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The forgotten ones of ports : The filter feeders at the heart of siltation processes

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29 matter produced was constant between seasons at approximately 130 g/m²/d; marina-wide,
30 this amount represents a total daily production of 3.2 tons. However, the production amount
31 varies spatially and temporally in relation to marine hydrodynamics and the organisms
32 involved. Bioproduction was taxon-dependent: areas abundant in oysters and mussels were
33 the areas with the most pronounced bioproduction, whereas there was no significant
34 relationship between bioproduction and the presence of tunicates or scallops. If we consider
35 bioproduction on a seasonal scale, we can see that the campaigns with the greatest production
36 correspond to the periods when the sediment supply was the highest, i.e. when the tidal range
37 was the highest. The quality of the bioproducts (organic matter content) differed between
38 seasons, which can be explained by both environmental and metabolic changes.
39 Understanding the role of filter feeders in siltation processes appears to be essential in port
40 environments that need to be regularly dredged to ensure safe navigation.

41 **Keywords:** Siltation, Port, Mud, Filter feeders, Bivalves, Ascidians.

42 **1. Introduction**

43 Ports are dynamic, constantly evolving socio-ecosystems, tugged on the one hand by
44 environmental conditions and on the other hand by anthropic developments. Sediments and
45 their flow have been at the heart of this turmoil. The sediments are carried by the water
46 entering the port (Eysink, 1989; Van Rijn, 2016) and are partially trapped by port
47 infrastructure (Van Maren *et al.*, 2009; Van Rijn, 2016; Huguet *et al.*, 2020). These sediments
48 are part of the siltation process and must be dredged regularly to avoid disturbing the
49 navigation channels. This siltation is influenced by many environmental factors, widely
50 described in the literature: sediment inputs, internal and external hydrodynamics, weather,
51 salinity etc. (Langendoen, 1992; Van Maren *et al.*, 2009; Van Rijn, 2016; Huguet *et al.*,
52 2020). Numerous studies have been conducted on the physical factors influencing siltation in
53 port areas. However, few studies have focused on the role of biotic factors in siltation

54 processes. To our knowledge, between 2000 and 2020 (search conducted on 15 April 2021 by
55 combining the keywords Mud, Siltation, and Sediment with Port, Marina, and Harbour
56 yielding 680 articles), only four articles explored this topic (Droppo *et al.*, 2001; Friend *et al.*,
57 2003; Kirby *et al.*, 2008; Gerbersdorf *et al.*, 2020). Among these four studies, none addressed
58 the role of macro-organisms in mud formation. However, research in other contexts has
59 shown that organisms that are abundant in pontoons, such as bivalves and tunicates (Connell,
60 2000), could play an important role in the siltation process (Giles *et al.*, 2006; Forrest *et al.*,
61 2007; McKindsey *et al.*, 2009; Wang *et al.*, 2018).

62 The sediments sucked in by the filter feeders are excreted after digestion as faeces or
63 mucus-covered pseudo-faeces (Beninger *et al.*, 1999; Ward and Shumway, 2004). These
64 excretions are referred to as bioproducts. The bioproducts generated by filter feeders strongly
65 influence the amount of mud; small particles are aggregated into larger flocs that settle
66 quickly and successfully (Giles *et al.*, 2006; McKindsey *et al.*, 2009; Wang *et al.*, 2018). A
67 study carried out on a mussel farm showed that the presence of mussels led to a two-to-five
68 times increase in sedimentation (Weise *et al.*, 2009). McKindsey *et al.* (2009) reported that
69 tunicates present on mussel lines tended to double their sedimentation rate. The bioproducts
70 also influence the settling velocity (McKindsey *et al.*, 2009; Walker *et al.*, 2014); the
71 agglomerates formed by these bioproducts are heavy and sink rapidly through the water
72 column. This change in speed also affects the spatial distribution of the mud (McKindsey *et*
73 *al.*, 2009). As sediments reach the bottom fast, their propagation distance is short (McKindsey
74 *et al.*, 2009). Bioproducts also affect the structure and composition of mud (McKindsey *et al.*,
75 2011; Walker *et al.*, 2014; Wang *et al.*, 2018). A study of mud collected near mussel farms
76 showed that the rate of erosion was higher in the presence of mussels; this could be linked, in
77 particular, to changes in the composition of the mud (Walker *et al.*, 2014). As bioproducts are
78 notably the result of digestion processes, their composition is directly influenced by the

79 metabolism of organisms. Changes in the carbohydrate and protein content of the bioproducts,
80 both of which are correlated with sediment cohesion (Malarkey *et al.*, 2015; Kameda and
81 Yohei, 2021), could explain this behavioural change in the resulting mud.

82 The amount of bioproducts produced depends on the species (Fiala-Médioni, 1974;
83 Hawkins *et al.*, 1998; Ward and Shumway, 2004; McKindsey *et al.*, 2009) and is related to
84 the filtration rate (Hawkins *et al.*, 1998; Ward and Shumway, 2004). The filtration rate varies
85 according to each organism's metabolism, which is influenced by environmental factors, such
86 as sediment supply, amount of organic matter, season, temperature, and salinity (Ward and
87 Shumway, 2004; Riisgård *et al.*, 2014; Zuñiga *et al.*, 2014, Ehrich and Harris, 2015).

88 Filter feeders appear predominantly during siltation in some contexts. Therefore, it is
89 important to not neglect their role in the siltation of port areas. This study aimed to highlight
90 the role of filter feeders in the siltation process in port areas and to determine the factors that
91 influence their production in bioproducts. An experimental analysis was performed at La
92 Rochelle marina. The bioproducts of the filter feeders were collected and analysed using
93 sediment traps fixed under the pontoons. The study was performed over a period of 2 months,
94 in two distinct seasons, to precisely determine the evolution of this production.

95 The La Rochelle marina is the largest marina in Europe, with an area of 70 ha. Its
96 maintenance requires the dredging of approximately 200,000 m³ of mud per year (Direction
97 Départementale des Territoires et de la Mer de la Charente-Maritime, 2018). It is divided into
98 four basins with distinct filter feeder communities and environmental conditions, allowing for
99 a detailed study of the environmental factors that influence the production of bioproducts.
100 This makes it an ideal site for studying the role of filter feeders in the siltation process in port
101 areas.

102 **2. Materials and methods**

103 **2.1. Study site**

104 The La Rochelle marina is located along the French Atlantic coast in the central part
105 of the Bay of Biscay (Fig.1). This port was created in 1972 and is one of the largest marinas
106 in the world with 5,000 moorings. Huguet et al. (2020) described the hydrosedimentary
107 dynamics of this port. Five sampling points were selected in areas with different
108 hydrosedimentary profiles (Fig.1) (Huguet *et al.*, 2020):

109 Pontoon 13 (200 m), in the centre of the Lazaret Basin, is characterised by strong tidal
110 currents and considerable siltation. Far behind the breakwater, it is protected from winds and
111 waves.

112 Pontoon 43 (150 m) was the most distant from the marina openings at the end of the
113 Marillac basin. At the back of the basin, the hydrodynamics are low, and the siltation is
114 constant and low.

115 Pontoon 51 (125 m), at the west of the Tamaris basin, is located close to the channel
116 but is protected by a breakwater. The hydrodynamics and siltation are considerable.

117 Pontoon 61 (170 m), at the east of the Tamaris basin, is close to an opening to the sea.
118 It is also characterised by considerable siltation, and its hydrodynamics are strongly
119 influenced by wind.

