fig. 1). Bivalve recruits were sampled within 1 m of the paired rows of ‘bouchots’ as the influence of these culture structures on bivalve abundance has been shown to be restricted to this zone (Grant...
No active shellfish farming operations (i.e., harvesting or other manipulations) occurred during the sampling period within cultivated sites, where 1 year-old mussels were growing out.

2.4. Sampling design

The influence of both anthropogenic activities on bivalve recruitment was evaluated by assessing the abundance of recruits in disturbed (described earlier) and near-by, paired, 3 x 3 m reference parcels; the distance between paired parcels varied from 10 to 12 m for ‘hand-raking’ and 50–130 m for ‘bouchot’ treatments (Fig. 1).

Bivalve meiofaunal recruitment dynamics were monitored throughout the bivalve settlement season by sampling 8 randomly positioned sediment cores (5.4 x 1 cm, diameter x depth; 0.018 m² total surface area) from each parcel during each of 4 sampling dates (June 22–23, July 7–8 and 21–22, and August 6–7, 2013). To the extent possible, cores were analyzed immediately after sampling; the remainder was preserved in 4% buffered formalin until sorting.

Bivalve macrofaunal recruitment efficiency was assessed at the end of the reproductive season by sampling 8 randomly positioned sediment cores (15.2 x 2 cm, diameter x depth; 0.15 m² total surface area) from each parcel from September 18 to 22, 2013. Samples were sieved in the field on a 1 mm square mesh and the retained material fixed in 4% buffered formalin until laboratory analysis. Cores were considered to be independent as the whole sampled surface during the study accounted for a maximum of 1.6% of a parcel.

Temperature kinetics in surficial sediments within studied habitats were assessed using temperature loggers (Onset® HOBO® Pro v2; Onset Corp., Bourne (MA), USA) that were placed in sediments (at 2 cm depth) in both sampling areas (n = 2, 1 per area) to continually record (8 min frequency) temperature from April to September 2013.

2.5. Laboratory procedures

Meiofaunal recruits. Sediment cores were rinsed through a column of two square mesh sieves (200 and 1 000 μm) and the retained material elutriated according to a method modified from Burgess (2001) that uses a colloidal silica solution to optimize segregation of organic material from sediments. Briefly, retained
material was mixed in a 175 mL vial with 120 mL of Ludox® solution (HS-40) on a variable speed vortex mixer. The speed was first set to maximum for 30 s to ensure homogenization was complete and then slowly decreased to a low level for 4 min 30 s. In contrast to maximum for 30 s to ensure homogenization was complete and then slowly decreased to a low level for 4 min 30 s. Sorting, identifying, and counting of young bivalves were done using a dissecting microscope and Dollflus plate; post-larvae thus obtained were preserved in 75% ethanol. For this study, post-larvae were considered as settled metamorphosed individuals, characterized by well-visible dissoconch shell and/or gills. A high resolution (2–54 MPixels) digital microscope equipped with a 100–1000 × magnitude objective (VHX-2000® with VH-Z100R, respectively, Keyence Corp. Osaka, Japan) was used to identify dominant taxa to the lowest taxonomic level possible.

Macrofaunal recruits. To optimize sediment sample sorting and because most post-larvae are expected to reach 2 mm (length) by about the end of the sampling season (September 18), only the 2–5 mm fraction was analyzed. Based on the few studies that have examined bivalve post-larval growth (Chicharo and Chicharo, 2001; Bownes and McQuaid, 2009; van der Geest et al., 2011; Andresen et al., 2013; Martel et al., 2014), and despite the great variability between and within species, we considered an approximate mean growth rate of 30 μm.d−1, and a mean size at metamorphosis of 300 μm. Thus, the youngest (300 μm in August 07) and the oldest (1 mm in June 22) meiofaunal cohorts should be 2 and 4 mm in mid-September (44 and 90 days later), respectively. Sediment cores were sieved through a column of two rounded mesh sieves (2 and 5 mm) and the retained material sorted to collect bivalves. Post-larvae were counted, identified to the lowest taxonomic level possible, and then preserved in 75% ethanol.

