Estuarine, Coastal and Shelf Science 235 (2020) 106581

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: http://www.elsevier.com/locate/ecss

Swinging boat moorings: Spatial heterogeneous damage to eelgrass beds in a tidal ecosystem

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ARTICLE INFO

Keywords:
Boat mooring
Zostera marina
Seagrass ecology
Anthropogenic disturbances
SCUBA-Diving
Modeling approach

ABSTRACT

Seagrass meadows are currently known to be subjected to huge physical disturbances including boat moorings in shallow bays. We aimed to identify the impact of permanent swing mooring on the fast-growing seagrass *Zostera marina* in a mega-tidal area. Coupling the hydrodynamic MARS3D model to simulate mooring chain movements and *in situ* measurements of plant traits, we analyzed the structural responses of the eelgrass bed to scraping disturbance in the western English Channel (France). A comparison of the results with a reference site without any permanent swing boat mooring showed a significant impact on eelgrass structure (shoot density, leaf size, leaf dry weight), depending on the direction and distance from the mooring. *Zostera marina* was absent close to the mooring fixation point in three out of the four directions we evaluated. Beyond 5 m, the canopy height remained lower than in the reference site, most likely due to regular disturbances by mooring chains. Conversely, shoot density beyond 5 m was higher than in the reference site. This adaptive response counter-balanced the decrease in canopy height at these distances. The fluctuations of the structure of the eelgrass cover (number of shoots, leaf length) at a small spatial scale was clearly in accordance with the scraping intensity simulated by the MARS3D model. The tidal currents coupled to tidal amplitude variability imply a small-scale heterogeneous effect of permanent mooring on the benthic compartment, previously undetected by an aerial survey. The present results highlight the interest of coupling approaches so as to understand how physical pressure influences fast-growing species traits. The resulting important modifications could imply a more functional impact such as biodiversity loss and carbon sequestration, which is beyond the scope of the present paper.

1. Introduction

Despite their high ecological, economical and conservation value (Costanza et al., 1997; Jackson et al., 2013), seagrass meadows are known to be largely impacted by a wide range of direct and indirect human-induced disturbances (Orth et al., 2006 and reference therein) leading to accelerated seagrass losses across the world over the last decades (Short and Wyllie-Echeverria, 1996; Waycott et al., 2009). Among the major causes, repeated physical disturbances such as those caused by swinging boat moorings are one of the major reasons of local decline (Orth et al., 2006). Damage occurs when the heavy mooring chains rotate with the tidal current and wind movements associated with the buoy. This movement causes the chain to scrape up the surrounding substrate, uprooting seagrasses and resulting in clear damage on the seagrass cover around the fixing point of the mooring (Walker et al., 1989; Hastings et al., 1995; Demers et al., 2013; Unsworth et al., 2017; Sagerman et al., 2019). This always produces long-lasting impacts due to direct regular physical disturbance such as sediment erosion, and partial or total destruction of the seagrass cover (see Jackson et al., 2013). This has been clearly demonstrated on both slow-growing tropical species such as *Posidonia sp.* and *Amphibolis sp.* (Walker et al., 1989; Hastings et al., 1995; Demers et al., 2013) and temperate eelgrass such as *Zostera marina* (Collins et al., 2010; Unsworth et al., 2017). However, a recent systematic review on the effects of mooring infrastructure on benthic vegetation concluded that (1) the effects could vary according to the study and (2) there were too few studies to identify the reasons (Sagerman et al., 2019).

Even if the loss of seagrass habitats seems to be relatively restricted

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https://doi.org/10.1016/j.ecss.2020.106581
Received 23 January 2019; Received in revised form 23 August 2019; Accepted 1 January 2020

to a few meters surrounding the mooring, at least 18% of the seagrass lost between 1941 and 1992 at a regional scale are thought to be the consequence of boat mooring in Western Australia (Hastings et al., 1995). The over-dispersion of mooring areas along the coastline still largely constitutes a substantial source of repeated destruction of seagrass beds (Walker et al., 1989; Unsworth et al., 2017; Sagerman et al., 2019). In addition, seagrass loss must also be considered by including the critical alteration of the functional role of seagrass at the local and regional scales. It is well known that the loss of surface area as well as increased fragmentation could modify the functions and ecosystem services supported by the seagrass bed. This could therefore affect the associated biodiversity (Backhurst and Cole, 2000), and more generally ecosystem functioning. The decline of the dominant Atlantic species *Zostera marina* L. (1753), which is widespread across Europe, could notably affect the carbon storage capacity (Martin et al., 2005; Ouisse et al., 2011 for example) and reduce resuspension and turbidity (Widdows et al., 2008; Reidenbach and Thomas, 2018 for example). Habitat loss may also result in loss of refuge for juveniles, thereby directly or indirectly diminishing the role of this area as a nursery and its feeding functions for many organisms (Boström et al., 2014), including epifauna and flora (Reed and Hovel, 2006; Gustafsson and Boström, 2009), infauna (Silberberger et al., 2016), benthic macrofauna (Fredriksen et al., 2010), fish and birds (Plummer et al., 2013). It is also well known that these highly productive areas provide important carbon sources that directly or indirectly sustain coastal food webs (Jaschinski et al., 2008; Jephson et al., 2008; Baeta et al., 2009; Ouisse et al., 2012), related biodiversity and commercial resources (Wennhage and Pihl, 2002; Cole and Moksnes, 2016).

Initiatives proposed by international conventions on biological diversity (Ramsar Convention, Bern Convention) and then European directives (Habitat Directive EU, Ospar Convention) have led to eelgrass habitats being specifically targeted for conservation and restoration (Wynne et al., 1995). More recently, policy and management aimed at protecting *Z. marina* habitats in France was tiered from an international scale down to a regional scale. Although seagrass beds have been recorded all around the western coasts of France, they consist of more or less isolated population units growing best when located in shallow subtidal (10–15 m maximum) or intertidal water areas, on muddy-sandy seabeds (and sometimes even on gravel) (Borum et al., 2004). Unfortunately, despite the European directives, these sheltered bays and estuaries represent excellent sites for the expansion of new marina moorings.

While there is a wealth of information on the impacts of anchoring and boat mooring on growth and reproductive success processes, especially for slow-growing seagrasses (Francour et al., 1999; Hastings et al., 1995; Montefalcone et al., 2006; Demers et al., 2013), studies of boat mooring damage on faster-growing seagrasses such as *Z. marina* are relatively scarce. Aerial satellite imaging and *in situ* video imaging evidenced that boat mooring led to complete destruction of the *Z. marina* cover up to 5 m around the weighted mooring point in mega-tidal ecosystems (Unsworth et al., 2017). Nevertheless, size range of vessels, depth and maintenance on boat mooring can be modify the impact on seagrass bed (Glasby and West, 2018). In addition, tidal amplitude and current direction variability over each tidal cycle could influence the distance and the direction of scraping by the mooring chain. This repeated circular non-regular movement of the mooring chain could thus entail non-homogeneous disturbances on *Z. marina* according to the direction and the distance from the fixing point of the mooring. In addition, *Z. marina* has a relatively huge capacity to recover from repeated environmental disturbances such as clam harvesting (Qin et al., 2016) by adapting its energy allocation according to environmental conditions. This phenotypical plasticity (number of leaves, canopy height, biomass) could thus result in more complex responses of seagrasses to human-induced disturbances than just the scarred area.