120 The Capitainerie pontoon (150 m) is at the centre of the channel. The hydrodynamics
121 are the strongest at this level. Siltation is constant and considerable.



Fig.1. Study area, La Rochelle marina (Les Minimes). Surrounded by red: the sampled

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131 **2.2. Experimental design and sample analysis**

132 To sample the bioproducts rejected by the filter feeders living under the pontoons, we
133 created an experimental protocol. Sixteen campaigns were conducted in two different seasons
134 (eight from January to March 2020 and eight from May to July 2020). For each campaign, 50
135 sediment traps were deployed for 24 h under five pontoons (Fig.1), that is, 10 traps per
136 pontoon. As the sampled pontoons were of different sizes, the traps were distributed
137 equidistant from each other along the length of the pontoons. This process allowed precise
138 monitoring of bioproduct production within each pontoon. To avoid damage to the organisms
139 living under the pontoons, the traps were carefully placed and removed by a professional
140 diver. The diver first cleaned the organisms by stirring the surrounding water. This ensured
141 that only bioproducts were recovered and not the sediment deposited on the organisms. Of
142 these 10 traps, two were used as controls and were
143 placed in areas of the pontoon that were devoid of
144 organisms (the organisms being previously removed by
145 the diver).

146 To prevent the loss of bioproducts or external
147 incoming fluxes from the surrounding environment, the
148 traps were made of 25-cm diameter plastic cylinders

149 and placed as close as possible to the pontoon (Fig.2). The traps were set for 24 h – this is the
150 optimal duration to maximize the harvest of bioproducts; beyond this time, the average
151 quantity of bioproducts harvested per trap decreases (Personal observation, obtained during a
152 preliminary study conducted in May 2019, to optimize the protocol under the same pontoons).



Fig.2. Photograph of a trap placed under the pontoon

153 To allow decantation while preventing degradation of the samples, the contents of the
154 traps were placed in a cold room at 3 °C for 24 h. After decanting (by pouring off or
155 aspiration), the remaining sediment was centrifuged at 1500 ×g for 3 min. After removing the
156 supernatant (by pouring off and aspiration), the pellet was placed in an oven at 60 °C for 72 h
157 and then weighed to obtain the total dry mass of the bioproducts of each sample. Loss on
158 ignition analysis was then carried out for 5 h at 550 °C to obtain the mineral content. The
159 organic content was calculated by subtracting the mineral content from the total dry mass. To
160 obtain only the quantity of matter produced by the organisms, the average mass of matter in
161 the control traps per pontoon was subtracted from that of each sample.

162 2.3. Environmental data

163 To precisely understand the elements that influence the quantity of the bioproducts, a
164 census of the filter feeders present under each pontoon was carried out. Three samples per
165 season were collected from each pontoon: one from each end and one from the centre. To
166 carry out this sampling, a 0.64-m² floating quadrat was placed under the pontoon, and all the
167 organisms found therein were collected by a scientific diver. Only the four most abundant
168 taxa were counted (Fig.3).

169 - Mussels: *Mytilus edulis* (Linnaeus, 1758).

170 - Oysters: *Crassostrea gigas* (Thunberg, 1793).

171 - Scallops: *Mimachlamys varia* (Linnaeus, 1758).

172 - Ascidians: *Ciona intestinalis* (Linnaeus, 1767) and *Clavelina sp.* (Müller, 1776).

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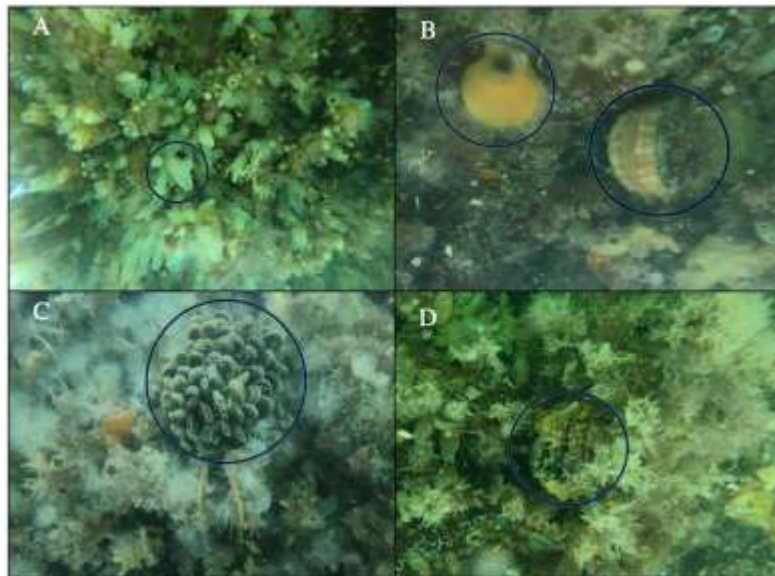


Fig.3. Photographs of ascidians (A), scallops (B), mussels (C), and oysters (D) under pontoons

The size (width \times length \times height) of the bivalves was recorded. Individuals below 1 cm were considered juveniles and were not measured. During the two sampling periods, the multiparameter YSI 6600 V2 probes were positioned under pontoons 43 and 51. The same probe was also placed under pontoon 13 in summer. This probe provides the temperature, oxygen, salinity, and turbidity data (Table 1, Fig.A.1). Meteorological and hydrodynamic data were also collected for all the campaigns (Table 1, Fig.A.1).

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Table.1. Environmental variables of the study area and their sources

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Variable	Units	Sources
Precipitation height	Meter	Météo France
Duration of precipitation	Minutes, seconds	Météo France
Air temperature	Degrees Celsius	Météo France
Atmospheric pressure	Hectopascal	Météo France
Wind speed	Meter/second	Météo France
Wind direction	360-degree wheel	Météo France
Exposure time	Minutes, seconds	Météo France
Global radiation	Joules	Météo France
Tidal height	Meter	Service Hydrographique et Océanographique de la Marine (SHOM)
Offshore swell	Significant height; period; direction	Centre d'Archivage National de Données de Houle In Situ (CANDHIS)
Sediment flow	Milligram/liter/day	Numerical results (Huguet <i>et al.</i> 2020)

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During the second sampling period, the sestonic charge was measured to estimate the organic and mineral matter available for the filter feeders. At the port entrance, the day before each sampling, a water sample was collected from just under the pontoon using a horizontal Niskin bottle. The water was filtered through a 0.7- μ m gf/f filter, and the collected sediments were analysed according to the same protocol as for the sediment traps. This sample was used to calibrate the probes and models.

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2.4. Data analysis

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The production of bioproducts has been studied at different scales. It has been examined between different pontoons as well as between different campaigns and seasons. We analysed the bioproducts as a whole using the dry matter produced, and the composition of the bioproducts was determined through the percentage of organic matter. The results of

227 campaign 6 are not presented here because the field conditions did not allow us to recover all
228 traps correctly.

229 All statistical tests were carried out using R software (Version 3.6.3 "Holding the
230 Windsock") with a rejection threshold of 5%. As the data did not satisfy the conditions for
231 applying parametric tests (normality of the distributions and homoscedasticity), non-
232 parametric tests were used. The Wilcoxon–Mann–Whitney test was used to compare the
233 average production of the controls and replicas as well as to compare the average amounts of
234 dry and organic matter produced between seasons for each pontoon. For multiple
235 comparisons, the Kruskal–Wallis test and Wilcoxon pairwise *post-hoc* test were used.

