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1 **Influence of parasitism on bioturbation: from host to ecosystem**  
2 **functioning**

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9 **Running page head:** Parasitism in bioturbation studies

10

11 **Abstract**

12 Bioturbating species represent a typical example of ecosystem engineer species in marine benthic environments. These  
13 abundant endo- or epibenthic organisms modify the physical structure and geochemical properties of sediments, and at  
14 broader ecosystem scale impact nutrient flows and benthic community structure. The ecological importance of  
15 bioturbators depends on (1) their abundance and (2) the magnitude of their bioturbation activity. We suggest that parasitism has  
16 a substantial impact on bioturbators, and cascading effects on their role in ecosystem functioning. Reviewing 5940 papers  
17 concerning bioturbation and using a set of selective criteria, we identified 176 bioturbating species, with 31 % of  
18 these potentially parasitized (micro- and macroparasites). However, there is significant discrepancy in the research effort on  
19 parasites among bioturbating groups, the highest effort being devoted to molluscs whereas studies on annelids and  
20 arthropods are rare. Furthermore, studies addressing the impacts of parasites on their bioturbating hosts are still scarce, but  
21 evidence we do have indicates that parasites impair their hosts' physiological state, fecundity, behaviour and survival.  
22 Because of impacts of parasites on phenotypic traits related to the bioturbation engineering activity of their hosts, parasitism  
23 could play a key role on ecosystem functioning through cascade effects. Yet, studies assessing the intricate link between  
24 parasites and their hosts' bioturbation activity, including potential effects on ecosystem functioning, are virtually non-existent.

25 **Keys words:** bioturbation, parasitism, ecosystem functioning, behaviour modifications, cascade effects

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31 **1. INTRODUCTION**

32 The structure and dynamics of ecosystems are shaped by myriad ecological and environmental factors, an  
33 important one of which is the activity of organisms. In 1994, Jones et al. defined ecosystem engineer species (EES) as species  
34 that modify their physical environment by their activity (allogenic engineers) or by their mere presence (autogenic engineers) in  
35 addition to their potential contribution to biotic interactions..

36 In marine benthic ecosystems, the role of bioturbating species as EES is well established (e.g., Krantzberg 1985;  
37 Levinton 1995; Lohrer et al. 2004; Mermillod-Blondin & Rosenberg 2006; Meysman et al. 2006). The process of  
38 bioturbation is described as any modification of the sediment matrix, including interstitial waters, due to the activities of  
39 organisms living mainly in or on the substratum (Kristensen et al. 2012). The locomotion, feeding and burrowing activities of  
40 bioturbators substantially displace sediment particles. These sediment reworking activities strongly affect the physical  
41 properties and geomorphology of sediments (e.g., Jones & Jago 1993; Rhoads & Young 1970; Volkenborn et al. 2007a).  
42 Bioturbators also significantly enhance the transport of water in sediments. This water input stimulates movements of solutes  
43 between pore- and overlying waters, a process named bioirrigation (Kristensen et al. 2012). In particular, sediment-  
44 dwelling organisms largely stimulate hydrological fluxes (Aller 1988; Volkenborn et al. 2012), since (1) biogenic structures,  
45 such as burrows, increase the surface of solute exchanges between the sediment and the overlying and porewaters and (2)  
46 the ventilation of the burrow stimulates advective irrigation. Thus, bioturbators play a key role in the biogeochemistry of  
47 sediments (e.g., Aller 1982; Webb & Eyre 2004; Volkenborn, Hedtkamp, et al. 2007; Volkenborn et al. 2012).

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53           The influence of bioturbators as EES on ecosystems depends on (1) their abundance and  
54 (2) the magnitude of their activities and thus on the physiological state of these organisms. In natural environments,  
55 organisms are seldom in optimal environmental conditions and different abiotic and biotic factors can adversely affect the  
56 physiology and the behaviour of bioturbating organisms, altering ecosystem functioning through cascade effects. The role of  
57 environmental factors such as temperature, salinity, food and oxygen availability is well established (e.g., Berkenbusch &  
58 Rowden 1999; Ouellette et al. 2004; Maire et al. 2007; Przeslawski et al. 2009). Biotic interactions can also have a large influence  
59 on the individual behaviour of organisms and can play a key role in bioturbation processes (e.g., Braeckman et al. 2010; Maire  
60 et al. 2010; Premo & Tyler 2013; Campbell & Lindsay 2014).

61           Among biotic factors influencing faunal EES, one major concern is the role played by parasites and associated  
62 infectious diseases. In the context of global climate change, it has been suggested that warmer conditions could increase the  
63 frequency and intensity of disease events (Harvell et al. 2002; Marcogliese 2001). For example, increase in seawater temperature  
64 enhances infection success of the trematode *Maritrema novaezealandense* in the amphipod host *Paracalliope*  
65 *novizealandiae*. A larger parasite burden is associated with a higher mortality rate of amphipods (Studer & Poulin 2013).  
66 Although many parasites and associated infectious diseases can produce mass mortality events in host populations (e.g.,  
67 Jensen & Mouritsen 1992; Jonsson & Andé 1992; Fredensborg et al. 2004), parasites can also have a wide range of sub-lethal  
68 effects, especially on the physiological status and behaviour of infected organisms. For example, the health of parasitized  
69 organisms is often impaired as reflected in reduced growth rate and condition index (e.g., Thieltges 2006; Dang et al. 2013;  
70 O'Connell-Milne et al. 2016). This pattern could be due to parasites directly interfering with food uptake (Flye-Sainte-Marie et  
71 al.