The present study aims to address how irregular movements of mooring chains induced by the tidal cycle affect the structure of *Z. marina* bed responses, in order to understand a key issue for the management of boat mooring areas along European coasts. We tested the hypothesis that mooring impact in mega-tidal system would (1) depend on distance and direction from the fixing point of each mooring and (2) vary over the neap and spring tides cycle. To test these hypothesis we first mimicked the theoretical scraping movement of the mooring chain to highlight the critical scraping phases of the tidal cycle based on the results of the hydrodynamic model. Second, shoot density, seagrass canopy height and leaf dry weight were analyzed to detect the potential variations of the impact of the chain according to distance and direction to the mooring.

2. Materials and methods

2.1. *Study area*

The extensive swinging boat moorings of Dinard (Brittany, France) cover 200 ha (gray area in Fig. 1A). The 130 permanent moorings, separated by approximately 30 m, are regularly distributed all over the bay (Fig. 1B). Each swinging mooring is composed of a heavy chain (15 m long) rotating around a large concrete block completely buried in the sediment. The chains and blocks are permanently positioned. Most of moorings are used throughout the *Zostera* growing season (Spring to Autumn) by pleasure boats under 8 m in length. *Zostera marina* is well developed and covers 11.5 ha of the bay. Boat moorings have been set up for more than thirty years, and losses of seagrass cover clearly detected by aerial photography (Fournier, 2002; Gerla, 2006).

This area is subjected to huge semi-diurnal marine tidal currents (up to 10 knots locally) enforced by the tidal hydropower dam of the Rance Estuary in the south. The tidal current is the main driver of hydrodynamic movements as compared to currents induced by local wind. The maximum tidal amplitude is approximately 13 m during spring tides.

2.2. *MARS3D model and simulated movements of the mooring chains*

The three-dimensional (3D) hydrodynamic model MARS (Model for Applications at a Regional Scale, Lazure and Dumas (2008)) was used to simulate the tide-induced coastal circulation in the study area. MARS-3D was previously validated and successfully applied in the Bay of Saint-Malo (GIRAC project – Pôle Mer Bretagne). In the present study, the model was used with a regular horizontal grid (grid mesh of 151 x 101, resolution 30 m, spatial limits 02°00′29″W, 02°04′10″W, 48°39′02″N, 48°37′25″N, dotted polygon in Fig. 1A). The coastline and bathymetry were provided by the SHOM (Hydrological and Oceanographic Service of the French Navy). The open boundary conditions were obtained from a larger model based on tidal harmonic constants. The wind was not taken into account in the simulation due to its relatively low impact on the mooring chain movements in comparison with the tidal currents.

Water circulation was simulated using tidal forcing from 12^{th} to November 26, 2015. This period included tidal cycles during neap and spring tides, which are the main drivers of the hydrodynamic of mega-tidal systems. This simulation period could be considered as almost similar all over the year from a hydrodynamic point of view. Barotropic currents (intensity and direction) and free surface elevation were recorded every 6 min. The scouring distance (from the fixing point of the mooring) and direction were calculated for each time point as a combination of instantaneous current direction, water height, and length of the mooring chain. The theoretical impact frequency over the whole simulation period was finally calculated for each of the 16 directions.

2.3. *In situ seagrass sampling strategy*

Two sampling sites were selected in the eastern part of the swinging boat mooring area: i) the impacted mooring site located within moorings (2°02′35″W, 48°37′57″N) and nearby, and ii) the reference site close to

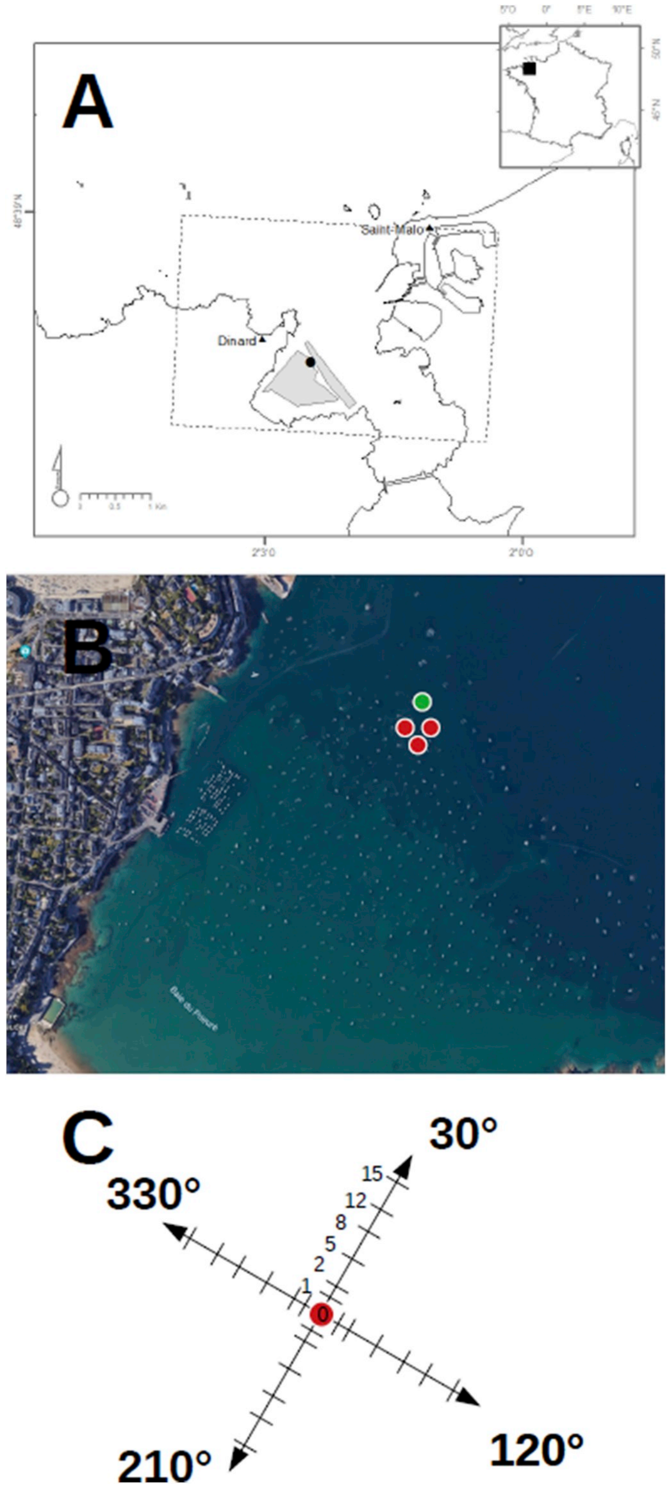

Fig. 1. (A) Location of the sampling site in the Bay of Saint-Malo (black point), western English Channel, France. The gray polygons correspond to the permanent boat mooring area. The rectangular area (dotted lines) correspond to the spatial limits of the hydrodynamic MARS3D model. (B) Satellite image from Google Earth (2019) of bay of the permanent boat mooring area in the Bay of Saint-Malo. Each white points correspond to a boat mooring. The red and green points indicate the three impacted sites studied and the reference site, respectively. (C) Schematic representation of sampling strategy for each mooring. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the moorings but not within their immediate influence (50 m from a mooring and located in the adjacent channel reserved for boating). In the reference site, loss of seagrass cover or habitat fragmentation of the seagrass cover was undetectable by aerial photography (Fournier, 2002; Gerla, 2006). The two sampling sites were situated in an area considered as homogeneous for bathymetry (1.2–1.6 m above chart datum) and granulometry (muddy-sandy sediment). All samples were collected by SCUBA diving in spring, between 9th and April 11, 2015.