236 To estimate the relationships between the average dry matter production rate and
237 environmental conditions, the Pearson correlation test was used with a rejection threshold (r)
238 of 0.5 to estimate the relationships between the average dry matter rate produced and
239 environmental conditions.

240 **3. Results**

241 **Preamble**

242 For each season and pontoon, the amount of dry matter in the controls was
243 significantly lower than that in the replicates. The average amount of total dry matter per trap
244 was 9.45 ± 10.6 g for the replicas and 1.81 ± 2.85 g for the control traps in winter and 6.60 ± 6.97
245 g for the replicas and 0.902 ± 0.787 g for the control traps in summer. The organism-free
246 control traps allowed us to verify that the data pertaining to the replica traps were indeed
247 related to bioproduction. In both seasons, the production of bioproducts was homogeneous
248 within each pontoon, allowing accurate comparisons between the pontoons.

249 All data presented hereafter are expressed as the amount of matter produced by the
250 organisms per square meter, that is, the average mass of materials in the control traps per
251 pontoon subtracted from the mass in each sample.

3.1. Study of bioproduction

The amount of dry matter produced differed between winter (chi-squared = 80.72, df = 4, $p < 2.2e-16$) and summer (chi-squared = 118.29, df = 4, $p < 2.2e-16$). In both seasons, the average dry matter produced in the Capitainerie pontoon was significantly higher than that produced in the other pontoons, whereas that of pontoon 43 was significantly lower (Fig.4 A, B). The bioproduction in Capitainerie pontoon was, on average, eight times greater than that in pontoon 43 in winter and almost 10 times greater in summer (Fig.4 A and B).

For all pontoons, the average dry matter production was different between winter campaigns (chi-squared = 87.65, df = 6, p-value $< 2.2e-16$) and between summer campaigns (chi-squared = 66.46, df = 7, p-value = $7.619e-12$) (Fig.4 C and D). However, this difference seemed to be pronounced for the winter season; the weekly cyclicity showed an alternating increase and decrease in average production (Fig.4 C and D).

The average dry matter production did not differ between the two seasons, both for the pontoons as a whole ($W = 40431$, $p = 0.054$) and per pontoon. The amount of organic matter found in the bioproducts was found to be similar between pontoons (Fig.4 A and B). In winter, the amount fluctuated from $11.97 \pm 2.65\%$ for pontoon 61 to $15.97 \pm 4.09\%$ for pontoon 43. In summer, the amount fluctuated from $15.53 \pm 6.2\%$ for pontoon 61 to $19.32 \pm 6.33\%$ for pontoon 13. For all pontoons, the amount of organic matter found in the bioproducts was higher in summer ($17.4 \pm 5.62\%$) than in winter ($13.8 \pm 3.43\%$) ($W = 12023$, p-value $< 2.2e-16$). The within-season variation between campaigns was low (Fig.4 C and D), with organic matter amounts ranging between $12.89 \pm 1.44\%$ and $15.92 \pm 4.57\%$ in the winter campaigns and $13.34 \pm 4.53\%$ and $19.67 \pm 8.69\%$ in the summer campaigns.

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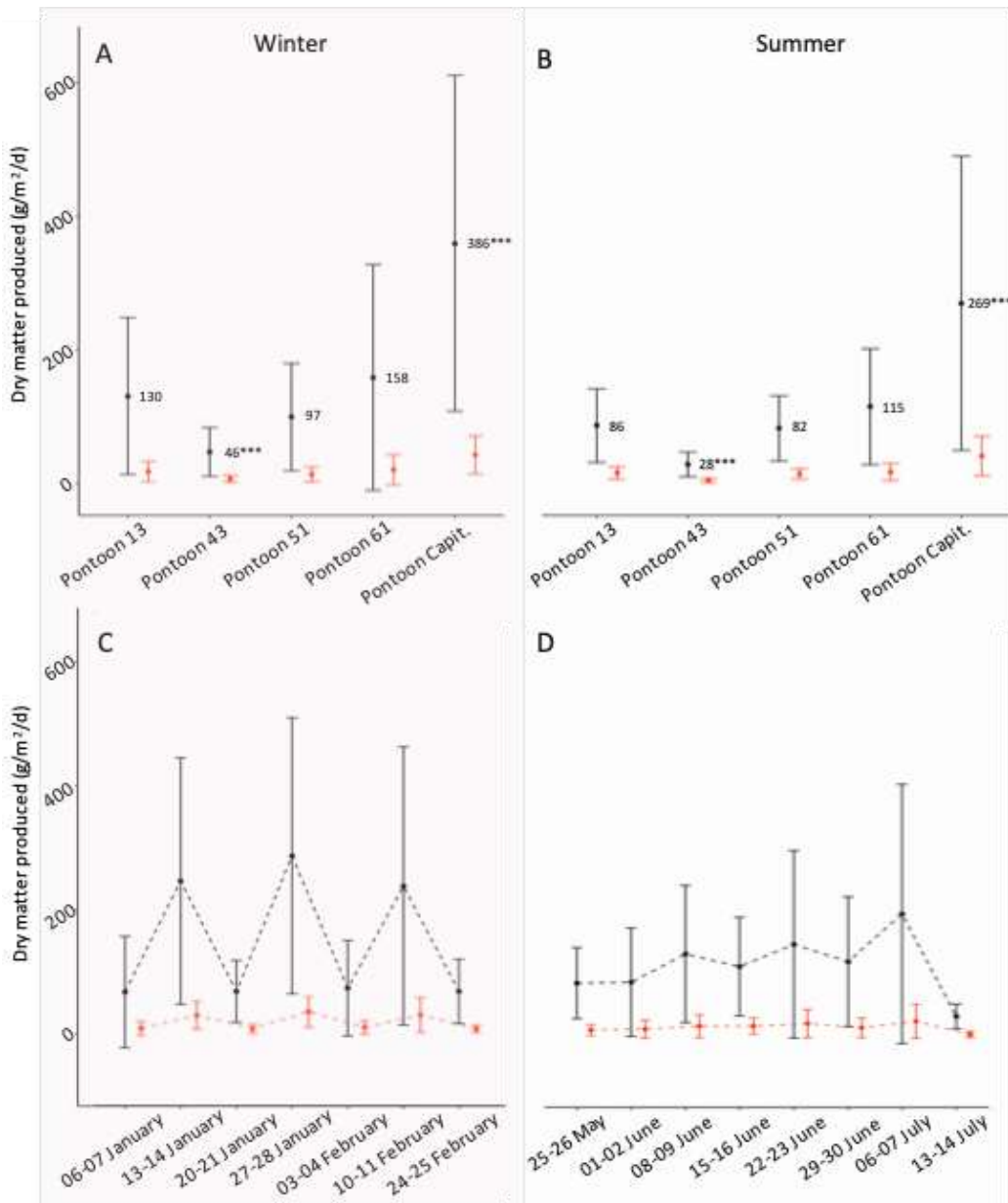


Fig.4. Averages of dry matter produced and associated standard deviation in two different seasons, per pontoon (A and B) and per campaign (C and D). ***statistically distinct average. In red the average fraction of associated organic matter and its standard deviation

3.2. Factors influencing bioproduction

3.2.1. Filter feeders

In both seasons, production was not related to the number of organisms present under the pontoons (winter: $t = 2.98$, $df = 58$, $r = 0.36$; summer: $t = 1.54$, $df = 58$, $r = 0.19$). Whereas the average production between winter and summer seasons was similar, yet the number of individuals present under the pontoons was four times higher in summer than in winter (Fig.5 and Table 2).