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76 2007; Stier et al. 2015) or impairing a host's metabolism (Anderson 1977; Repetto & Griffen 2012). Behaviour  
77 modifications can also result from parasitism, with infected organisms exhibiting aberrant behaviour compared to  
78 unparasitized individuals (e.g., Thomas & Poulin 1998; Pascal 2017). If parasites are prevalent in the population of  
79 their host, their effects on individual organisms can produce broad impacts at the ecosystem level, with parasites playing a  
80 key role in structuring communities of free-living organisms (Minchella & Scott 1991; Mouritsen & Poulin 2002; Poulin 1999;  
81 Price et al. 1986).

82         The role of parasites on EES acting by bioturbation appears as a crucial issue in the understanding of marine  
83 ecosystems. The aim of this paper is to review current knowledge on parasites and associated infectious diseases in  
84 common bioturbators, to highlight some scientific gaps and propose a general framework for future studies. We examined the  
85 relationship between parasites and bioturbators by answering four questions: (1) what are the commonly studied  
86 bioturbating species, (2) are there any parasites known to infect these bioturbating species, (3) what are the effects of  
87 parasites on their host, and (4) do parasites infecting bioturbating species have any consequence on the functioning of  
88 ecosystems?

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91 **2. DEFINITIONS**

92 **2.1. Type of bioturbators**

93 In this study, bioturbating species were restricted to epi- or endobenthic faunal organisms influencing the physical  
94 structure (i.e. grain size, porosity, organic matter content, etc.) and/or biogeochemical properties (i.e. nutrient and solute  
95 contents, redox status, etc.) of sediments. In addition, this literature review was limited to invertebrates occurring in  
96 coastal environments, including mangrove forests. Taking these restrictions into account, publications were searched in  
97 Scopus using the terms “bioturbation”, “sediment reworking” and “bioirrigation”. Because of the very high number of  
98 related papers, the search was further constrained to publications belonging to the “environmental science” subject  
99 area for the items “sediment reworking” and “bioirrigation”. A list of 4912, 732 and 296 publications for the terms  
100 “bioturbation”, “sediment reworking” and “bioirrigation” were gathered (May 11<sup>th</sup>, 2018), respectively. Bioturbators were  
101 taxonomically classified based on the World Register of Marine Species (WoRMS Editorial Board 2018). Our search  
102 found a total of 176 bioturbating species studied in coastal environments worldwide (Fig. 1; see ESM 1 for a full list of the  
103 bioturbators). Species belonging to the phyla Arthropoda, Annelida and Mollusca were the most extensively studied,  
104 representing 37, 27 and 23 % of the total number of bioturbator species richness, respectively (Fig. 1).

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108 **2.2. Type of parasites**

109 Parasites were broadly defined as organisms exploiting other organisms (the hosts) and  
110 can include viruses (Combes 1995). This study investigated both microparasites (viruses and unicellular organisms)  
111 and macroparasites (mainly helminths and arthropods) of bioturbating species (Anderson & May 1979). For each of  
112 the bioturbating species identified in our first search, a second search for publications mentioning parasites occurring  
113 in these organisms was made by using the name of the bioturbating species in combination with the terms “parasite”,

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115 “infection”, “bacteria” and “virus”. In addition, we collected data related to prevalence, intensity and/or abundance of parasitic  
116 infections when available. In a sampled population, prevalence is defined as the percentage of infected individuals, intensity of  
117 infection as the mean number of parasites per parasitized hosts, and abundance as the mean number of parasites per potential host  
118 (including both parasite-infected and uninfected) (Margolis et al. 1982). Furthermore, the influence of parasites on the  
119 physiological state, behaviour and bioturbating activity of their host was also recorded.

### 120 **3. PARASITE SPECIES INFECTING BIOTURBATING ORGANISMS**

121 Of the 176 species of bioturbators identified, 55 species (i.e. 31 %) were reputed as being parasitized with at least one  
122 macro- or microparasite species (Fig. 1). More specifically, 27 (i.e. 15 %) and 11 (i.e. 6 %) bioturbating species are infected with  
123 at least one macro- or microparasite species only, respectively and 17 bioturbators (i.e. 10 %) with both macro- and  
124 microparasites (Fig. 1; see ESMs 2 and 3, respectively, for a full list of macro- and microparasites of bioturbating  
125 species). There is an important disparity regarding the distribution of parasites across the phyla of bioturbators, with highly  
126 parasitized, such as molluscs (51 % of the species harbouring at least one parasite species), and others apparently less  
127 parasitized, for example echinoderms (22 %) and arthropods (23 %) (Fig. 1). Similarly, the number of parasite species  
128 identified per bioturbating host strongly differed among phyla (Fig. 2). Numerous studies were devoted to bioturbating  
129 molluscs and highlighted that they were diversely parasitized, with on average ( $\pm$  SE)  $8.2 \pm 2.9$  macroparasite species (Fig.  
130 2A) and  $8.6 \pm 2.8$  microparasite species (Fig. 2B) identified per individual species. To the contrary, only a few parasites  
131 species have been documented in annelids, with on average  $1.4 \pm 0.3$  macroparasite species (Fig. 2A) and  $1.8 \pm 0.4$  microparasite  
132 species (Fig. 2B) identified per annelid species. Finally, there was also a large

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138 variability in parasite species richness per bioturbating species within a given phylum (Fig. 2).  
139 For example, the number of macro- and microparasites identified in molluscan bioturbators  
140 ranged from 1–55 and 1–26, respectively (ESMs 2 and 3).