2.6. Data analysis

For the meiofaunal fraction, taxonomic richness and bivalve recruit abundance (individuals m−2) were calculated for each core, the latter for all (total), dominant, and rare taxa (≥ and <5% of total cumulative abundances, all taxa pooled, respectively). Results for dominant taxa were detailed, whereas those for rare taxa were pooled. Some rare taxa were also examined individually when they were also present in the macrofaunal fraction. All data are presented as means ± standard errors (SE).

Data were analyzed separately for hand-raking and ‘bouchot’ parts of the experiment using PERMANOVA using PRIMER and PERMANOVA- (versions 6.1.12 and 1.0.2, respectively; PRIMER-E Ltd; Ivybridge, UK) as data did not conform to assumptions of parametric analyses. Natural variation in recruitment (i.e., to reference parcels) was evaluated at 94% in reference parcels for both areas. With maximum values of 2620 and 165 ind. m−2 for meio- and macrofaunal recruitment, respectively, the maximum loss ratio occurring between post-larval ontogeny was evaluated at 94% in reference parcels for both areas.

3. Results

3.1. Environmental data and natural recruitment

From April to October 2013, the temperature ranged from 6 to 28 °C in subsurface sediments and 8–20 °C in surface waters, with a similar seasonal mean of 16–17 °C. Over the sampling period (late June to early August 2013), average subsurface sediment temperatures were similar in ‘hand-raking’ and ‘bouchot’ areas, globally ranging from 15 to 20 °C. Wide thermal ranges were recorded within 24 h periods (maximum of 11 °C in ‘hand-raking’ and 5 °C in ‘bouchot’ areas, respectively), such that subsurface sediment warming during emersion was greater in ‘hand-raking’ than in ‘bouchot’ areas, with maximum temperatures of 28 and 22 °C, respectively.

A total of 31 meiofaunal (200 μm–1 mm) and 5 macrofaunal (2–5 mm) taxa were identified as bivalve recruits. The dominant meiofaunal recruits were mussels (family Mytilidae — not including the genus Mytilus, the post-larvae of which are characterized by a prominent umbo, and is treated separately) and Nucula sp.1, whereas the dominant recruiting macrofaunal taxa was Littorina borealis.

Natural variation in recruitment was not great, such that the total abundance of meiofaunal bivalves in reference parcels did not vary as a function of Areas (p-F(1) = 0.44; p(perm) = 0.526), Dates (p-F(2) = 29.53; p(perm) = 0.109) or their interaction (p-F(2) = 0.10; p(perm) = 0.954), with a mean recruit abundance of 384 ± 33 ind. m−2 (n = 224) from late June to early August. Likewise, the total abundance of macrofaunal recruits in reference parcels did not vary significantly between ‘hand-raking’ and ‘bouchot’ areas (p-F(1) = 5.08; p(perm) = 0.088), with a mean abundance of 17 ± 5 ind. m−2 (n = 56) in September. With maximum values of 2620 and 165 ind. m−2 for meio- and macrofaunal recruitment, respectively, the maximum loss ratio occurring between post-larval ontogeny was evaluated at 94% in reference parcels for both areas.

3.2. Bivalve hand-raking

Over the sampling period, the meiofaunal bivalve recruit community in the ‘hand-raking’ area included 24 taxa, with 6 dominant ones accounting for 76% of the total abundance, including, in order of decreasing mean abundance, i) Mytilidae spp., ii) Nucula sp.1, iii) Abra tenuis, iv) L. borealis, v) Mactridae sp1, and vi) Loparia lucinalis. Taxonomic richness was greater in reference than in hand-raked parcels, with a total of 21 and 16 taxa, respectively. Of these, 13 taxa were common to both treatment parcels, while 8 and 3 were restricted to reference and hand-raked treatment parcels, respectively, where they accounted for 11 and 4% of the total abundance of bivalve recruits. Of the taxa restricted to reference parcels, four were cockles, which were pooled as the group “Cardiidae spp.” for subsequent analyses and interpretation.