Table.2. The average number of individuals and their size, as well as the average number of juveniles, collected under the pontoons for each season

		Winter			Summer			
		Number (/m ²)	Size (cm)	Juvenile (/m ²)	Number (/m ²)	Size (cm)	Juvenile (/m ²)	
304	Pontoon 13	Mussels	35.31±10.31	11.89±5.93	2.08±2.38	89.53±47.03	14.93±7.44	14.06±1.56
		Oysters	62.04±19.68	179.07±172.07	0	81.71±23.59	171.64±168.17	2.08±2.38
		Ascidians	346.25±147.34	NA	NA	902.03±509.531	NA	NA
		Scallops	13.43±6.40	23.58±14.05	4.68±1.56	28.0±28.12	26.23±13.13	1.04±1.80
306	Pontoon 43	Mussels	6.25±7.03	5.48±3.30	4.68±2.70	64.53±44.21	6.07±4.65	16.66±5.02
		Oysters	14.68±12.96	76.08±53.95	0	32.1875±13.12	83.47±60.55	4.68±1.56
		Ascidians	173.90±20.31	NA	NA	971.87±161.56	NA	NA
		Scallops	38.43±36.87	1.02±2.14	29.16±9.54	18.12±19.06	3.45±2.74	0.52±0.92
308	Pontoon 51	Mussels	77.03±39.84	5.36±3.52	0	1270.31±549.68	5.63±2.89	145.83±41.40
		Oysters	27.5±13.43	114.40±80.54	0	78.06±12.96	102.81±73.08	3.64±0.90
		Ascidians	41.56±19.84	NA	NA	766.56±49.21	NA	NA
		Scallops	11.40±6.25	9.85±11.27	3.12±3.12	10.93±11.25	5.70±4.86	2.60±2.38
310	Pontoon 61	Mussels	494.21±34.37	8.88±5.75	2.08±0.9	1561.40±409.06	11.85±6.34	282.81±78.87
		Oysters	35.93±9.37	114.18±79.09	0	77.03±12.65	119.04±83.84	5.72±1.80
		Ascidians	53.59±23.43	NA	NA	1222.35±830.31	NA	NA
		Scallops	0	0	0	2.50±2.34	0	0
312	Pontoon Capit.	Mussels	707.81±298.28	6.70±4.99	7.81±1.56	2527.03±2824.53	7.11±4.96	641.66±144.70
		Oysters	58.75±27.18	99.52±71.57	0	80.15±8.90	109.03±72.84	10.93±5.41
		Ascidians	195.78±91.71	NA	NA	552.50±439.37	NA	NA
		Scallops	33.28±18.75	8.10±7.70	6.77±1.80	28.12±14.84	4.56±6.84	8.85±1.80

Production appeared to be taxon-dependent (Fig.5). There was more production in areas where mussels were present during winter ($t = 5.38$, $df = 13$, $r = 0.83$) and summer ($t = 2.57$, $df = 13$, $r = 0.58$). Production also correlated with the presence of oysters in winter ($t = 2.34$, $df = 13$, $r = 0.54$).

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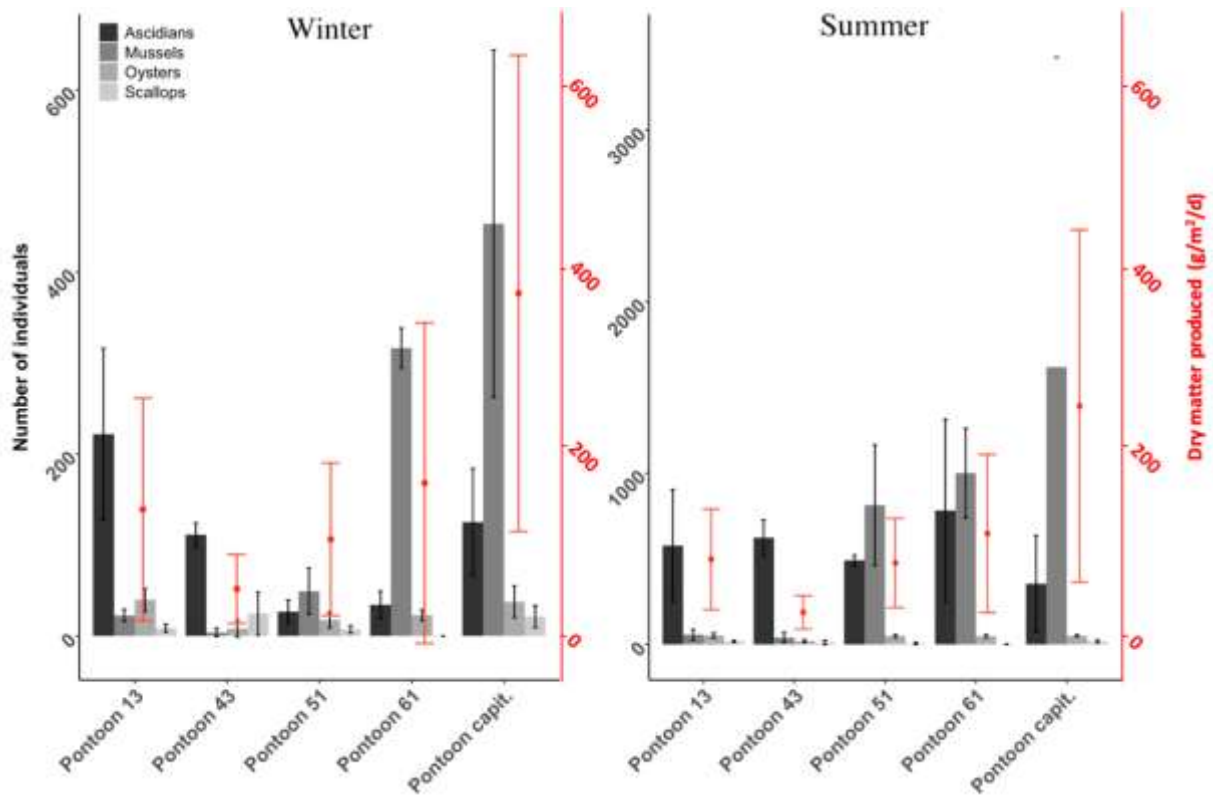


Fig.5. Average number of individuals and associated standard deviation, per pontoon and per taxon. In red, the average dry matter produced per pontoon and their standard deviation