We choose a reference site close to the moorings but not within their immediate influence (50 m from a mooring). This imply that seagrasses are submitted to the same environmental conditions as bathymetric, granulometric and hydrodynamic currents. We thus consider our sampling as pseudo-replication which has the advantage of limiting the influence of spatial or temporal co-variables (Oksanen, 2001).

The sampling strategy was conducted on three permanent moorings randomly chosen in the impacted site and on one random fixing point in the reference site (Fig. 1B). Seagrass was sampled in four regularly distributed directions (30°, 120°, 210°, and 300° N, E, S, and W, respectively) 0, 1, 2, 5, 8, 12, and 15 m away from the fixing point of each mooring or reference site (Fig. 1C). These uneven increments were determined from the maximum theoretical impacted area (15 m along the mooring chain) and the results of the hydrodynamic model. At each distance, three cores (12 cm inner diameter, 5 cm depth) arranged perpendicularly to the transect (50 cm apart) were carefully collected and stored in a plastic bag. The core size was adapted from seagrass monitoring methods (Avery, 1999; McKenzie et al., 2001; Ganthy et al., 2013), to be adjusted to the density and the maximum leaf length of *Zostera marina* in temperate areas in spring.

2.4. *Laboratory measurements*

Each sample was rinsed with clear water, and the leaves were separated from the roots and rhizomes. Then the number of shoots *per* sample (shoot density, D) and the length of each leaf was measured (±1 mm). The canopy height (CH) was defined as the maximum leaf length of each sample. Finally, leaves were dried separately at 60 °C to a constant weight (leaf dry weight, LDW, ± 0.001 mg).

2.5. *Data treatment and statistical analyses*

Data from the three moorings were pooled according to distance (0, 1, 2, 5, 8, 12, and 15 m) and direction (N, E, S, and W) for all analyses. Shoot density (D), canopy height (CH) and leaf dry weight (LDW) were used to test the mooring effect on *Zostera marina*. The mooring effect was firstly tested by comparing values from the impacted site to the reference site with an F-test and a *t*-test (or a Welch test if the variance was unequal) after verifying the normality of the data (Shapiro test, $p < 0.05$). The effects of distance, direction, and the interaction between distance and direction were then tested using two-way ANOVA with replication both on the impacted and reference sites. Tukey's HSD post-hoc tests were used to identify the differences within directions and distances. Finally, one-sample *t*-test was used to test differences in shoot density, canopy height and leaf dry weight between each sampling point of the impacted site and the reference value estimated from the reference site. All treatments were analyzed with R 3.1.2, and figures were drawn with SigmaPlot 12.5.

3. Results

3.1. *MARS3D model simulation*

The theoretical scouring effect on the seagrass bed simulated from the 3D hydrodynamic model MARS varied both in direction and distance over each tide cycle. This variation resulted from the combination of the mooring chain length (fixed parameter), the current direction, and the sea level which varied at each time point. As illustrated during a neap tide from November 20, 2015 at 12:11 p.m. to November 21, 2015 at 01:11 a.m. (Fig. 2a), the theoretical mooring chain trajectory was composed of four alternative periods over one tide cycle, *i.e.* two periods with slow variation of the mooring chain length in contact with the sediment, and two periods of fast shifting direction of the mooring chain. During the ebb tide (from 1:00 p.m. to 5:00 p.m. in the present case), the theoretical direction of the mooring chain did not vary (299 ± 8°) and the length of the mooring chain in contact with the sediment increased slowly from 6.8 m at 1:00 p.m. to 10.9 m at 5:00 p.m. (Fig. 2a). The shift of the current direction between the ebb tide and the next rising tide induced a fast movement of the mooring chain from 325° to 87° over 1 h (from 6:00 p.m. to 7:00 p.m.), without any change of the chain length in contact with the bottom (12.1 ± 0.1 m). The theoretical direction of the mooring chain remained constant (105 ± 8°) during the next rising tide (8:00 p.m. to 12:00 a.m.), and the mooring chain length in contact with the sediment decreased from 12.2 to 7.0 m. The last period resulting from a shift of the current direction corresponded to a fast movement of the mooring chain (from 116° to 280°) and a short mooring chain length in contact with the seagrass bed (less than 7 m). The theoretical mooring chain trajectory was similar in the spring tide and in the neap tide, yet with a higher amplitude (Fig. 2b). The theoretical distance of the impact exceeded 14 m during low tide. The simulation results revealed a rapid movement of the chain at the end of the ebbing tide resulting from a change in the current direction (see trajectory after 10:00 p.m.).

The theoretical scraping distance of the mooring chain over the simulation period (including neap and spring tide) was evaluated by calculation of the minimum, median and maximal impacted areas (Fig. 3). It corresponds respectively to the area impacted during 90%, 50% and 10% of time over the simulation period. The theoretical scraping distance was at least 3.3 m (minimal impacted area in the south-west) whatever the direction, corresponding to the difference between the length of the mooring chain (15 m) and the maximum sea level on the site (Fig. 3). The impacted area varied little over the simulation period (small difference between minimal and maximal impacted area) between 160° and 270° (approximately from south to west, less than 7 m) and between 330° and 90° (approximately from north to east, more than 12 m). In contrast, the impacted area largely varied with natural conditions (amplitude of the tidal cycle) in the north-west (270–330°) and south-east (90–160°) directions, corresponding to the position of the mooring chain during the ebb and rising tides (Fig. 2).

3.2. Eelgrass parameters

The mean canopy height was significantly higher (Welch test, $p < 0.001$) and less variable (F test, $p < 0.001$) in the reference site (270 ± 68 mm) than in the impacted site (98 ± 91 mm). The mean leaf dry weight was also significantly higher (*t*-test, $p < 0.001$) in the reference site (34.03 ± 21.90 g m^{-2}) than in the impacted site (17.93 ± 22.13 g m^{-2}). Conversely, shoot density was more variable (F test, $p < 0.001$) in the impacted site, but the mean values were similar to those of reference site (363 ± 448 shoots m^{-2} and 364 ± 220 shoots m^{-2}, respectively).

In the reference site, the structure of the seagrass bed was relatively homogeneous (Table 1). There was no significant effect of the distance from the origin (a point randomly fixed for sampling) on shoot density, leaf dry weight or canopy height (two-way ANOVA, Table 2). The mean canopy height was the only variable that differed significantly along directions (two-way ANOVA, $n = 65$, $p = 0.007$, Table 2). We thus used the global mean value (±SD) of shoot density (364 ± 220 shoots. m^{-2}) and leaf dry weight (34.03 ± 21.90 gDW. m^{-2}) as the unique reference values for further analyses in the impacted site, except for the mean canopy height; in that case, we used the mean value according to the four directions as a reference value (dotted lines and gray polygons in Fig. 4).