141         Several factors explain the discrepancy in parasite species richness recorded among and  
142 within the phyla of bioturbators. First, through a large meta-analysis, Kamiya et al. (2014)  
143 highlighted a positive association between parasite species richness and host body size,  
144 population density and geographical range. Second, difference in sensitivity and susceptibility of  
145 bioturbating species to parasites could also explain interspecific variation in parasite species  
146 richness (Dang et al. 2009). On the other hand, we suggest that the large disparity in parasite  
147 species richness we observed among and within phyla of bioturbators is more likely related to a  
148 bias in research effort on parasites occurring in these organisms. Notably, the higher the  
149 economic value of a species, the more intensive are the research efforts to identify any potential  
150 pathogens or other stressors that could influence the sustainability of the production and/or the  
151 quality of the resource. For instance, numerous studies have been conducted in molluscs, a  
152 phylum of broad interest for fisheries and aquaculture, with the common cockle *C. edule* and the  
153 Manila clam *R. philippinarum* being two important species. Although a small proportion of  
154 echinoderms have been described as being parasitized so far, there is a proportionally extensive  
155 literature on parasites infecting bioturbating species with a commercial value, such as the sea  
156 cucumber *Apostichopus (Stichopus) japonicus*. Accordingly, annelids are poorly exploited and  
157 have rarely been studied with regard to parasites and associated infectious diseases.

158         Bioturbators harbour a large diversity of macro- and microparasites species with large  
159 differences in the relative frequency among parasite phyla (Fig. 3, ESMs 2 and 3).  
160 Platyhelminthes are the most common macroparasites infecting bioturbators, with 75 % of the

161 reported parasites species belonging to this phylum. Platyhelminthes infect molluscs,  
162 echinoderms and annelids, and to a lesser extent arthropods (Fig. 3A). Platyhelminthes includes  
163 about 30,000 species (Caira & Littlewood 2013), of which many are parasites (Dobson et al.  
164 2008), such as members of the Trematoda or Cestoda. Moreover, it is one of the most important  
165 groups of marine parasites (Rohde 2005) which makes it unsurprising that infections with  
166 Platyhelminthes have been noted in bioturbators to such extent. On the other hand, only a few  
167 studies highlighted the occurrence of parasitic annelids or nemerteans in bioturbators. As these  
168 two groups mainly consist of free-living organisms, they represent minor parasite group in  
169 marine environments (Rohde 2005). Regarding microparasites, 53 % of the species identified are  
170 eukaryotes and 36 % are bacteria. Eukaryotic microparasites encompass a large diversity of  
171 phyla, while bacteria are mainly represented by Proteobacteria (Fig. 3B). Finally, a few viral  
172 syndromes and infectious diseases for which the etiological agent has not yet been fully  
173 characterized (e.g. various neoplasias, viscera ejection syndrome, brown muscle disease; ESM 3)  
174 have been noted in bioturbating organisms as well.

#### 175 **4. DIRECT EFFECTS OF PARASITES ON BIOTURBATING SPECIES**

176 Parasites have direct effects on their host, i.e. pathological impacts on individuals. The  
177 literature is limited concerning bioturbating species. Our literature survey documented that 376  
178 macroparasites ( $N = 108$  studies) and 188 microparasites and associated infectious diseases ( $N =$   
179 132 studies) parasitize 55 coastal bioturbating species. Among these parasites, impacts on the  
180 host were recognized in 32 % and 36 % of the studies highlighting the occurrence of macro- and  
181 microparasites (and associated infectious diseases) in bioturbating species, respectively. These  
182 direct effects included alterations of physiological state (i.e. modulation of gene expression and  
183 cellular functions, initiation of inflammatory responses, tissue damages, etc.), modifications of

184 reproductive functions (i.e. partial or total castration, changes in reproductive success, etc.),  
185 increase of the mortality rate of the host and modifications of host behaviour (reduced activity  
186 levels, abnormal behaviours, etc.) (Fig. 4, ESL 2 and 3). More than 82 % of the known impacts of  
187 macroparasites are due to Platyhelminthes (ESM 2). Most studies on microparasites focused on  
188 Proteobacteria (36 %) and Myzozoa (30 %) (ESM 3). These patterns are in accordance with those  
189 showing that Platyhelminthes, Proteobacteria and Myzozoa are the most commonly described  
190 macro- and microparasites in bioturbating species (Fig. 3).

#### 191 **4.1. Impacts of parasites on bioturbator physiology**

192 Numerous parasites are documented to impact the physiological state of their bioturbating  
193 host (Fig. 4). At the molecular scale, parasites interfere with gene regulation, thereby either up- or  
194 down-regulating their expression. For example, the trematode *Himasthla elongata* up-regulates  
195 the expression of several genes related to mitochondrial metabolism and oxidative responses in  
196 infected cockles *C. edule*, a reputed bioturbator. These modulations in gene expression are  
197 considered to be a molecular response to parasites causing energetic losses and oxidative stress in  
198 cockles (Paul-Pont et al. 2010). Parasites can also impair the host's physical integrity if  
199 physiological alterations are concomitant with physical injuries. While developing and residing  
200 inside their host, parasites cause significant histopathological damages to host tissue (Lauckner  
201 1980, Robaldo et al. 1999, Dang et al. 2008). For instance, the protozoan parasites *Perkinsus* spp.  
202 induce histological lesions in gills, digestive gland and gonad gland of the sand gaper clam *Mya*  
203 *arenaria* (McLaughlin & Faisal 1998). As the gills and the digestive gland play a key role in  
204 nutrients absorption, such tissue alterations are expected to be energetically costly for the host,  
205 and may have direct repercussions on its growth. In fact, a caging experiment conducted at two  
206 sites impacted by perkinsosis along the northeast Atlantic coast of France demonstrated that