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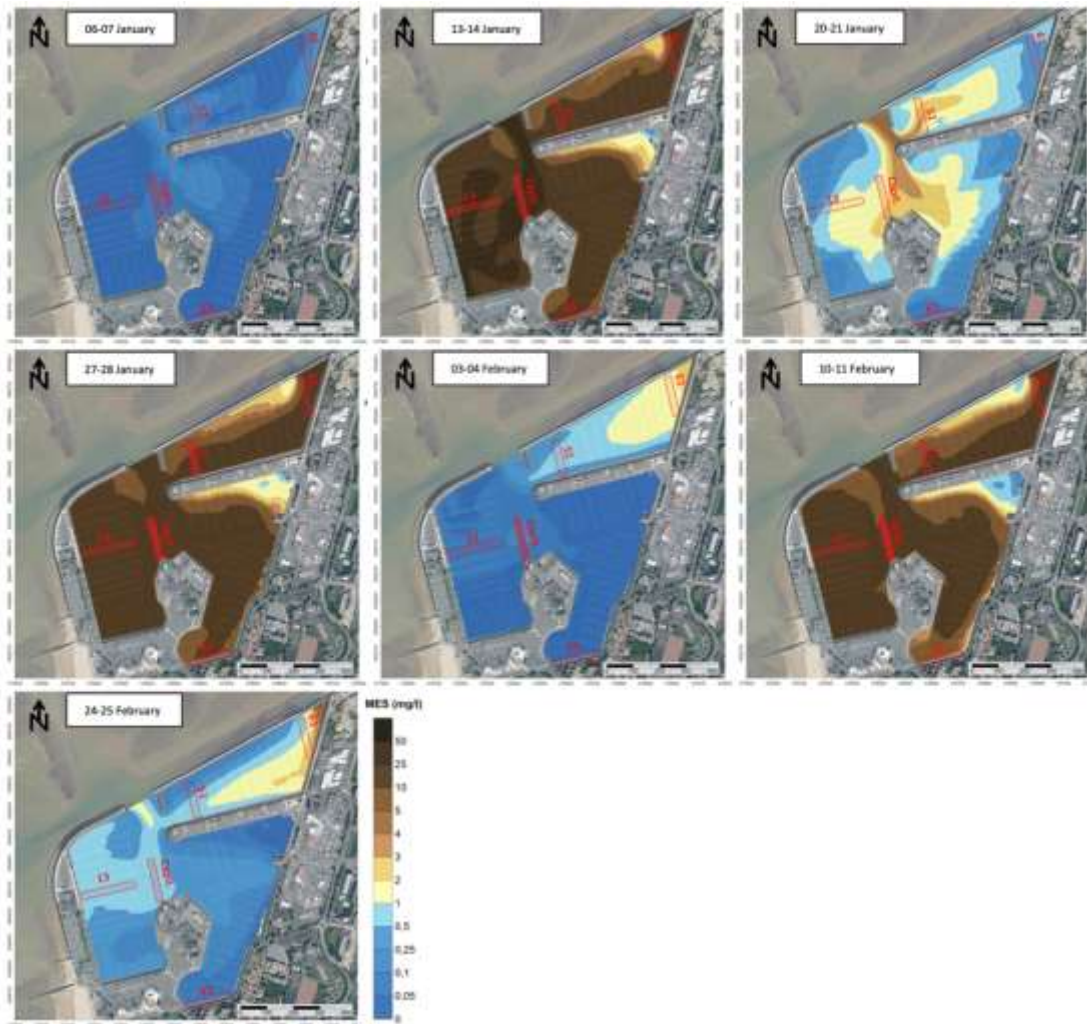


Fig.6. Maps of average environmental sediment concentration and average daily bioproduction (in red) for the 7 winter campaigns. The intensity of the red is proportional to the amount of bioproducts formed.

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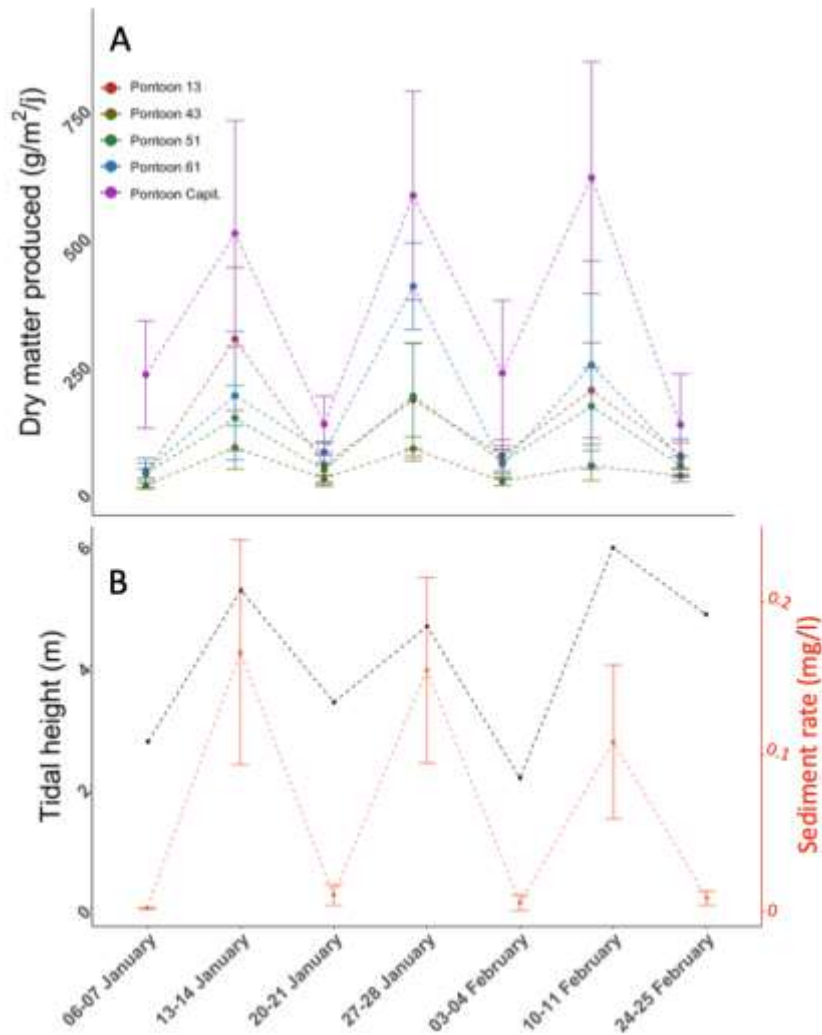


Fig.7. Top (A): average dry matter produced was associated standard deviation per winter campaign for each pontoon. Bottom (B): trends of two abiotic factors – tidal range (in black) and average sediment concentration (in red) – over the winter campaigns

For the Capitainerie pontoon, which was the most exposed, production was also correlated with wind direction ($t = 4.16$, $df = 40$, $r = 0.55$). For pontoon 43, production was also related to other factors such as salinity ($t = 3.95$, $df = 19$, $r = 0.67$), amount of dissolved oxygen ($t = -4.40$, $df = 19$, $r = -0.71$), and wave height ($t = 5.28$, $df = 48$, $r = 0.60$).

In summer, production did not seem to correlate with the selected factors ($r \in [-0.5 > < 0.5]$). Except for the Capitainerie pontoon, where production was correlated with sediment concentration and tidal range ($t = 5.46$, $df = 54$, $r = 0.59$; $t = 4.71$, $df = 54$, $r = 0.54$) (Fig.A.2).

402 **4. Discussion**

403 Filter feeders are often overlooked in studies on the sedimentary process. In La
404 Rochelle marina, considering the 15 km stretch of pontoons that make up this port, filter
405 feeders release nearly 3.2 tons of bioproducts per day (130 g/m²/d of dry matter). The
406 distribution of the bioproducts among the pontoons was spatiotemporally heterogeneous. The
407 factors influencing the distribution can be classified into two categories: abundance of various
408 organisms and sediment availability.

409 **4.1. Filter feeders' contribution**

410 The filter feeders are heterogeneously distributed in the La Rochelle marina, and the
411 areas abundant in oysters and mussels seem to be the areas with the most pronounced
412 bioproduction. Thus, the hypothesis that bioproduction is a taxa-dependent process seems to
413 be valid. In this sense, a study by McKindsey *et al.* (2009) showed that sedimentation rates
414 are influenced by the species present; sedimentation rates had almost doubled from 3.9 g/d to
415 7.2 g/d when tunicates were present in addition to mussel populations (McKindsey *et al.*,
416 2009). This study highlights the fact that bioproduction should be examined not only on a
417 species-by-species basis but also at a community scale. However, given the small number of
418 replicates available and the complexity of the filter feeder communities present under the
419 pontoons, we only examined the taxa that seemed to be strongly correlated with
420 bioproduction.