In the impacted site, the structure of seagrass patches varied strongly both in direction and distance from the fixing point according to the simulation results. Seagrasses were scarcely present close to the fixing point of the mooring chain in the north, east and south directions (Fig. 4). However, the absence of *Zostera marina* in the first few meters was less marked to the west. There was a significant effect of distance, direction, and of the direction-distance interaction on canopy height, shoot density and leaf dry weight (two-way ANOVA, Table 3). The mean canopy height, shoot density and biomass were significantly lower (Tukey's HSD post-hoc test, $p < 0.01$) in the samples taken 0, 1, and 2 m from the fixing point than in the more distant samples in all four directions. The impact on the structure of the seagrass bed extended to 5 m to the north, with values similar to those measured close to the mooring. Beyond 8 m, the mean canopy height remained significantly lower than in the reference site (Table 1) in all four directions (one-sample t-tests, $p < 0.001$). Yet, shoot density was significantly higher in the impacted site than in the reference site (one-sample t-tests, $p < 0.001$, Fig. 4), except 12 and 15 m to the west. Mean biomass (leaf dry weight) remained lower (or equal at 15 m distance, Fig. 4) but not significantly different than in the reference zone (34.03 ± 21.90 gDW. m^{-2}).

4. Discussion

The present study aims to address how irregular movements of mooring chains induced by tidal circulation affect the structure of *Z. marina* bed responses. Coupling hydrodynamic model simulation and *in situ* observation approaches, we describe non-circular and predictable effects of mooring chains on seagrass meadows resulting from the shift of the current direction and the variation of the mooring chain length in contact with the sediment during tidal cycles. An effect of the disturbance was also detectable beyond 5 m, but less visible. The measurements performed in the present study show an increase in canopy height, in density, and consequently in biomass with increasing distance. However, the canopy height remained below the reference value (from the reference site) while density exceeded the reference density estimated in the reference site. Leaf dry weight, which integrates these two antagonistic tendencies, was comparable to the estimated biomass in the reference site.

4.1. Impacts on Z. marina as a function of distance and direction

The absence of the fast-growing seagrass *Zostera marina* close to the mooring (less than 5 m around it) is in agreement with aerial photographs taken in the study area (Fournier, 2002; Gerla, 2006). Nevertheless, seagrass beds were less impacted in the 300° direction, corresponding to the landing zone of the chain. This zone clearly differed from the 30°, 120° and 210° directions for which the tidal currents led to rapid changes of direction of the chain and therefore to intense scraping. Large scours in eelgrass beds caused by anchoring or mooring have been previously observed on *Zostera* marina (Unsworth et al., 2017; Glasby and West, 2018), *Posidonia* sp. (Walker et al., 1989; Hastings et al., 1995; Francour et al., 1999; Montefalcone et al., 2006; Glasby and West, 2018), *Amphibolis* sp. (Walker et al., 1989; Hastings et al., 1995) or *Halodule* sp. (Creed and Amado Filho, 1999). This result from physical disturbances due to the scraping of the chain. Clear areas surrounding 'swing' moorings can be generated by the continuous dragging of the mooring chains, and the concrete block itself causes a loss of seagrass due to its large surface area. The spatial extent of damage can be also exacerbates by lift and replacement of the blocks with chain in some places (Glasby and West, 2018). In our study, this scraping hypothesis is reinforced by the MARS 3D hydrodynamic model simulations which illustrate that the zone close to the mooring (less than 5 m, Fig. 2) was subjected to huge impacts of the chain during the tidal cycle in all four studied directions.

In addition, we illustrated more diffusive effects of the mooring chains on seagrass meadows. Moorings seemed to have a lower effect than the total loss of seagrass bed in the first few meters, but did have effects on a wider spatial scale. The canopy height beyond 5 m was

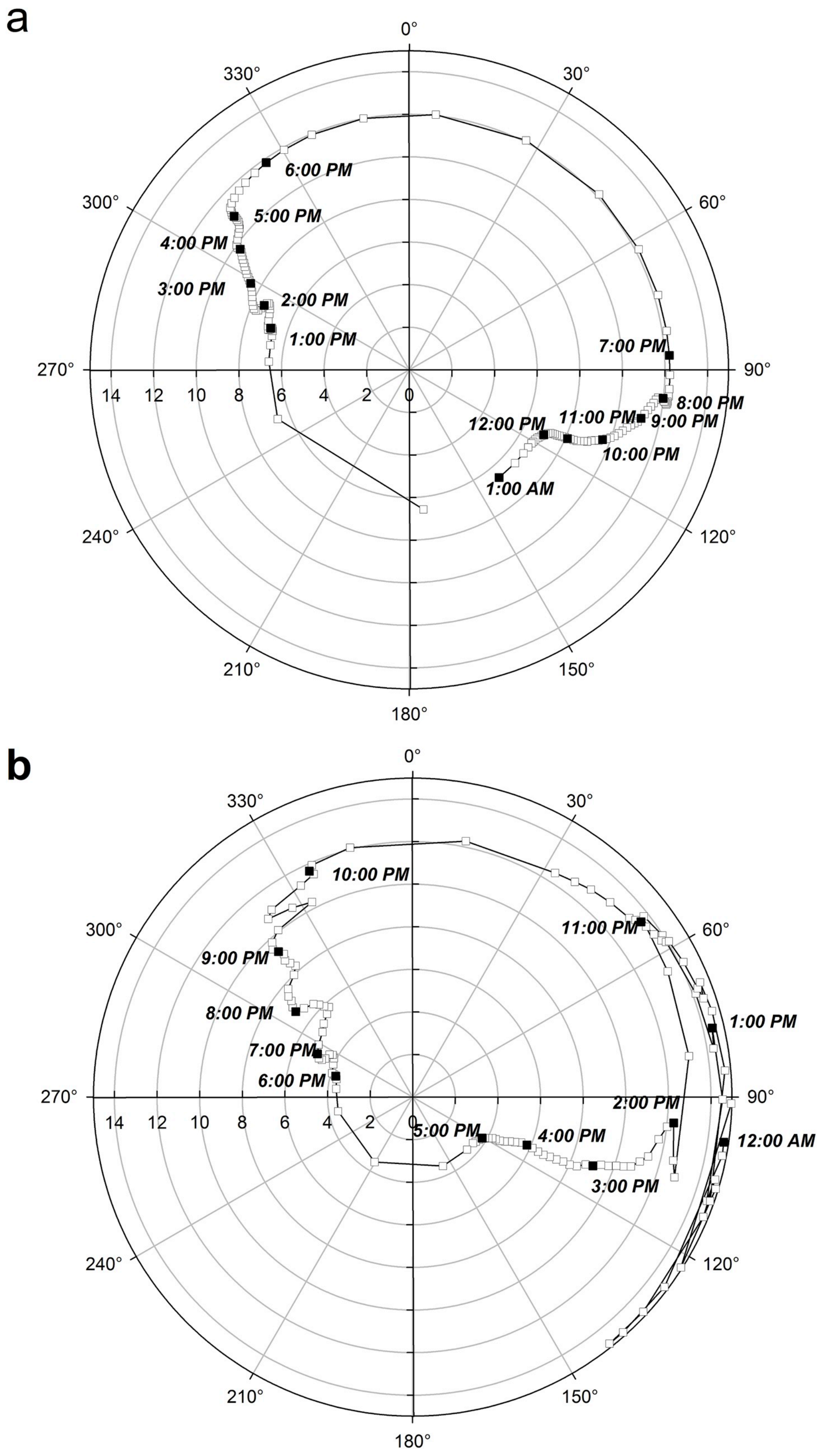

Fig. 2. Theoretical impact of the mooring chains simulated with the MARS 3D hydrodynamic model every 6 min as a combination of current direction, water height and mooring chain length. Theoretical direction and mooring chain length in contact with the seagrass bed (a) over a neap tide cycle (from November 20, 2015 at 12:11 p.m. to November 21, 2015 at 01:11 a.m.) and (b) over a spring tide (from November 25, 2015 at 12:00 a.m. to November 26, 2015 at 00:25 a.m.).