207 growth rates of the bioturbators *R. decussatus* and *R. philippinarum* are significantly  
208 compromised as a result of *Perkinsus* spp. infections (Dang et al. 2013). Macroparasites  
209 impacting the growth of their bioturbating host have also been broadly documented (e.g.,  
210 Mouritsen & Jensen 1994; Pascal et al. 2016; Smith et al. 2008). The mud shrimp *Upogebia* cf.  
211 *pusilla* displays reduced size when infected with the epicaridean isopod *Gyge branchialis* (Pascal  
212 et al. 2016). The negative effect of the parasite is probably not related to histological lesions but to  
213 the parasite directly feeding at the expense of its host (Tucker 1930). By doing so, the parasite  
214 strongly affects host energetics (Hughes 1940) and consequently its physiological state (Williams  
215 & Boyko 2012). Parasites do not always diminish their host's growth rate. The bioturbators  
216 *Peringia (Hydrobia) ulvae* infected with trematodes grow to larger sizes than their unparasitized  
217 conspecifics (Mouritsen & Jensen 1994). Such cases of gigantism have been reported in several  
218 host-parasite association involving parasitic castrators (de Montaudouin et al. 2003; Pearre 1976;  
219 Sluiter et al. 1980).

#### 220 **4.2. Impacts of parasites on bioturbator reproduction**

221 Evidence for alterations to host fecundity are common and has been found in 31 % and 6  
222 % of the studies on effects of macro- and microparasites, respectively (Fig. 4). Macroparasites,  
223 and especially digenean trematodes (Platyhelminthes), are often associated with impairment of  
224 the host reproductive function (ESM 2). Digenean trematodes have complex life cycles. One of  
225 the stages, called sporocyst or rediae according to digenean species, is fundamentally damaging  
226 for the fecundity of the host (Lauckner 1980, 1983). Digenean trematodes infect the digestive  
227 gland and/or the gonad of their host (Probst & Kube 1999), causing partial or complete castration  
228 *via* mechanical or chemical damages to host reproductive tissue (Hurd 1990). For instance,  
229 infection with trematodes leads to an important reduction of the penis size of the mud snail *P.*

230 *ulvae* and to almost non-existent oviposition in females (Mouritsen & Jensen 1994). Castration is  
231 not only caused by digenean trematodes; crustacean parasites like epicaridean isopods have also  
232 strong influences on the fecundity of their bioturbator hosts (Dumbauld et al. 2011; Tucker  
233 1930). However, castration of hosts by isopods seems to be related to the parasite lowering the  
234 condition index of the host and/or interfering with the secretion of host reproductive hormones  
235 (Reinhard 1956; Williams & Boyko 2012). In sharp contrast, some parasites such as  
236 microsporidian can enhance the fecundity of their bioturbating host (Mautner et al. 2007), but  
237 these example are more rare.

#### 238 **4.3. Impacts of parasites on host mortality**

239 As a result of their pathological effects, parasites can compromise the survival of their  
240 bioturbating hosts. An increase in mortality rate has been noticed in 17 % and 49 % of the studies  
241 evaluating the influence of macro- and microparasites, respectively (Fig. 4). For instance, the  
242 Galician population of the common cockle *C. edule* showed an important decline in spring 2012,  
243 with mortality up to 100 %. At this time, juvenile and adult cockles were heavily infected (up to  
244 100 % prevalence) with the protistan parasite *Marteilia cochillia*, which is probably the cause of  
245 the population collapse (Villalba et al. 2014). Marteiliosis is associated with substantial  
246 physiological alterations in infected organisms. The parasite infects the digestive gland of its host  
247 and interferes with its energetic balance (Pérez Camacho et al. 1997), weakens organisms and  
248 eventually kill them.

249 Among macroparasites, digenean trematodes have been recognized to deeply affect the  
250 survival of their hosts, at time causing collapses of natural populations. For instance, the  
251 trematodes *Microphallus claviformis* and *Maritrema subdolum* are considered to be the main  
252 cause of the 40 % population decline of the bioturbating mud snail *P. ulvae* observed in the

253 Danish Wadden Sea during Spring 1990 (Jensen & Mouritsen 1992). Digenean trematodes can  
254 also modulate the population size structure of their bioturbating hosts because of differential  
255 susceptibility to parasitism of small and large organisms. An extensive field survey conducted in  
256 Arcachon Bay, France, over the years 1998–1999 indicated an important decline of the largest  
257 mud snails *P. ulvae* during the winter 1998-1999 which were also the most parasitized (up to 100  
258 %). A laboratory experiment conducted in parallel highlighted higher mortality rates of  
259 parasitized organisms as compared to unparasitized individuals. Together, these results  
260 demonstrate that digenean parasites substantially influence the population size structure of the  
261 bioturbator *P. ulvae* (de Montaudouin et al. 2003).

#### 262 **4.4. Impacts of parasites on bioturbator behaviour**

263 Parasites can have more subtle effects on their hosts such as behaviour alteration. Such  
264 effects have been reported in 46 % and 11 % of the studies evaluating the influence of macro-  
265 and microparasites on their bioturbating hosts, respectively (Fig. 4; ESMs 2 and 3).