421 The maximum filtration rate (found in literature) of a mussel (*Mytilus edulis*) is almost
422 twice that of an oyster (*Crassostrea gigas*), respectively, at 0.014 m³/g/h (Riva and Massé,
423 1983) and 0.007 m³/g/h (Ehrich and Harris, 2015). Thus, mussels are expected to capture and
424 release more sediments than oysters do. This hypothesis is in accordance with the results of
425 the present study, where the correlation between bioproduction and the presence of mussels
426 (*Mytilus edulis*) was stronger than that between bioproduction and the presence of oysters

427 (*Crassostrea gigas*). This hypothesis also supports the fact that bioproduction is a species-
428 dependent process.

429 The amount of bioproducts formed is directly related to the filtration rate (Hawkins *et*
430 *al.*, 1998; Ward and Shumway, 2004), which depends on the metabolism of the organism,
431 which in turn is modulated by environmental conditions (Riisgård *et al.*, 2014; Zuñiga *et al.*,
432 2014; Ehrich and Harris, 2015). In the present study, the rate of bioproduct formation in one
433 pontoon was found to be related to salinity and oxygen levels. Oxygen is a basic requirement
434 for metabolism; therefore, the hypothesis that production rates are inversely correlated with
435 oxygen levels seems coherent. Oxygen content has been found to limit the filtration rate in
436 oysters in some models (Cercó and Noel, 2005).

437 Salinity also affects the filtration rate. Riisgård *et al.* (2014) demonstrated that the
438 filtration rate of the two mussel species was closely related to salinity. In their review, Ehrich
439 and Harris (2015) showed that salinity had an impact on the filtration rate of oysters; in fact,
440 similar to our results, several studies showed that an increase in salinity increased the
441 filtration rate and vice versa (Powell *et al.*, 1992; Cercó and Noel, 2005; Fulford *et al.*, 2007).
442 Lavaud *et al.* showed that changes in salinity had an impact on the filtration rate of oysters,
443 and any disturbance in the filtration rate affected the growth and reproduction of organisms
444 (Lavaud *et al.*, 2017).

445 Studies on pearl oysters (*Pinctada margaritifera*) and mussels (*Mytilus edulis*) have
446 shown that the rates of filtration and clearance are size dependent (Pouvreau *et al.*, 1999;
447 Jacobs *et al.*, 2015). This result could explain the correlation between bioproduction and the
448 number of oysters in winter, but not in summer. Indeed, if we only examine the number of
449 oysters, we can see that some areas rich in oysters are not very productive. However,
450 considering the size of the oysters in parallel, we notice that it is mainly the areas with small
451 oysters that are less productive in summer. This is probably linked to the hazard of

452 recruitment: oyster larvae settle where they find support, but this is not necessarily the most
453 suitable place for their survival. Long-term monitoring would provide a better understanding
454 of the evolution of communities and their relationship to bioproduction.

455 For each taxon and pontoon, the amount of matter produced did not depend on the
456 number of individuals present under the pontoons. If we consider the example of mussels, we
457 can see that they are 10 times more densely present in summer than in winter, yet their
458 bioproduction amounts are the same between the two seasons. Size is an important factor, as
459 we have seen previously, and the number of juveniles is important in summer. However,
460 mussels live for several years, so we expect to find a large proportion of mussels in winter and
461 summer. This shows that production is not limited by the number of individuals, but by
462 another factor: sediment availability.

463 **4 .2. Contribution of sediments**

464 The availability of sediments is a limiting factor for bioproduction. Organisms that
465 produce bioproducts must have sedimentary input. Filter feeders do not create material,
466 instead they trap it, consume some of it, and release some of the modified material as waste.
467 In the present study, we found that the distribution of these sediment inputs was spatially and
468 temporally heterogeneous, and that filter feeder bioproducts are closely correlated with
469 sediment availability. Indeed, if we look at the bioproduction on a seasonal scale, we notice
470 that although the average quantity is relatively similar, the campaigns with the highest
471 production corresponded to the times when the sediment supply was the highest (Fig.6 and
472 Fig.7). Similarly, the pontoon with the least amount of production (pontoon 43) had the least
473 sediment input, and the pontoon with the highest production (Capitainerie pontoon) had the
474 highest input. Several studies have shown that the filtration rates of oysters and mussels are
475 strongly influenced by sediment input (Ward and Shumway, 2004; Ehrich and Harris 2015).
476 For these two species, the filtration rate tends to increase up to a threshold with the sestonic

477 charge (Ward and Shumway, 2004; Ehrich and Harris 2015) and is also modulated by the size
478 of the particles (Benniger *et al.*, 1999; Ward and Shumway, 2004) and organic input
479 (Hawkins *et al.*, 1998; Jacobs *et al.*, 2015). These saturation and sorting phenomena are
480 regulated by several mechanisms, which are well documented in the literature, and depend on
481 both the quantity and quality of the available sediment (Ward and Shumway, 2004; Ehrich
482 and Harris, 2015; Jacobs *et al.*, 2015). Indeed, bivalves filter water with their gills to recover
483 nutrient particles. The gills have dual functions: respiratory and alimentary. They ensure the
484 circulation of seawater through the movement of the lateral gill cilia. The particles were
485 transported to the mouth by the action of the lateral and frontal cilia. Before being carried to
486 the mouth, the labial palps (which surround the mouth) select particles; those that are not
487 ingested are rejected in aggregates, known as pseudo-faeces. The ingested particles are
488 digested, a fraction is used for metabolism by the organism, and the rejects are evacuated
489 through the anus in the form of faeces. (Wildish *et al.*, 1998; Castrec, 2018). Several studies
490 have shown that the filtration rate and particle selection process can be affected by variables,
491 such as particle content, size and type of particles ingested, and the presence of trace elements
492 in the environment (Cognie *et al.*, 2001; Loayza-Muro and Elías-Letts, 2007; Enriquez-
493 oceña *et al.*, 2012; Rosa *et al.*, 2018). The quantity and quality of available plankton as well
494 as the ratio of plankton-to-mineral matter, influence the particle selection, filtration, and
495 assimilation of organisms (Hawkins *et al.*, 1998; Jacobs *et al.*, 2015; Rosa *et al.*, 2018). This
496 directly affects the type of bioproducts (faeces vs. pseudo-faeces) and their compositions and
497 quantity (Smaal *et al.*, 2019). Several bivalves, for example, increase the proportion of
498 pseudo-faeces in their rejects when the particulate content of the environment is high or low
499 in organic matter (Ward and Shumway, 2004; Smaal *et al.*, 2019). It is thus expected that
500 summer waters, which are richer in plankton, are better assimilated by organisms and that the
501 quality and quantity as well as the type of bioproducts rejected, are directly impacted.

502 Considering the composition of the bioproducts, we can see that they contain a higher
503 proportion of organic matter in summer than in winter. This result is in accordance with that
504 of a study conducted in the Iberian Peninsula on mussels (*Mytilus galloprovincialis*) (Zuñiga
505 *et al.*, 2014). This difference could be related to the presence of plankton, which are more
506 abundant and of higher nutritional quality in summer than in winter (Zuñiga *et al.*, 2014).
507 However, we did not discriminate between pseudo-faeces and faeces produced nor analyse
508 their precise composition. Furthermore, the precise sediment composition of the La Rochelle
509 marina is unknown. Additional studies on the composition of the available sediments in
510 relation to the composition of the bioproducts would allow for further analysis and would help
511 to understand the inter-seasonal differences in the organic matter produced. These results may
512 be related to the metabolic needs of the organisms, which will also directly affect the
513 composition of the bioproducts.