Total meiofaunal bivalve abundance and the abundance of Mytilidae spp. were significantly (two-fold) greater in reference than in hand-raked parcels (Table 1; Fig. 2a, b). The abundance of L. borealis also differed significantly between treatments (Table 1), such that its abundance in reference parcels was about one fifth that observed in hand-raked parcels (Fig. 2c). Taxonomic richness of meiofaunal bivalves and Nucula sp1 abundance were quite variable at small spatial scales (i.e., significant Parcel effects, Table 1). Although two reference parcels had significantly greater taxonomic richness than that observed in hand-raked parcels, overall, hand-raked and reference parcels did not differ significantly (Fig. 2d). Nucula sp1 was highly concentrated in only one reference parcel and did not differ between hand-raked and reference parcels (Fig. 2e). Neither variable varied through time or as a function of the
interaction between Date and Treatment. The abundance of rare taxa increased significantly in reference parcels at the beginning of July (Table 1, Fig. 2f) whereas abundances of *A. tenuis*, *Mactridae* sp.1, and *L. lucinalis* did not vary significantly between treatments (Tables 1 and 2).

At the end of the season, the assemblage of macrofaunal recruits was composed of 3 taxa, 2 of them (*A. tenuis* and *L. borealis*) being common in both treatments. As for meiofaunal *Cardiidae* spp., macrofaunal *C. edule* was restricted to reference parcels, accounting for 8% of the total abundance in that treatment. Taxonomic richness and abundances of other taxa did not differ between treatments (Table 3). Globally, there were 1 ± 0.1 taxa per sampling core and macrofaunal recruits accounted for 6–10% of the mean meiofaunal bivalve abundance (Table 2).

### 3.3. ‘Bouchot’ mussel culture

Over the sampling period, meiofaunal bivalves included 28 taxa in all ‘bouchot’ areas examined, with 5 dominant species accounting for 71% of the total mean abundance, including, by order of decreasing mean abundance, i) Mytilidae spp., ii) *Nucula* sp1, iii) *Mytilus* spp., iv) *Veneridae* sp1, and v) *L. lucinalis*. The absolute number of taxa observed was similar for both treatments with a total of 23 and 24 taxa in reference and ‘bouchot’ parcels, respectively. As previously, 19 taxa were common to both treatments while 4 taxa were restricted to reference parcels (including *G. glycymeris*; Table 2) and 5 restricted to ‘bouchot’ parcels, accounting for 2 and 8% of total bivalve abundances, respectively.

The abundances of *Nucula* sp1, *L. lucinalis*, and *L. borealis* were significantly higher in ‘bouchot’ than in reference parcels (Table 1, Fig. 3a, b, c). There was considerable variation in bivalve communities at small spatial scales (i.e., significant Parcl effects) such that the factor Parcel was significant for taxonomic richness, total abundance, and the abundance of *Mytilidae* spp., rare taxa, and *Cardiidae* spp. (Table 1). Taxonomic richness, total abundance, and the abundance of *Mytilidae* spp. were greater in two bouchot parcels than all other parcels (Fig. 3d, e, f). Variation in the abundances of rare taxa and *Cardiidae* spp. showed no particular pattern (Fig. 4a, b). Abundances of *Mytilus* spp. and *Veneridae* sp1 were similar in every treatment (Table 2).