266 Modifications of the behaviour of the host can be a side effect of parasitism, that is  
267 phenotypic alterations with no adaptive value for either the parasite or the host (Ewald 1980).  
268 Few examples report how parasites impair the behaviour of bioturbators and their activities (Fig.  
269 4; ESM 2 and 3). For instance, mud snails *P. ulvae* infected with trematode parasites experience  
270 modifications of locomotory behaviour, with parasitized snails moving slower and crawling over  
271 shorter distances as compared to uninfected organisms (Mouritsen & Jensen 1994). This  
272 behavioural modification could be a side effect of parasites interfering with the host energy  
273 allocation. Indeed, mud snails exhibited increased growth rates (“gigantism”). Since locomotory  
274 activity is a highly costly behaviour, it has been suggested that parasites stimulating host growth  
275 reduce the energy available for the host to crawl (Mouritsen & Jensen 1994).

276           Regarding the impacts of microparasites on host behaviour, the literature is even more  
277 scarce, with altered behaviour recognized in only 11 % of the studies documenting the occurrence  
278 of microparasites or infectious diseases in bioturbators (Fig. 4; ESM 3). Given the large influence  
279 of microparasites on the physiological status of their hosts (ESM 3) it is likely that microparasites  
280 have side effects on host behaviour as well. For instance, brown muscle disease causes a serious  
281 atrophy of the posterior adductor muscle of the Manila clam *R. philippinarum* (Dang et al. 2008).  
282 Any alterations to this muscle is expected to disturb clam feeding and respiration, as well as  
283 locomotion. Such modifications of locomotory activity were observed in Manila clams infected  
284 with the protozoan *Perkinus olseni*. This parasite promotes the emergence of *R. philippinaum* at  
285 the sediment surface and limits its ability to re-burrow in thermally stressful condition (Nam et al.  
286 2018).

287           Modifications of the behaviour of the host can also be adaptive manipulation. This  
288 typically involves parasites with complex life cycles as host behaviour modifications are  
289 expected to enhance the transmission success of parasites (Combes 1991; Lafferty 1999; Moore  
290 2002). One of the most detailed examples of adaptive manipulation in bioturbators involves the  
291 New Zealand cockle *Austrovenus stutchburyi*, which is commonly found at the sediment surface  
292 of tidal flats, with organisms showing difficulty in burrowing (Thomas & Poulin 1998). Surfacing  
293 cockles (i.e., in abnormal position) are heavily infected with the trematode *Curtuteria australis*,  
294 compared to buried cockles (i.e., in normal position) (Thomas & Poulin 1998). The trematode  
295 needs the cockle to be eaten by marine birds to complete its life cycle, which is facilitated by its  
296 altered behaviour at the surface of the sediment. Together, these results suggest that the parasite  
297 alters the cockle phenotype so as to enhance its own transmission success (Thomas & Poulin  
298 1998).

299 **5. INFLUENCE OF PARASITES ON BIOTURBATION ACTIVITY AND**  
300 **ECOSYSTEM FUNCTIONING**

301 The direct effects exerted by parasites on individuals can have knock-on effect on the  
302 population of bioturbators, then influencing their role as EES. These indirect effects of parasites  
303 on ecosystem functioning can be classified as density- and trait-mediated effects (Mouritsen &  
304 Poulin 2002; Preston et al. 2016). First, parasites can modify traits of their hosts involved in their  
305 functional role within ecosystem. These trait-mediated effects occur as side effect of pathology or  
306 are adaptive parasite manipulation. Secondly, through their impacts on the mortality and  
307 fecundity of their host, parasites can be main drivers of host density and regulate population size  
308 structure.

309 **5.1. Trait-mediated effects**

310 Out the 215 studies evidencing the occurrence of 376 macro- and 188 microparasites in  
311 55 bioturbating species over 176 bioturbators commonly studied in coastal environments, 82  
312 studies showed that parasites can impair the physiological state, reproductive capacity, behaviour  
313 and/or the mortality of their bioturbating hosts. Of these studies, only 21 studies depicted effects  
314 of parasites on the behaviour of their bioturbating host. Within these 21 studies just seven  
315 focused on the link between the occurrence of parasites and their role in modulating the  
316 bioturbating activity of their hosts, with potential outputs on the community of free-living  
317 organisms and ecosystem functioning, the so-called trait-mediated effects (Table 1).  
318 Nevertheless, these few papers strongly support the idea that parasites can act as EES themselves  
319 by modifying functional traits of their host involved in bioturbation activities (Thomas et al.  
320 1999) (Table 1, Fig. 5). For instance, Pascal (2017) monitored the influence of the epicaridean  
321 parasite *G. branchialis* on the behaviour of the mud shrimp *U. cf. pusilla* through video  
322 recording. He defined four main behavioural states for the mud shrimp species as “resting”,

323 “burrowing”, “ventilating” and “walking”. “Burrowing” and “ventilating” are the two behaviours  
324 associated with bioturbation activities of the mud shrimp. Pascal (2017) demonstrated that  
325 parasitized mud shrimp spend 1.8- and 2.3-fold less “burrowing” and “ventilating” than healthy  
326 organisms. These behavioural modifications are associated with negative impacts on the intensity  
327 of the bioturbating activity: the sediment reworking rate of parasitized organisms is 4.6-fold  
328 lower and the bioirrigation rate 2.9-fold lower compared to unparasitized organisms. As a result,  
329 biogeochemical fluxes are also strongly modified. The total oxygen and nitrate uptake are  
330 reduced and there is a diminished release of ammonium at the sediment-water interface. This  
331 suggests, therefore, that parasitized mud shrimp have a much lower influence on organic matter  
332 mineralization and nutrient turnover than uninfected organisms (Pascal 2017). At the ecosystem  
333 level, these findings can be highly relevant (Fig. 5) as (1) mud shrimp can attain high densities  
334 (e.g., Nates & Felder 1998) and (2) epicarideans are widespread in natural populations of mud  
335 shrimp (Pascal et al. 2016; Smith et al. 2008).