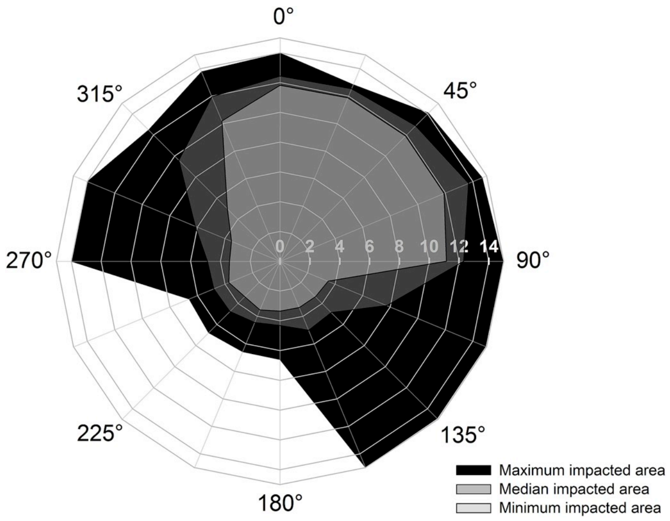

Fig. 3. Surface of the theoretical impacted areas over the complete simulation period (including the neap and spring tides of 12th and November 26, 2015). The minimum (light gray), median (dark gray) and maximal (black) impacted area correspond respectively to the area impacted in 90%, 50% and 10% of time over the simulation period.

Table 1

(n) number of values, Mean (±SD) Canopy height, Shoot density and Leaf dry weight in the reference and impacted sites along the four directions (North, Est, South and West).

Direction	n	Canopy height (*mm*)	Shoot density (*Shoot .m^{-2}*)	Leaf dry weight (*gDW .m^{-2}*)
Reference Site				
N	24	304 ± 62	354 ± 186	33.23 ± 27.62
E	24	261 ± 52	328 ± 189	36.20 ± 20.24
S	20	242 ± 95	385 ± 271	31.16 ± 21.56
W	24	269 ± 48	394 ± 242	35.09 ± 17.91
Impacted Site				
N	63	77 ± 87	261 ± 352	12.08 ± 16.90
E	60	89 ± 93	380 ± 516	19.48 ± 27.01
S	62	103 ± 90	415 ± 494	19.62 ± 21.16
W	59	123 ± 90	399 ± 408	20.79 ± 21.97

Table 2

Results of univariate two-factorial ANOVAs on canopy height, shoot density and leaf biomass in the reference site.

Source of variation	DF	MS	F-ratio	p-level
Canopy height				
Direction	3	15076	4.4	0.007
Distance	6	5827	1.7	0.132
Direction x Distance	17	7046	2.1	0.019
Error	65	3399		
Shoot density				
Direction	3	21416	0.4	0.757
Distance	6	58579	1.1	0.382
Direction x Distance	17	28747	0.5	0.927
Error	65	54125		
Leaf dry weight				
Direction	3	106	0.2	0.907
Distance	6	311	0.5	0.778
Direction x Distance	17	227	0.4	0.983
Error	64	580		

probably limited by the regular passage of the chain near the bottom; this physical disturbance, though less frequent, particularly between 90° and 330°, was probably a stress factor for *Zostera marina*. There seemed to be some compensation by the plants, which favored a greater number of shoots rather than a higher canopy. This fast-growing seagrass species is known for its plasticity in terms of energy allocation according to environmental conditions (Olesen and Sand-Jensen, 1994a). Biomass in stable eelgrass populations is predominantly allocated to increasing shoot size rather than shoot density. However, the severe disturbance that reduced leaf dry weight and opened the canopy prior to spring growth enhanced the growth and survival of new small shoots. Under natural conditions, a clear relationship between the increase of the number of shoots and the decrease in maximum leaf length in *Z. marina* was pointed out by Jacobs (1979). Thus, *Zostera marina* populations may display a wide range of growth strategies including larger leaves *per* shoot, or branching and expansion of the rhizome and development of many new shoots (Olesen and Sand-Jensen, 1994a, 1994b). An increase in the number of shoots in late spring resulting from physical disturbance was also demonstrated in *Halodule wrightii* (Creed and Amado Filho, 1999). Concerning *Zostera marina*, repeated stress, if not lethal, could induce an adaptive response aimed at increasing the number of germinative shoots (Erftemeijer and Robin Lewis, 2006). The major differences observed in eelgrass structures are strongly linked to the chain movement effects, although very local hydrodynamic conditions may also influence leaf growth, as suggested before.

If mooring chains have a direct impact on eelgrass through repeated contacts, indirect impacts may also exist. Flexible plants as seagrasses are actually describe to reduce the hydrodynamic depending the distance and the structure of the seagrass bed (Abderlrhman, 2007; Ganthy et al., 2013; Serra et al., 2018). Permanent scraping generate large bare soil surrounding 'swing' moorings which induce an increase of hydrodynamic which enhance the resuspension. This will impact the turbidity, reducing the water clarity which can limit photosynthesis (and growth) by enhancing turbidity.

4.2. Hydrodynamic model to identify critical phases and thresholds

The results from *in situ* observations are consistent with the results from model simulations. Although relatively simple, the modeling of the movement of the chain on the bottom explains a large part of the spatial variability of the swing boat mooring. At this stage, the model gives clues about the critical phases of the movement of the chain. Rapid changes in the direction of the current induce a scraping movement of the mooring chain at a variable distance from the point of attachment. The simulation also highlights the effect of the disturbance frequency on the seagrass bed. Although some areas suffered from the effects of the scraping chain movement, the movement did not cause the seagrass to totally disappear, but changed the phenology of *Zostera marina* by increasing the number of shoots and decreasing the seagrass canopy height. The potential overestimation of the mooring chain impact could ensue from the simplicity of the physical indicators we used and from the simplified hydrodynamic forcing applied for the simulation. This could be refined, both in terms of impact distance (length in contact with the bottom) and trajectory. For this latter point, the effect of the wind, especially in the presence of a boat, could change the response time of the chain trajectory in the presence of a current; however, it is often admitted that the current is the main force in this region subjected to mega-tidal currents. Moreover, taking into account a finer modeling of the chain movement would be quite time-consuming, induce more hypotheses and would not bring any new elements.