At the end of the season, the macrofaunal community of bivalve recruits included 5 taxa, the two most abundant of which were common to both treatments, including, in decreasing order of mean abundance, i) *L. borealis* and ii) *C. edule*. The dog-cockle, *G. glycymeris*, was found only in reference parcels, accounting for 40% of the total abundance in this treatment. By contrast, the warty venus, *Venus verrucosa*, and *A. tenuis* were restricted to ‘bouchot’ parcels, where they accounted for 17 and 8% of the total abundance in those treatments, respectively. Taxonomic richness and abundances of other taxa did not differ between treatments (Table 3). Globally, there were 0.5 ± 0.1 taxa per sampling core (0.018 m²) and the density of macrofaunal recruits was roughly equivalent to 1–6% of the mean meiofaunal bivalve abundance (Table 2). The abundance of *L. borealis* varied among parcels but not as a function of other factors (Table 3, Fig. 5).

### 4. Discussion

#### 4.1. Natural recruitment

The study areas (‘hand-raking’ and ‘bouchots’) were situated on the same type of benthic habitat, i.e. coarse sands dominated by the bivalves *C. edule* and *G. glycymeris*. Temperature monitoring confirmed that organisms living in tidal flats are submitted to high temperature variations (Perez et al., 2013) — up to 11 °C within a 24 h period. Bivalve recruitment and the composition of dominant taxa assemblages were similar in reference treatment areas, indicating a common recruitment pattern in this habitat. The total recruitment rate was rather low as compared to previous studies done elsewhere (Beukema and Dekker, 2014; van der Heide et al., 2014) and in the same area (Olivier and Retiere, 1998), which might be explained by high inter-annual variability (Pouvreau et al., 2015; Barbier, 2016) or fine-scale habitat differences, such as fine versus coarse sediments. Interestingly, bivalve community
structure changed between initial and final recruitment as dominant recruiting meiofaunal (i.e. < 1 mm) taxa (L. lucinalis, Mytilidae, and Nucula sp.1) did not remain dominant; other species became dominant at the macrofaunal stage (2–5 mm), including C. edule and L. borealis. Similar shifts also occurred for dominant taxa that were uncommon to both areas, likely due to small-scale variation in environmental conditions.

The observed taxonomic composition and turnover through the recruitment season highlight the great importance of early post-settlement processes, including mortality (i.e. predation, starvation, competition) and active and/or passive post-larval dispersion (Olivier et al., 1996; Palmer et al., 1996; Hunt and Scheibling, 1997; Olivier and Retière, 1998) to the success of bivalve recruitment. All mechanisms combined, the overall loss ratio evaluated during the post-larval period exceeded 90%, in accordance with the rates observed in previous classic studies on the subject (Thorson, 1950; Pedersen et al., 2008). In highly dynamic environments, such as Chausey, hydro-sedimentary dynamics may strongly influence the spatial patterns of early recruitment by modulating both settlement and post-larval resuspension (Bouma et al., 2001). Moreover, for juvenile bivalves, Norkko et al. (2001) suggested that dispersal is potentially of greater importance than mortality over small- and meso-spatiotemporal scales, and highlighted the importance of behavior by observing a decoupling between dispersal and

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**Fig. 2. ‘Hand-raking’ experiment.** Mean densities (±SE) of meiofaunal bivalve recruits as a function of treatment for (a) total abundance, (b) Mytilidae spp., (c) Lucinoma borealis, (d) taxonomic richness, (e) Nucula sp.1, and (f) abundance of rare taxa. Bars in Fig. 2d and e represent results observed in the different experimental parcels. Letters indicate significant differences (p < 0.05).
The capacity to disperse may benefit post-larvae by allowing them to avoid habitat deterioration, select a more suitable habitat for the next life stage (Commisso et al., 1995), and/or return to adult populations when primary settlement has occurred on less suitable substrates (Armonies, 1994; Olivier et al., 1996; Olivier and Retiere, 1998; Hiddink, 2003).