336 Mouritsen & Poulin (2005, 2010) addressed the influence of parasitism on animal  
337 community structure (Table 1). Over a long-term field experiment, they highlighted a positive  
338 relationship between macrozoobenthic species richness (and density) and the presence of  
339 parasitized cockles *A. stutchburyi* (Mouritsen & Poulin 2005). A similar pattern was reported at a  
340 larger spatial scale (Mouritsen & Poulin 2010). The bivalve *A. stutchburyi* harbours multiple  
341 parasites, some of which can manipulate the behaviour of cockles to facilitate transmission.  
342 These behaviour modifications can also change the role of cockles as EES. Heavily parasitized  
343 organisms are more likely found at the sediment surface than buried in the sediment and show  
344 reduced ability to rebury in the sediment (Thomas & Poulin 1998). Moreover, heavily parasitized  
345 cockles exhibit reduced crawling activity compared to moderately infected conspecifics

346 (Mouritsen & Poulin 2005). Cockles exhibit important reworking activity in subsurface  
347 sediments, where they also strongly impact nutrients cycling and the production of primary  
348 producers (Sandwell et al. 2009). Mouritsen & Poulin (2005, 2010) suggested that the positive  
349 association between macrozoobenthic species richness and parasitized cockles could be related to  
350 (1) a lower disturbance of the sediment *via* parasites reducing bioturbating activities of cockles  
351 and (2) surfacing cockles acting as physical ecosystem engineers (Jones et al. 1997; Thomas et al.  
352 1998).

353         There is no general rule regarding the influence of bioturbators on macrofaunal  
354 communities. Inhibitory and facilitative effects of bioturbators on the community diversity of  
355 free-living organisms have both been reported and depend on the bioturbating species (Posey et  
356 al. 1991, Dittmann 1996, Kanaya 2014). Mouritsen & Haun (2008) evaluated how parasitism  
357 interferes with the role of the bioturbating gastropod *P. ulvae* as an EES. Parasitized snails have a  
358 negative impact on primary producers whereas unparasitized organisms enhance primary  
359 production. The authors suggest that the sediment mixing activity of parasitized snails is reduced,  
360 lowering nutrient supply to benthic primary producers. Faunal community structure is also  
361 different in sediment bioturbated by parasitized and unparasitized snails, probably because of  
362 trophic cascading effects.

## 363         **5.2. Density-mediated effects**

364         The effect of bioturbators as EES relies on their activities but also on their abundance.  
365 Therefore, parasites can affect ecosystem functioning *via* density effects on major EES  
366 (Mouritsen & Poulin 2002; Poulin 1999) as bioturbators (Fig. 5). We reported several examples  
367 of parasites reducing the fecundity and/or the survival of their host (ESMs 2 and 3). The intensity  
368 of the bioturbation activity can vary according to population biomass and bioturbator density

369 (e.g., Duport et al. 2006; Sandwell et al. 2009; Braeckman et al. 2010), with potential impacts on  
370 ecosystem functioning (Fig. 5). As an illustration, Lohrer et al. (2004) evaluated the influence of  
371 a declining density of the irregular urchin *Echinocardium* sp. on nutrient cycling. They  
372 highlighted a positive influence of density of urchins on ammonium efflux, and on oxygen, nitrite  
373 and nitrate and phosphorus influxes at the sediment-water interface. These nutrients being of  
374 fundamental importance for primary production, the microphytobenthic primary production  
375 increased with the density of *Echinocardium* sp.. Considering the intricate link between  
376 bioturbators and microphytobenthos, one would expect that the reduction of the abundance of  
377 bioturbators related to parasitic infection could be ecologically relevant (Fig. 5).

378 Parasites can also interfere with the engineering role of their bioturbating hosts by shaping  
379 the size structure of their host populations. Concomitantly, the magnitude of the bioturbation  
380 activities of organisms depends on their individual size (Bachteram et al. 2005; Bosch et al.  
381 2015). In a laboratory experiment, Bosch et al. (2015) evaluated the influence of the nereid  
382 polychaete *Alitta (Neanthes) succinea* biomass on nitrogen cycling by manipulating the density  
383 and size of worms. They found that at similar density, large polychaetes (high biomass)  
384 stimulated nitrogen solute fluxes at the sediment-water interface to a greater extent than small  
385 worms (low biomass). Moreover, large organisms enhanced solute diffusion in deeper horizons  
386 of the sediment column compared to small worms. This pattern is probably the result of larger  
387 organisms building larger and deeper burrows than small organisms (Davey 1994), which would  
388 boost bioirrigation processes (Bosch et al. 2015; Mermillod-Blondin et al. 2004). These examples  
389 suggest that parasites could also theoretically interfere with the role of bioturbators in nutrient  
390 cycling and/or in shaping benthic environments (*via* reduction of sediment reworking) by  
391 modifying the size structure of the population of their bioturbating hosts (Fig. 5).