5. Conclusions

Our study is one of the first focused on the impacts of mooring on a fast-growing species in a temperate area subjected to macro-tidal currents. We specifically analyzed the structure of seagrass patches still in

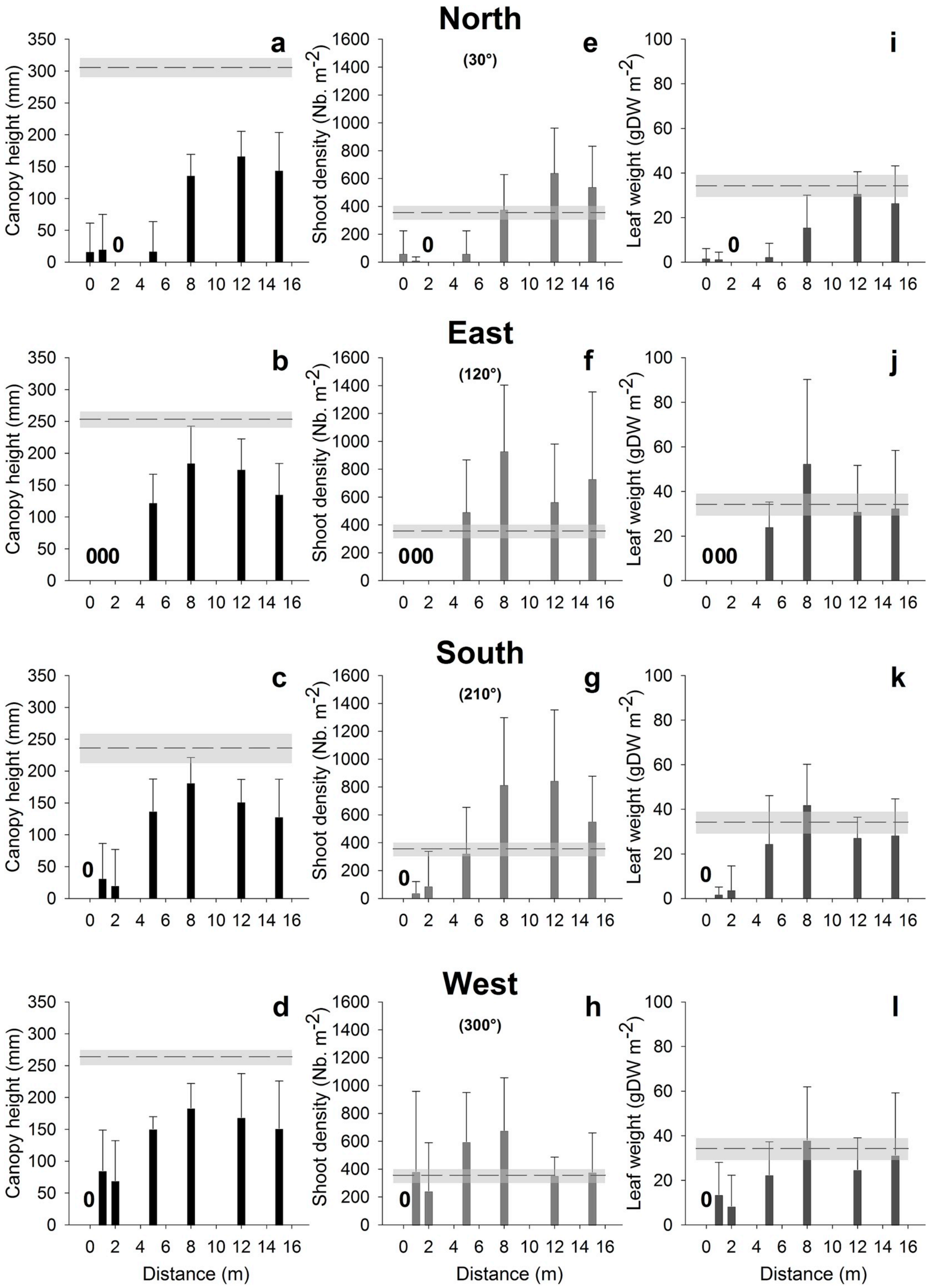

Fig. 4. Mean (±SD) canopy height (a, b, c, d), shoot density (e, f, g, h) and leaf dry weight (i, j, k, l) 0, 1, 2, 5, 8, 12, and 15 m from the mooring in the impacted site along the four directions (north, est, south and west). The dotted line and gray area correspond to the mean (±SE) Canopy height (see Table 1), shoot density (364 ± 220 shoots. m^{-2}) and leaf dry weight (34.03 ± 21.90 gDW. m^{-2}) in the reference site. "0" indicates the absence of *Zostera marina*.

place and still growing under the continuous impact of a chain, at a very fine scale. Given the modeling of the chain trajectory, the four directions selected to monitor these impacts allowed us to analyze the responses of the seagrass cover under different scraping intensities. We did not estimate losses on a large scale, which could be done through an aerial survey (Unsworth et al., 2017), but the detected modifications of the eelgrass structure led to a better estimation of the impacts of swing boat mooring in our study site. Using model simulation, we hope to extrapolate our results to larger mooring coastal areas subjected to mega-tidal cycles. In order to limit the associated uncertainties related to this extrapolation, we will have to consider the influence of size range of vessels and depth as it was mentioned by Glasby and West (2018).

Solutions would undoubtedly be to remove moorings from seagrass beds. When that is not possible, it could be imagine to remove the heavy chains during long period of non using but taking care to limit impact the seagrass bed during maintenance. One other solution would be to

Table 3
Results of univariate two-factorial ANOVAs on canopy height, shoot density and leaf biomass in the impacted site.

Source of variation	DF	MS	F-ratio	p-level
Canopy height				
Direction	3	24325	9.9	<0.001
Distance	6	213870	86.8	<0.001
Direction x Distance	18	7248	2.9	<0.001
Error	216	2464		
Shoot density				
Direction	3	305053	2.7	0.044
Distance	6	3188635	28.7	<0.001
Direction x Distance	18	263444	2.4	0.002
Error	216	111105	5.0	
Leaf dry weight				
Direction	3	989	3.9	0.009
Distance	6	8902	35.4	<0.001
Direction x Distance	18	472	1.9	0.019
Error	217	252		

deploy other types of moorings such as those recommended by Demers et al. (2013), *i.e.* the so-called 'sea-grass-friendly boat mooring systems', especially in mooring areas submitted to strong current intensities. Our study reinforces the idea that ecological moorings would also allow us to ensure the recovery of a fast-growing seagrass species displaying the same characteristics as those of the reference sites. 'Screw' seagrass-friendly-moorings allow for the recovery of eelgrass, as observed in Australian bays (Gladstone, 2011). In mega-tidal regions, the main problem remains to transpose environmentally friendly moorings and find technical solutions to reduce the length of the chain that is directly in contact with the seabed when the tide recedes. This constitute an important challenge as these chain length are calculated according to water depth and boat size. Our study provides useful information to that end. Local recovery may sometimes occur rapidly, as shown in the Baltic Sea (Frederiksen et al., 2004a, 2004b), in both subtidal and intertidal areas of the Wadden Sea (Reise and Kohlus, 2008; van Katwijk et al., 2009), in the Atlantic Ocean (Glémarec et al., 1996; Godet et al., 2008; Furman et al., 2015; Orth et al., 2017). Even in the case of replacement by ecological moorings, we can however expect the recovery of the eelgrass cover to be variable depending on many others biological and environmental factors (seeds recruitment, disturbance intensity, others human pressures …) as suggested after huge impacts (Neckles et al., 2005; Qin et al., 2016 for example).