In the present study, Mytilidae spp. constitutes an interesting case study as they were the dominant recruiting meiofaunal taxon. Although Mytilidae are mostly associated with hard substrates at the adult stage, they also exhibit post-metamorphic recruitment onto soft sediments. This strategy may contribute to population renewal in soft-bottom mussel beds (Commisso et al., 2005), although such habitat is not common in the study site. In addition, Mytilidae spp. disappeared during post-larval ontogeny, becoming totally absent in macrofaunal samples. Mortality (due to predation, starvation and/or competition) may account for this disappearance, but settled juvenile mussels may also disperse from their initial habitat, with the suggestion that most drifting individuals are in the 1–2 mm size range (Newell et al., 2010). In fact, observations by Norkko et al. (2001) and the present study support the primary – secondary settlement hypothesis (Bayne, 1964; Buchanan and Babcock, 1997; Alfaro, 2006), underlining the great ability of mytilids to disperse via byssal-drifting (de Blok and Tan-Maas, 1976; Sigurdsson, 1976; Lane et al., 1985).

Because similar contrasting patterns between meio- and macrofaunal fractions were observed for several taxa, we hypothesize that secondary dispersal is an adaptive strategy during post-larval ontogeny that involves major changes in substrate/habitat selectivity. Nevertheless, our approach prevents us to conclude that this occurs for every identified taxa, given that late and/or low growth cohorts of bivalve recruits were not expected to contribute to the macrofaunal fraction (2–5 mm) in mid-September. In contrast to Lucinidae, Mytilidae and Cardiidae (van der Geest et al., 2011; Andresen et al., 2013; Martel et al., 2014), Nuculidae exhibit a low growth rate (Chardy et al., 1984), preventing us from further addressing the ontogenic development of Nucula sp.1 post-larvae. Further studies are needed to assess the relative importance of this phenomenon for the population dynamics of intertidal bivalves.

### 4.2. Bivalve hand-raking

We show that typical spring tide bivalve hand-raking practices have a major impact on the bivalve assemblages during the first steps of recruitment, largely due to the practice reducing the overall abundance of meiofaunal recruits, particularly that of mussels. When considering the primary – secondary settlement process, such activity may also indirectly limit secondary bivalve exchanges to other habitats. In addition, significant parcel effects suggest that such practices may regulate natural spatiotemporal recruitment patterns, which tended to be less variable in disturbed parcels. Whereas hand-raking reduced the recruitment of most species, it also strongly enhanced the recruitment of *L. borealis* and some species appear to be mostly restricted to disturbed parcels.

Such differences in recruitment may be due to differential sensitivity to raking (i.e., Coffen-Smot and Rees, 1999; Chicharo et al., 2002) and/or to habitat selection by larvae and post-larvae for disturbed sediments (i.e., Griffiths et al., 2006; Van Alstyne et al., 2011). Hand-raking practices modify the nature and structure of the substratum, as shown by Kaiser et al. (2001), who observed a trend of decreasing grain size and increased organic content of sediments 14 days after hand-raking. Moreover, Van Alstyne et al. (2011) showed that “shellfishers” pools (resulting from sediment destratification) promote nutrient releases originating from sediment porewater. Such conditions could inhibit the recruitment of filter-feeders, such as mussels, but promote the colonization of deposit-feeders such as *L. borealis*.

Despite these effects on early bivalve life-stages, fishing-related impacts on the total abundance of macrofaunal bivalve recruits were not evident, possibly suggesting compensatory post-sediment bedload transport. In fact, settled bivalve post-larvae may undertake secondary dispersal by crawling on the substratum or by secretion byssal threads that increase their buoyancy in the water column (Sigurdsson, 1976; Beukema and de Vlas, 1989; de Montaudouin et al., 2003; Shanks and Shearman, 2011). Drifting bivalve post-larvae may actively control their vertical position by producing byssus and/or opening their valves to different extents (de Montaudouin, 1997). Regardless of the dispersal mechanisms that may be involved (usually site- and species-specific), the turnover of juvenile bivalves may be quite rapid on tidal flats and may be an ongoing process (Hunt et al., 2007).