514 The sediment concentration is determined by many environmental factors. One of the
515 main factors related to sediment concentration on the Atlantic coast is the tide (Van Rijn,
516 2016; Huguet *et al.*, 2020). This explains the close correlation between the tidal range and
517 production rate. Huguet *et al.* (2020) showed that wind and waves are also significant factors
518 to be considered when studying sediment concentrations. This could explain the correlation
519 between wind direction and bioproduction rate in the Capitainerie pontoon and between wave
520 height and production in pontoon 43. The Capitainerie pontoon is in the fairway and is
521 probably the most exposed to the wind, which could explain why it is the only pontoon to be
522 directly influenced by this factor. Pontoon 43 is the least productive pontoon, but it is also the
523 pontoon whose production amounts showed the lowest variability; therefore, the small
524 variations, such as the contribution of the waves, may be easily observed.

525 **4.3. The future of bioproducts and their implications**

526 Our analysis of the impact of filter feeders on the composition of mud has highlighted
527 the fact that filter feeders interact with a considerable proportion of the sediment, trapping it
528 during feeding and releasing it as a bioproduct during excretion. However, before these
529 bioproducts become an integral part of mud, they are released into the water column where
530 they are affected by a number of environmental variables. These rejects flocculate and
531 aggregate with other particles; hence, their composition as well as their movement in the
532 water column changes (Jarvis *et al.*, 2005; Liu *et al.*, 2021). Conversely, they are also affected
533 by hydrodynamic variables and fragments (Jarvis *et al.*, 2005; Liu *et al.*, 2021). These
534 behaviours are constrained by variables such as pH, temperature, salinity, presence of
535 microalgae, and water flow (Xiao *et al.*, 2007; Verney *et al.*, 2009; Mietta *et al.*, 2009; Kumar
536 *et al.*, 2010). The study of their behaviour in relation to the variables of the La Rochelle
537 marina is, therefore, necessary to fully understand how bioproducts evolve before being
538 incorporated into the mud.

539 The behaviour of these bioproducts in the water column and mud is also influenced by
540 their initial structure and composition. Several studies (Mietta *et al.*, 2009; Larsen *et al.*,
541 2009) have shown that flocs containing a high proportion of organic matter, such as those
542 produced in the summer by the organisms in our study, would be larger in size. These larger
543 flocs are also more resistant to fragmentation owing to the high organic content (Eisma *et al.*,
544 1983; Jarvis *et al.*, 2005). This large size would also lead to quicker sedimentation (Fan *et al.*,
545 2020). Our analysis has provided some clues about their composition (share of organic and
546 mineral matter), but further studies on their structure (size, density, mineral, and organic
547 composition) would complete our data and inform us of the behaviour of these products in the
548 water column and in the mud.

549 Bioproducts settle to the bottom faster than suspended matter and thus increase the
550 flux of organic matter to the bottom, depending on the depth, currents, and resuspension

551 process (Chamberlain *et al.*, 2001; McKindsey *et al.*, 2009; Walker *et al.*, 2014). Thus, the
552 presence of filter feeders in port areas could affect the frequency of dredging. Similarly,
553 physicochemical changes in bioproducts can modify the texture of mud, making it more or
554 less cohesive and, therefore, more or less difficult to remove (Walker *et al.*, 2014; Wang *et*
555 *al.*, 2018). Dredging vessels are used for removing excess mud and maintaining a water depth
556 suitable for navigation. They can be divided into two categories: mechanical and hydraulic
557 dredgers (Vlasblom, 2003; Winterwep, 2005). Mechanical dredgers dig or collect mud from
558 the bottom surface using a bucket or grab (Vlasblom, 2003; Winterwep, 2005). Hydraulic
559 dredges suck up or resuspend the mud that has accumulated at the bottom (Vlasblom, 2003;
560 Winterwep, 2005). Both methods are directly influenced by the texture and structure of the
561 mud that needs to be removed. The former can be used is only on very cohesive muds, and the
562 latter on less cohesive muds. Knowledge of the factors affecting the behaviour of muds, such
563 as those presented in this study, is therefore an advantage for port managers and would allow
564 them to anticipate and improve dredging operations by studying the communities present
565 under the pontoons. This is all the more important because dredging activities have numerous
566 impacts on the marine environment. By removing bottom sediments, dredging destroys
567 habitats and modifies the topography and hydrography of the seabed (Miller and Payne, 2004;
568 Becker *et al.*, 2015; Manap and Voulvoulis, 2015). Similarly, the dredging industry presents a
569 real economic challenge to ports. The costs of dredging and processing of dredged materials
570 represent a considerable part of the port budget. For example, in 2021, these costs amounted
571 to 5.33 billion euros worldwide (IADC 2021). Given the economic and environmental
572 challenges, ports need to adapt their dredging strategy to achieve a balance between
573 profitability, environmental impact, and efficiency, which could involve studying the filter
574 feeder communities present under the pontoons and analysing their rejects.

575 **5. Conclusion**

576 Understanding the factors that govern the production and behaviour of mud is a major
577 aspect in port operations. In these hyper-anthropic environments, where life seems to have no
578 place, the roles of the organisms that live there are often ignored. However, considerable
579 communities grow in these areas, protected by pontoons and some, as highlighted here, play
580 an important role in siltation processes, such as filter feeders. These organisms are able to trap
581 and release a large amount of sediment, approximately 3.2 tons per day, if we extrapolate our
582 results to the scale of the port.

583 Our study showed that bioproduction is modulated by many factors, such as the taxa
584 of the organisms, tidal range, and environmental sediment concentration. However, in
585 addition to their capacity to collect and release sediment, filter feeders also modify the
586 physicochemical properties of sediments (Walker *et al.*, 2014; McLean *et al.*, 2018; Wang *et*
587 *al.*, 2018). Thus, it is important to focus on the future of these rejects. How will the changes in
588 their physicochemical properties influence their behaviour in the water column and mud?
589 Similarly, as shown in other contexts, filter feeder bioproducts have an influence on benthic
590 communities and their exchange with different compartments (Callier *et al.*, 2009; Lavoie *et*
591 *al.*, 2016; Murphy *et al.*, 2019). But what about in harbour areas? This study and all the
592 questions it raises (and the list is not exhaustive) show that the involvement of organisms such
593 as filter feeders in the hydro-sedimentation and siltation processes must not be ignored. This
594 study may also help port management by providing managers with a better understanding of
595 the factors governing their environment.