Acknowledgements

This study forms part of the Master's degree of I. Marchand-Jouravleff. The authors would like to thank J. Guillaudeau, C. Ronval, T. Diméglio and V. Danet for their field participation, M. Jouan (ACRI-HE) for producing MARS3D simulations, G. Messiaen for his help on cartography artworks and Annie Buchwalter for improving English redaction.

References

Abderlrhman, M.A., 2007. Modeling coupling between eelgrass Zostera marina and water flow. Mar. Ecol. Prog. Ser. 338, 81–96.

Avery, W., 1999. Monitoring submerged aquatic vegetation in Hillsborough bay, Floride. Chapter 10. In: Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press, Washington, D.C., pp. 137–155

Backhurst, M., Cole, R., 2000. Biological impacts of boating at Kawau Island, north-eastern New Zealand. J. Environ. Manag. 60, 239–251. https://doi.org/10.1006/jema.2000.0382.

Baeta, A., Pinto, R., Valiela, I., Richard, P., Niquil, N., Marques, J.C., 2009. δ15N and δ13C in the Mondego estuary food web: seasonal variation in producers and consumers. Mar. Environ. Res. 67, 109–116. https://doi.org/10.1016/j.marenvres.2008.11.005.

Borum, J., Duarte, C.M., Krause-Jensen, D., Greve, T.M. (Eds.), 2004. European Seagrasses: an Introduction to Monitoring and Management. The M&MS project, S. l.

Boström, C., Baden, S., Bockelmann, A.-C., Dromph, K., Fredriksen, S., Gustafsson, C., Krause-Jensen, D., Möller, T., Nielsen, S.L., Olesen, B., Olsen, J., Pihl, L., Rinde, E., 2014. Distribution, structure and function of Nordic eelgrass (*Zostera marina*) ecosystems: implications for coastal management and conservation. Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 410–434. https://doi.org/10.1002/aqc.2424.

Cole, S.G., Moksnes, P.-O., 2016. Valuing multiple eelgrass ecosystem services in Sweden: fish production and uptake of carbon and nitrogen. Front. Mar. Sci. 2 https://doi.org/10.3389/fmars.2015.00121.

Collins, K.J., Suonpää, A.M., Mallinson, J.J., 2010. The impacts of anchoring and mooring in seagrass, Studland Bay, Dorset, UK. Underw. Technol. 29, 117–123. https://doi.org/10.3723/ut.29.117.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253.

Creed, J.C., Amado Filho, G.M., 1999. Disturbance and recovery of the macroflora of a seagrass (Halodule wrightii Ascherson) meadow in the Abrolhos Marine National Park, Brazil: an experimental evaluation of anchor damage. J. Exp. Mar. Biol. Ecol. 235, 285–306. https://doi.org/10.1016/S0022-0981(98)00188-9.

Demers, M.C.A., Davis, A.R., Knott, N.A., 2013. A comparison of the impact of "seagrass-friendly" boat mooring systems on *Posidonia australis*. Mar. Environ. Res. 83, 54–62. https://doi.org/10.1016/j.marenvres2012.10.010.

Erftemeijer, P.L.A., Robin Lewis, R.R., 2006. Environmental impacts of dredging on seagrasses: a review. Mar. Pollut. Bull. 52, 1553–1572. https://doi.org/10.1016/j.marpolbul.2006.09.006.

Fournier, J., 2002. Analyse spatiale de l'impact d'une perturbation anthropique sur un herbier de zostères en baie de Locquirec (Bretagne nord). Norois 189, 47–55.

Francour, P., Ganteaume, A., Poulain, M., 1999. Effects of boat anchoring in *Posidonia oceanica* seagrass buds in the Port-Cros National Park (north-western Mediterranean sea). Aquat. Conserv. Mar. Freshw. Ecosyst. 9, 391–400. https://doi.org/10.1002/(sici)1099-0755(199907/08)9:4<391::aid-aqc356>3.3.co;2-#.

Frederiksen, M., Krause-Jensen, D., Holmer, M., Laursen, J.S., 2004. Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. Aquat. Bot. 78, 167–181. https://doi.org/10.1016/j.aquabot.2003.10.002.

Frederiksen, M., Krause-Jensen, D., Holmer, M., Laursen, J.S., 2004. Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: influence of physical setting. Aquat. Bot. 78, 147–165. https://doi.org/10.1016/j.aquabot.2003.10.003.

Fredriksen, S., De Backer, A., Boström, C., Christie, H., 2010. Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. Mar. Biol. Res. 6, 189–200. https://doi.org/10.1080/17451000903042461.

Furman, B.T., Jackson, L.J., Bricker, E., Peterson, B.J., 2015. Sexual recruitment in *Zostera marina*: a patch to landscape-scale investigation. Limnol. Oceanogr. 60, 584–599. https://doi.org/10.1002/lno.10043.

Ganthy, F., Sottolichio, A., Verney, R., 2013. Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). J. Mar. Syst. 109–110, S233–S240. https://doi.org/10.1016/j.jmarsys.2011.11.027.

Gerla, D., 2006. Inventaire des herbiers de zostères. Baie de Saint-Malo/Rance/Haut estuaire du Trieux (No. RST.DOP-LER/SM/06.004). Ifremer.

Gladstone, W., 2011. Monitoring of Seagrass Friendly Moorings in Shoal Bay – Report of 2010 Monitoring. Final report to OnWater Marine Services Pty Ltd, Sidney.

Glasby, T.M., West, G., 2018. Dragging the chain: quantifying continued losses of seagrasses from boat moorings. Aquat. Conserv. Mar. Freshw. Ecosyst. 28, 383–394.

Glémarec, M., Le Faou, Y., Cuq, F., 1996. Long-term changes of seagrass beds in the glenan archipelago (south brittany). Oceanol. Acta 20, 217–227.

Godet, L., Fournier, J., van Katwijk, M., Olivier, F., Le Mao, P., Retière, C., 2008. Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: a general overview and first accurate mapping. Dis. Aquat. Org. 79, 249–255. https://doi.org/10.3354/dao01897.

Gustafsson, C., Boström, C., 2009. Effects of plant species richness and composition on epifaunal colonization in brackish water angiosperm communities. J. Exp. Mar. Biol. Ecol. 382, 8–17. https://doi.org/10.1016/j.jembe.2009.10.013.

Hastings, K., Hesp, P., Kendrick, G.A., 1995. Seagrass loss associated with boat moorings at rottnest-island, western-Australia. Ocean Coast Manag. 26, 225–246. https://doi.org/10.1016/0964-5691(95)00012-q.

Jackson, E.L., Griffiths, C., Durkin, O., 2013. A Guide to Assessing and Managing Anthropogenic Impact on Marine Angiosperm Habitat-Part 1: Literature Review (No. 111). The Marine Biological Association of the United Kingdom, Plymouth, UK.