### Table 2

Global data for variables that did not exhibit significant variation and for taxa restricted to one treatment (* and ** to reference and disturbed parcels, respectively). Except for taxonomic richness, values are given as abundances (ind.m⁻²).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Global data</th>
<th>n</th>
<th>mean ± SE</th>
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<tr>
<td><strong>Hand-Raking</strong></td>
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<td><strong>Meiofaunal recruits</strong></td>
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<td>Cardiidae spp.*</td>
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<td>36 ± 12</td>
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<tr>
<td><strong>Macrofaunal recruits</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Taxonomic richness</td>
<td>24</td>
<td>1 ± 0.1</td>
<td></td>
</tr>
<tr>
<td>Total abundance</td>
<td>24</td>
<td>37 ± 6</td>
<td></td>
</tr>
<tr>
<td>Lucinoma borealis</td>
<td>24</td>
<td>25 ± 6</td>
<td></td>
</tr>
<tr>
<td>Abra tenuis</td>
<td>24</td>
<td>10 ± 3</td>
<td></td>
</tr>
<tr>
<td>Cerastoderma edule*</td>
<td>12</td>
<td>2 ± 2</td>
<td></td>
</tr>
<tr>
<td><strong>Bouchots</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mytilus spp.</td>
<td>256</td>
<td>49 ± 9</td>
<td></td>
</tr>
<tr>
<td>Veneridae sp.1</td>
<td>256</td>
<td>41 ± 8</td>
<td></td>
</tr>
<tr>
<td>Glycymeris glycymeris*</td>
<td>128</td>
<td>12 ± 4.5</td>
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<tr>
<td><strong>Macrofaunal recruits</strong></td>
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</tr>
<tr>
<td>Taxonomic richness</td>
<td>32</td>
<td>0.2 ± 0.1</td>
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</tr>
<tr>
<td>Total abundance</td>
<td>32</td>
<td>15 ± 4</td>
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<tr>
<td>Cerastoderma edule*</td>
<td>32</td>
<td>3 ± 1</td>
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<tr>
<td>Glycymeris glycymeris*</td>
<td>16</td>
<td>2 ± 2</td>
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</tr>
<tr>
<td>Abra tenuis</td>
<td>16</td>
<td>2 ± 2</td>
<td></td>
</tr>
<tr>
<td>Venus verrucosa*</td>
<td>16</td>
<td>1 ± 1</td>
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</table>

### Table 3

Results of PERMANOVAs testing the influence of treatment (Tr) and parcel (Pa) on macrofaunal bivalve recruits (2–5 mm) during ‘hand-raking’ and ‘bouchots’ experiments. Variation in taxonomic richness of several groupings of bivalves was evaluated. p-F – pseudo-F and bold indicate significant effects (P(perm) < 0.05).