392 Finally, it should be considered that parasites can have both trait-mediated and density  
393 effects on their bioturbating host. In particular, we documented that the bioturbators identified in  
394 this review host a large variety of parasites with complex life cycles (ESM 2 and 3), many of  
395 which need to be trophically transmitted (i.e., Platyhelminthes or Acanthocephala) to definitive  
396 hosts to reproduce. To facilitate their trophic transmission, parasites can drive significant  
397 modifications of behaviour similar to those reported previously for the cockle *A. stutchburyi* (i.e.  
398 reduced ability to burry, lower crawling activity). Therefore, such parasite species induce changes  
399 in bioturbating host traits and density, altering the functional role of the bioturbator host and  
400 ecosystem properties.

### 401 **5.3. What next?**

402 Over the last years, there has been a growing interest in developing indexes providing  
403 estimation of the impact of benthic community in the functioning of marine ecosystem. Among  
404 them, community bioturbation potential (BP<sub>c</sub>) and community bioirrigation potential (BIP<sub>c</sub>) are  
405 two metrics estimating the influence of benthic organisms on sediment mixing and solute  
406 exchanges, respectively (Renz et al. 2018; Solan et al. 2004; Wrede et al. 2018). Both of these  
407 scoring systems rely on a classification of marine infauna based on the (1) abundance, (2)  
408 biomass and (3) functional traits of organisms. For instance, the BIP<sub>c</sub> categorized species  
409 according to their feeding type, burrow type and burrowing depth. Our literature review  
410 highlights that parasites modulate the abundance, biomass and functional traits of their  
411 bioturbating hosts. For instance, mud shrimp *U. cf. pusilla* parasitized with the bopyrid *G.*  
412 *branchialis* show reduced ventilation rate and built smaller burrow than uninfected organisms.  
413 This has consequences on the influence of mud shrimp in driving solute exchange at the  
414 sediment-water interface (Pascal 2017). Thus, one would expect that the application of the BIP<sub>c</sub>

415 on macrofaunal communities dominated by the mud shrimp *U. cf. pusilla* without taking into  
416 account the presence of this parasite conducts to overestimation of the BIP<sub>c</sub> of such communities,  
417 with potential biases in the comparison of ecosystems. In our opinion, a successful application of  
418 trait-based indices such as the BP<sub>c</sub> and the BIP<sub>c</sub> would gain to take into account (1) the impact of  
419 parasites on their bioturbating hosts and (2) the prevalence of parasites in community of  
420 bioturbators.

## 421 **6. CONCLUSION**

422 The structure and function of benthic environments is substantially shaped by major  
423 ecosystem engineer species (Jones et al. 1994) such as bioturbators (e.g., Krantzberg 1985;  
424 Levinton 1995). These organisms play a key role in the physical structure of sediments, on their  
425 sediment biogeochemical properties and in nutrient cycling through intense sediment reworking  
426 and bioirrigation activities (e.g., Jones & Jago 1993; Rhoads & Young 1970; Volkenborn et al.  
427 2007; Webb & Eyre 2004). When abundant, bioturbators strongly influence the community  
428 structure of free-living organisms (e.g., Dahlgren et al. 1999; Pillay et al. 2007; Widdicombe et  
429 al. 2000) (Fig. 5). The impact of bioturbators on ecosystem functioning is related to (1) the  
430 intensity of their bioturbation and inherently on their physiological state and (2) their abundance.  
431 Several factors can interfere with the role of bioturbators as EES (e.g., Duport et al. 2006; Premo  
432 & Tyler 2013; Przeslawski et al. 2009), such as parasitism. Parasites are widespread in natural  
433 environments (Dobson et al. 2008), but so far only a small proportions of bioturbators have been  
434 studied in this regard. We pointed out the deficit of data on parasitism in bioturbating organisms.  
435 Moreover, we showed that few studies evaluated the influence of parasites on bioturbating  
436 organisms. Among these studies, parasites have been documented to strongly impair the  
437 physiological status, fecundity, behaviour and survival of their host. By doing so, parasites

438 certainly reduce the bioturbation activity of their host. Due to the impact of parasites on their  
439 bioturbating hosts and the fact that parasites can be highly prevalent in bioturbating host  
440 populations, parasites could have impacts on ecosystem functioning through cascading effects  
441 (Fig. 5). In fact, parasites should be considered EES (Thomas et al. 1999) just as bioturbating  
442 species are. Therefore, we strongly suggest that parasitism be taken into account when evaluating  
443 the role of bioturbators as ecosystem engineers.