Jacobs, R.P.W., 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquat. Bot. 7, 151–172. https://doi.org/10.1016/0304-3770(79)90019-6.

Jaschinski, S., Brepohl, D.C., Sommer, U., 2008. Carbon sources and trophic structure in an eelgrass Zostera marina bed, based on stable isotope and fatty acid analyses. Mar. Ecol. Prog. Ser. 358, 103–114. https://doi.org/10.3354/meps07327.

Jephson, T., Nystrom, P., Moksnes, P.-O., Baden, S.P., 2008. Trophic interactions in Zostera marina beds along the Swedish coast. Mar. Ecol. Prog. Ser. 369, 63–76. https://doi.org/10.3354/meps07646.

Lazure, P., Dumas, F., 2008. An external-internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). Adv. Water Resour. 31, 233–250. https://doi.org/10.1016/j.advwatres.2007.06.010.

Martin, S., Clavier, J., Guarini, J.-M., Chauvaud, L., Hily, C., Grall, J., Thouzeau, G., Jean, F., Richard, J., 2005. Comparison of *Zostera marina* and maerl community metabolism. Aquat. Bot. 83, 161–174. https://doi.org/10.1016/j.aquabot.2005.06.002.

McKenzie, L.J., Campbell, S.J., Roder, C.A., 2001. Seagrass-Watch: Manual for Mapping & Monitoring Seagrass Ressources by Community (Citizen) Volunteers, 100. QFS, NFC, Cairns).

Montefalcone, M., Lasagna, R., Bianchi, C.N., Morri, C., Albertelli, G., 2006. Anchoring damage on *Posidonia oceanica* meadow cover: a case study in Prelo cove (Ligurian

Sea, NW Mediterranean). Chem. Ecol. 22 (Suppl. 1), 207–217. https://doi.org/10.1080/02757540600571976.

Neckles, H., Short, F., Barker, S., Kopp, B., 2005. Disturbance of eelgrass *Zostera marina* by commercial mussel *Mytilus edulis* harvesting in Maine: dragging impacts and habitat recovery. Mar. Ecol. Prog. Ser. 285, 57–73. https://doi.org/10.3354/meps285057.

Oksanen, L., 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94, 27–38. https://doi.org/10.1034/j.1600-0706.2001.11311.x.

Olesen, B., Sand-Jensen, K., 1994. Biomass-density patterns in the temperate seagrass *Zostera marina*. Mar. Ecol. Prog. Ser. 109, 283–291.

Olesen, B., Sand-Jensen, K., 1994. Demography of shallow eelgrass (*Zostera marina*) populations-shoot dynamics and biomass development. J. Ecol. 82, 379. https://doi.org/10.2307/2261305.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K. L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2.

Orth, R.J., Lefcheck, J.S., Wilcox, D.J., 2017. Boat propeller scarring of seagrass beds in lower chesapeake bay, USA: patterns, causes, recovery, and management. Estuar. Coasts 40, 1666–1676. https://doi.org/10.1007/s12237-017-0239-9.

Ouisse, V., Migné, A., Davoult, D., 2011. Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Zostera noltii* beds. Mar. Ecol. Prog. Ser. 437, 79–87. https://doi.org/10.3354/meps09274.

Ouisse, V., Riera, P., Migné, A., Leroux, C., Davoult, D., 2012. Food web analysis in intertidal *Zostera marina* and *Zostera noltii* communities in winter and summer. Mar. Biol. 159, 165–175. https://doi.org/10.1007/s00227-011-1796-2.

Plummer, M.L., Harvey, C.J., Anderson, L.E., Guerry, A.D., Ruckelshaus, M.H., 2013. The role of eelgrass in marine community interactions and ecosystem services: results from ecosystem-scale food web models. Ecosystems 16, 237–251. https://doi.org/10.1007/s10021-012-9609-0.

Qin, L.-Z., Li, W.-T., Zhang, X., Zhang, P., Qiao, W., 2016. Recovery of the eelgrass *Zostera marina* following intense Manila clam *Ruditapes philippinarum* harvesting disturbance in China: the role and fate of seedlings. Aquat. Bot. 130, 27–36. https://doi.org/10.1016/j.aquabot.2016.01.002.

Reed, B., Hovel, K., 2006. Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influences epifaunal abundance and diversity. Mar. Ecol. Prog. Ser. 326, 133–143. https://doi.org/10.3354/meps326133.

Reidenbach, M.A., Thomas, E.L., 2018. Influence of the seagrass, *Zostera marina*, on wave attenuation and bed shear stress within a shallow coastal bay. Front. Mar. Sci. 5 https://doi.org/10.3389/fmars.2018.00397.

Reise, K., Kohlus, J., 2008. Seagrass recovery in the northern Wadden Sea? Helgol. Mar. Res. 62, 77–84. https://doi.org/10.1007/s10152-007-0088-1.

Sagerman, J., Hansen, J.P., Wikström, S.A., 2019. Effects of boat traffic and mooring infrastructure on aquatic vegetation: a systematic review and meta-analysis. Ambio. https://doi.org/10.1007/s13280-019-01215-9.

Serra, T., Oldham, C., Colomer, J., 2018. Local hydrodynamics at edges of marine canopies under oscillatory flows. PLoS One 13, e0201737. https://doi.org/10.1371/journal.pone.0201737.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. 23, 17–27. https://doi.org/10.1017/s0376892900038212.

Silberberger, M.J., Thormar, J., Fredriksen, S., 2016. Small-scale removal of seagrass (*Zostera marina* L.): effects on the infaunal community. Mar. Biol. Res. 12, 993–1002. https://doi.org/10.1080/17451000.2016.1225959.

Unsworth, R.K.F., Williams, B., Jones, B.L., Cullen-Unsworth, L.C., 2017. Rocking the boat: damage to eelgrass by swinging boat moorings. Front. Plant Sci. 8 https://doi.org/10.3389/fpls.2017.01309.

van Katwijk, M.M., Bos, A.R., de Jonge, V.N., Hanssen, L.S.A.M., Hermus, D.C.R., de Jong, D.J., 2009. Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar. Pollut. Bull. 58, 179–188. https://doi.org/10.1016/j.marpolbul.2008.09.028.

Walker, D.I., Lukatelich, R.J., Bastyan, G., McComb, A.J., 1989. Effect of boat moorings on seagrass beds near Perth, western-Australia. Aquat. Bot. 36, 69–77. https://doi.org/10.1016/0304-3770(89)90092-2.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. U.S.A. 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Wennhage, H., Pihl, L., 2002. Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. J. Fish Biol. 61, 207–228. https://doi.org/10.1111/j.1095-8649.2002.tb01772.x.

Widdows, J., Pope, N.D., Brinsley, M.D., Asmus, H., Asmus, R.M., 2008. Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. Mar. Ecol. Prog. Ser. 358, 125–136. https://doi.org/10.3354/meps07338.

Wynne, D., Avery, M., Campbell, L., Gubbay, S., Hawkswell, S., Juniper, T., King, M., Newbery, P., Smart, J., Steel, C., Stones, T., Taylor, J., Tydeman, C., Wynde, R., 1995. Proposed targets for habitat conservation. In: Biodiversity Challenge. RSPB, Sandy, Bedlordshire, p. 285.