<table>
<thead>
<tr>
<th>Variable</th>
<th>2-Ways models</th>
<th>1-Way models</th>
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<tr>
<td>Tr</td>
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<td>P(perm)</td>
<td>P_F</td>
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<td>Hand-Raking</td>
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<td>n = 8</td>
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<td>Taxonomic richness</td>
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<td>1.000</td>
<td>0.85</td>
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<tr>
<td>Total abundance</td>
<td>4.00</td>
<td>0.295</td>
<td>0.50</td>
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<tr>
<td>Lucinoma borealis</td>
<td>0.20</td>
<td>1.000</td>
<td>0.64</td>
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<tr>
<td>Abra tenuis</td>
<td>7.69</td>
<td>0.200</td>
<td>0.50</td>
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<tr>
<td>Bouchots</td>
<td>n = 8</td>
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<td>n = 32</td>
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<tr>
<td>Taxonomic richness</td>
<td>1.30</td>
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<td>0.96</td>
</tr>
<tr>
<td>Total abundance</td>
<td>1.13</td>
<td>0.385</td>
<td>0.88</td>
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<tr>
<td>Lucinoma borealis</td>
<td>1.14</td>
<td>0.495</td>
<td>0.83</td>
</tr>
<tr>
<td>Cerastoderma edule*</td>
<td>0.21</td>
<td>1.000</td>
<td>0.75</td>
</tr>
</tbody>
</table>
settlement processes. In fact, drastic decreases in total abundance (91%) and taxonomic richness (87%) between developmental stages highlight potential intra- and interspecific interactions, mortality and/or secondary migration, which are well known structuring mechanisms that regulate invertebrate populations and community organization of soft-sediment benthos (Olafsson et al., 1994). Although the overall effect of hand-raking could be considered negligible at the local scale as macrofaunal recruitment of most taxa was not affected by this activity, this was not true for Cardiidae, including the common cockle C. edule, which was not observed to recruit to disturbed areas. This is in agreement with the observations by Piersma et al. (2001) and Beukema and Dekker (2005), who found that a single suction-dredging event impacted cockle populations and recruitment in the Wadden Sea 4–6 years later, suggesting that the activity may lead to cockle recruitment failure in bivalve fishing areas. Indeed, harvesting seems to negatively impact population renewal of this species at three levels by: i) removing all adults larger than the legal landing-size as this is one of the major target taxa, ii) drastically reducing the abundances of under-sized individuals (Kaiser et al., 2001), and iii) strongly limiting the settlement of young stages (present study). Thus, the potential recolonization of such recurringly disturbed areas by > 5 mm C. edule would likely result largely from juvenile and/or adult dispersal (Günther, 1992) through active or passive processes.

Fig. 3. ‘Bouchot’ experiment. Mean densities (±SE) of meiofaunal bivalve recruits as a function of treatment for (a) Nucula sp.1, (b) Loripes lucinalis, (c) Lucinoma borealis, (d) taxonomic richness, (e) total abundance, and (f) Mytilidae spp. abundances. Bars in Fig. 3d, 3e, and 3f represent results observed in the different experimental parcels. Letters indicate significant differences (p ≤ 0.05).
Recruitment of three deposit-feeding species was enhanced at the foot of ‘bouchots’ relative to that observed in surrounding areas. Of these, the Protobranchia bivalve Nucula sp1 produces a lecithotrophic larval stage (pericalymma) with a short planktonic stage and, presumably, low dispersal ability (Zardus, 2002). This is in agreement with previous observations by Grant et al. (2012), who found that the greatest abundances of Goodallia triangularis were located in the vicinity of ‘bouchot’ structures. The other two species, L. lucinalis and L. borealis, belong to the Lucinidae family, and are reported to be short-lived taxa (estimated to 4.9 years for L. lucinalis; Veloso et al., 2007), with 20 and 39 mm of maximal shell length, respectively. Both are mixotrophic chemiosymbiotic bivalves, which may rely on heterotrophic deposit-feeding and/or chemoautotrophic production, thus uptaking particulate organic matter and sulfides, respectively, in sediment porewater (Dando et al., 1986; LePennec and Beninger, 2000), but recent studies provide evidence of a horizontal transfer of symbiotic bacteria (Roeselers and Newton, 2012; Espinosa et al., 2013), which may occur during post-metamorphic development (Gros et al., 1997). We hypothesize that meiofaunal Lucinidae post-larvae preferentially colonize reduced systems to acquire sulphide-oxidizing bacteria, which are more abundant in areas with greater concentrations of sulfides, such as areas impacted by benthic organic loading in mussel farms (Newell, 2004; McKindsey et al., 2011). This strongly suggests a local organic enrichment around ‘bouchots’, although further analyses are needed to confirm this in the highly dynamic study system with coarse and permeable sediments (Grant et al., 2012; and references therein).