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796 **Appendix**

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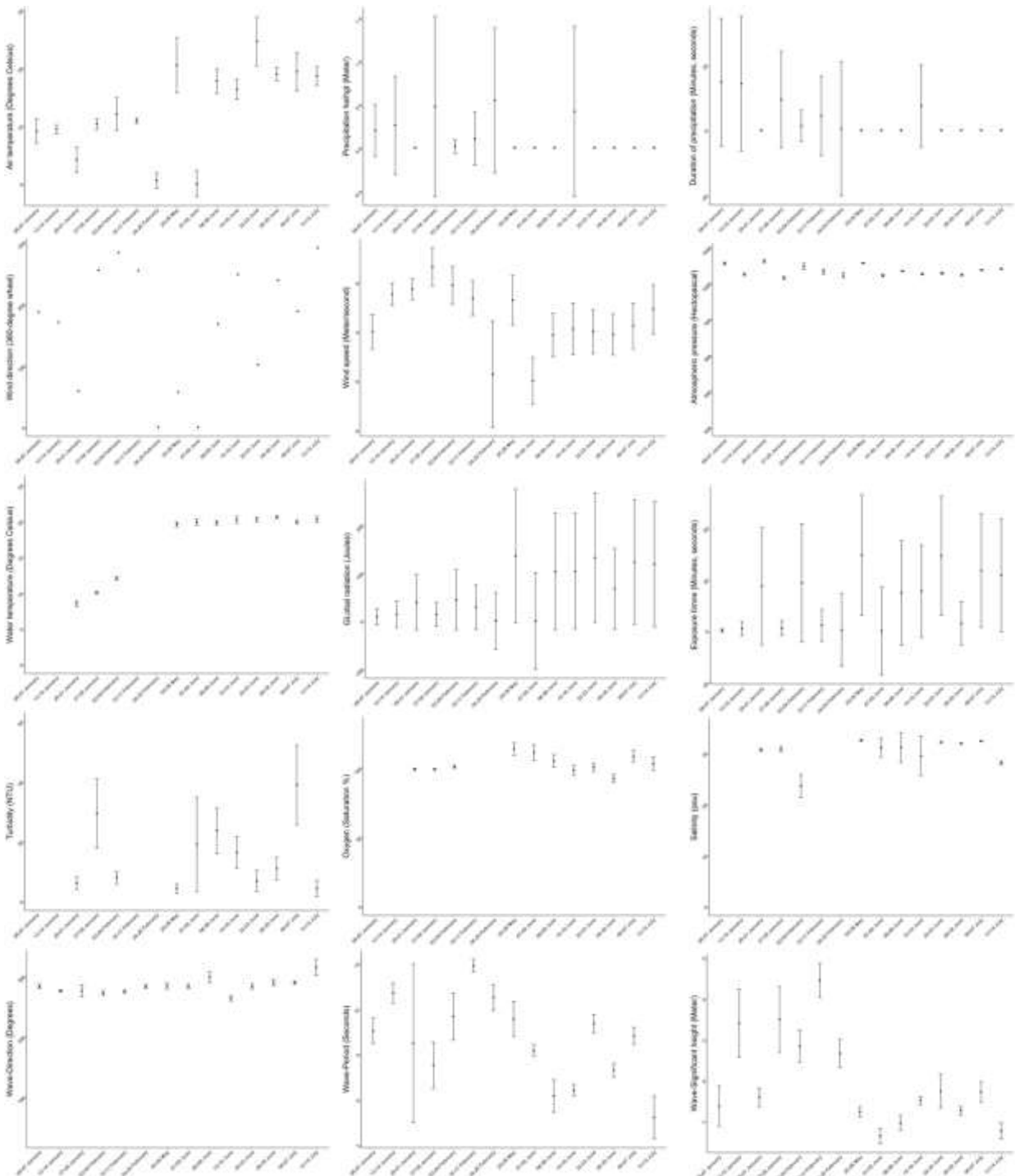
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Fig.A.1. Environmental data from all campaigns (from top to bottom and from right to left): air temperature, precipitations height, duration of precipitations, wind direction, wind speed, atmospheric pressure, water temperature, global radiation, exposure time, turbidity, oxygen, salinity, wave direction, wave period, wave significant height.

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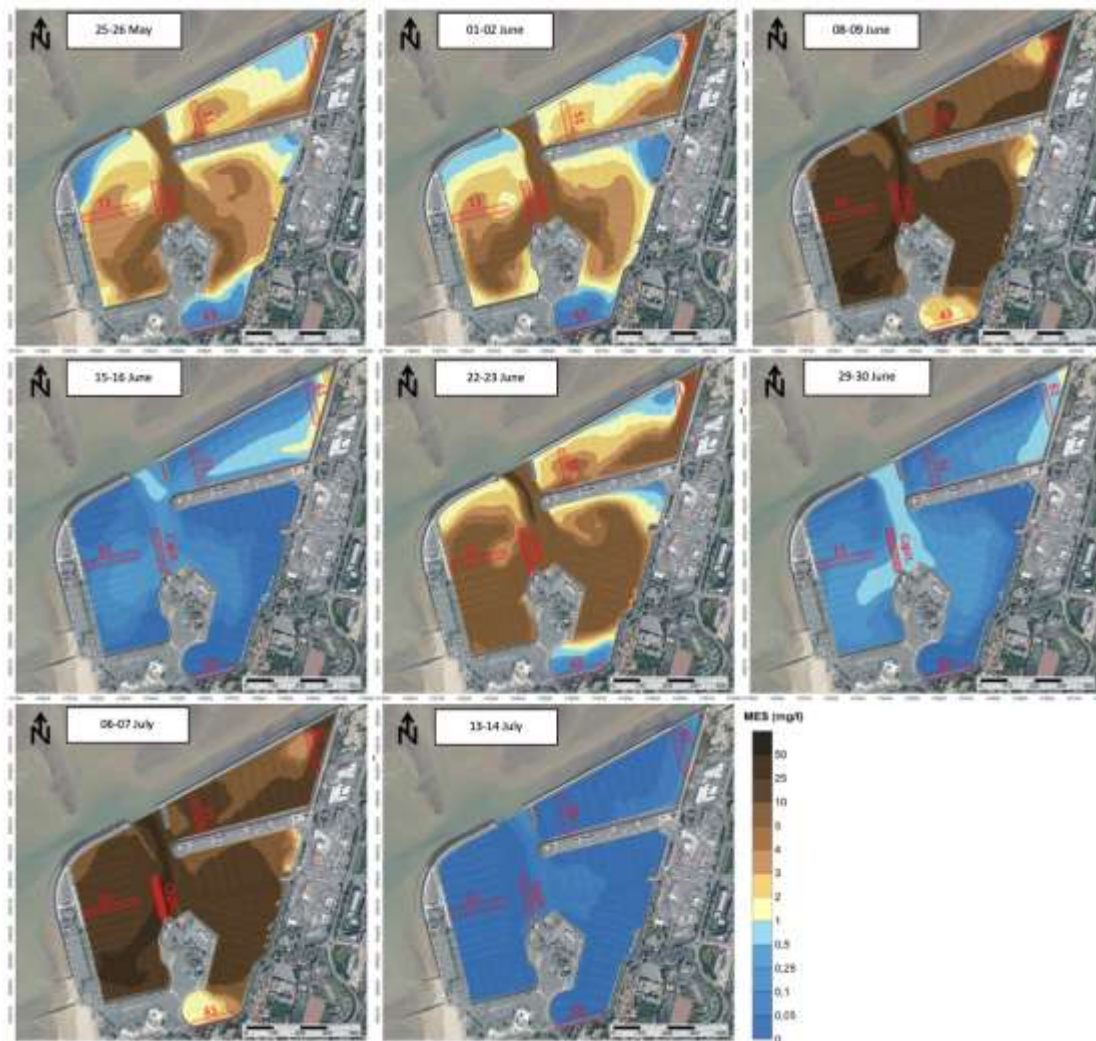


Fig.A.2. Maps of average environmental sediment concentration and average daily bioproduction (in red) for the summer campaigns. The intensity of the red is proportional to the amount of bioproducts formed.

The forgotten ones from the ports: The filter feeders at the heart of siltation processes.

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