The observed Parcel-level variation in total bivalve and mussel abundances was likely due to greater intra-treatment variability in the vicinity of the ‘bouchots’, implying that mussel farming increases habitat heterogeneity at a small spatial scale. This phenomenon may be related to modified hydro-sedimentary dynamics due to the farm structures (i.e. ‘bouchots’) within the benthic boundary layer (McKindsey et al., 2011) that influence the distribution of macro- and meiofaunal assemblages (Eckman et al., 1981; Jumars and Nowell, 1984). Such increased variability in community structure (beta diversity) could be an indicator of stress (Warwick and Clarke, 1993) and, more importantly, an early-warning signal of a critical transition of a system submitted to disturbance (Séguin et al., 2013). Infaunal macrobenthic communities were more heterogeneous in ‘bouchots’ than in reference sites (Grant et al., 2012). The modification of the spatial structure of meiofaunal bivalves due to anthropogenic disturbances is in agreement with work by Boldina et al. (2014), who suggested that such alteration may have important consequences for ecosystem functioning by modifying predator search behavior. Globally, changes in meiofaunal assemblages may modify interactions between macrofaunal species and, consequently, their impact on ecosystem properties (Piot et al., 2014).

As for bivalve hand-raaking, the influence of ‘bouchot’ mussel culture was not evident over the long-term and had disappeared by the bivalve post-larval stage, representing great losses in total abundance (ca. 98%). Nevertheless, a positive anthropogenic effect was observed for A. tenuis, whose macrofaunal “recruits” were restricted to ‘bouchot’ parcels and was probably composed of adults rather than recruits of the year. With a maximum size of 10 mm, A. tenuis attain a shell length of only about 1 mm at 1 year (Bachelet, 2014).
The recruitment of this species is therefore temporarily variable (i.e. limited in the study year) and occurs preferentially in mussel farming areas, which are commonly characterized by enhanced organic loading and/or reduced sediment grain-size (McKindsey et al., 2011). Likewise, Grant et al. (2012) observed that the structure of macrobenthic assemblages associated with ‘bouchot’ areas was related to the greater presence of finer sediments in reference sites.

5. Conclusion

Total primary bivalve recruitment was inhibited or promoted when submitted to hand-raking and ‘bouchot’ mussel culture, respectively. However, the effect of such activities changed by the end of the recruitment period as a consequence of post-settlement processes. Such contrasted responses to anthropogenic activities reveal the difficulties in assessing anthropogenic impacts on biologically complex life cycles. Notwithstanding this, the consequence of effects occurring during the first step of recruitment should not be minimized as they may affect bivalve communities over larger spatial scales (i.e., recruit availability for other habitats) and the wider ecosystem (Menge and Sutherland, 1987), including potential far-field benthic effects (McKindsey et al., 2011). The modulation of early recruitment may influence the trophic web via a trophic cascade by affecting predators (Beukema and Dekker, 2014), and ultimately secondary consumers (van Gils and Ahmedou Salem, 2015). In addition, intertidal coarse sediment habitats are subject to large hydrodynamic forces that constantly modify surficial sediments, potentially masking biotic interactions (Thrush et al., 1996) and the impact of temporarily or spatially discrete disturbances (Collie et al., 2000). In this context, the anthropogenic effects described in the present study are likely less pronounced than they may be in more sheltered systems, such as mudflats, or in systems where the anthropogenic activities are more wide-spread. The enhanced recruitment of deposit feeders (representative of fine organically rich sediments; Jumars and Nowell, 1984) and impaired recruitment of suspension feeders in disturbed areas suggest that mechanisms involved in the investigated anthropogenic disturbances are related to modifications of local-scale hydrodynamical dynamics. Finally, although the overall influence of ‘bouchot’ mussel culture is somewhat ambiguous (it may act as a reserve for young recruits), the fact that bivalve ‘hand-raking’ damages all life stages of one of the major target species (C. edule) suggests that the activity, typically considered to have low impact, should be managed with greater caution than is currently done.

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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.marenvres.2016.03.006.

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