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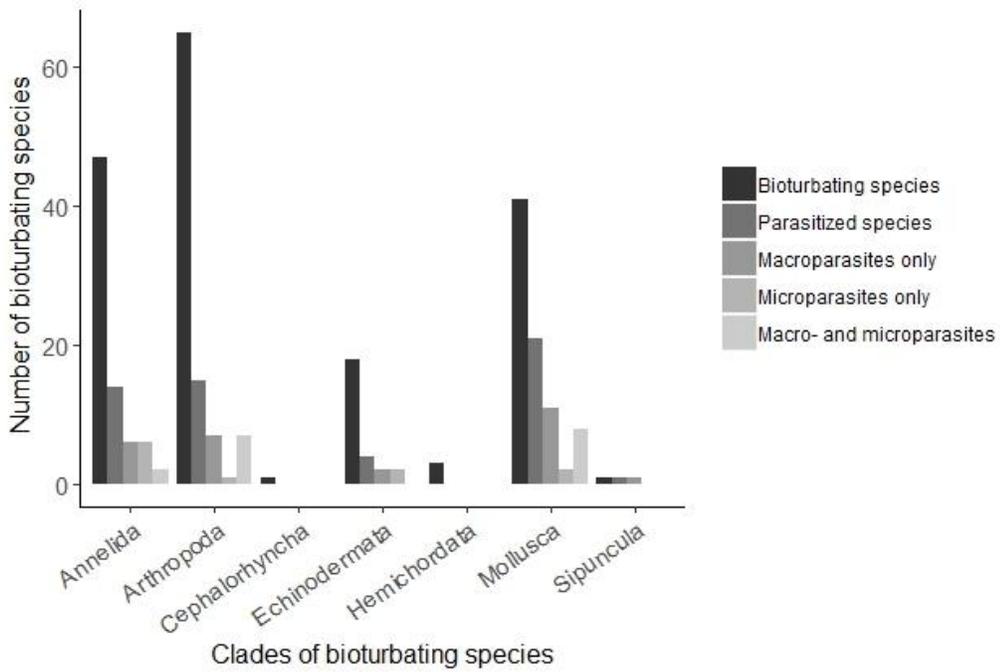
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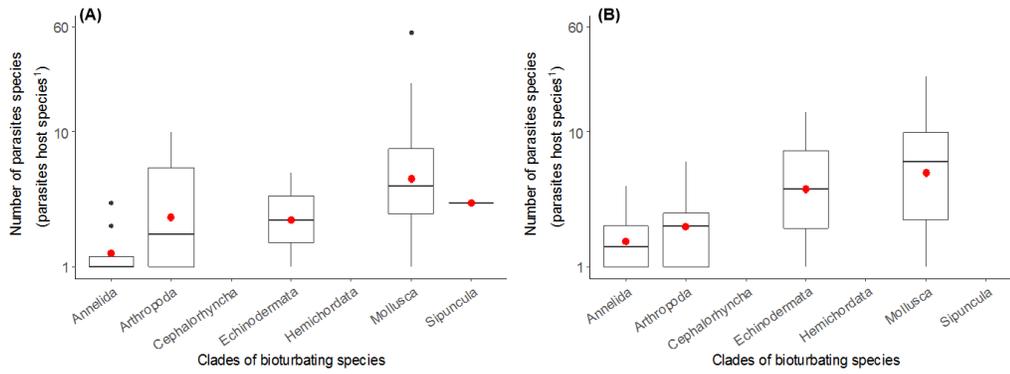
698 **Figure**



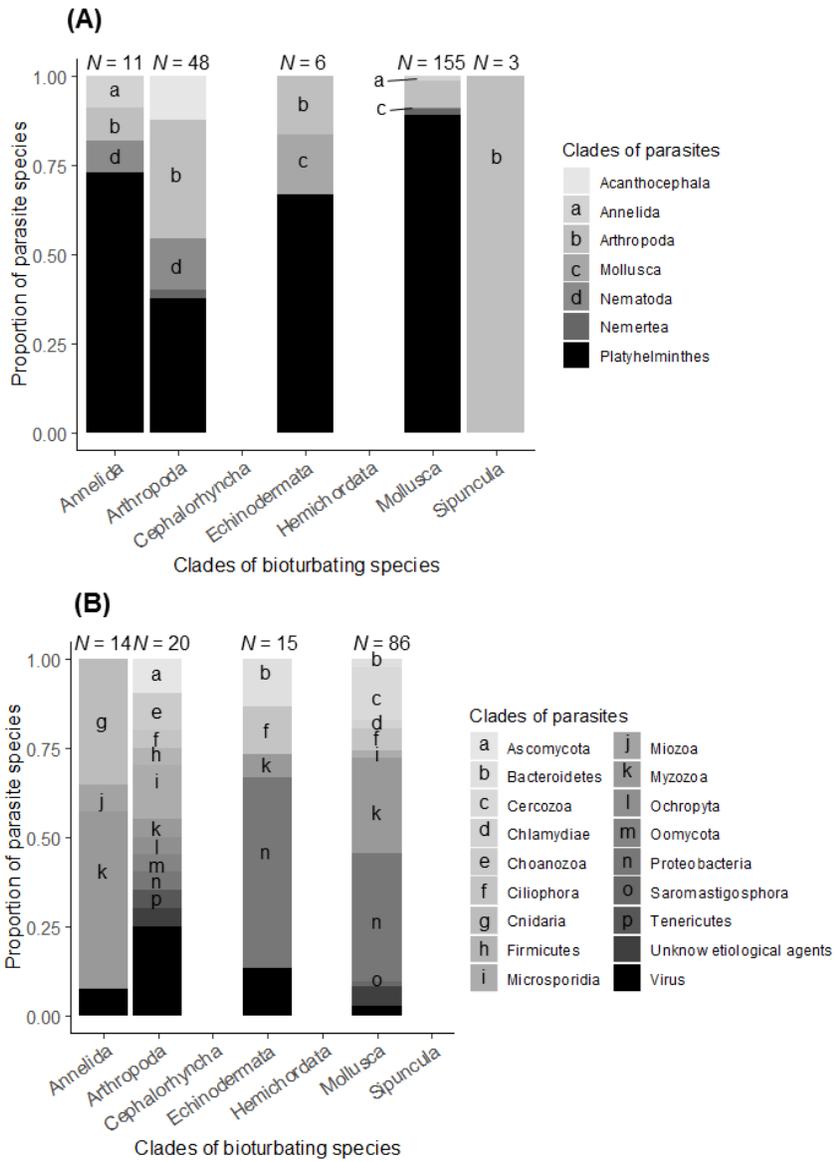
699

700 **Fig. 1** Number of coastal bioturbating species commonly studied and number of parasitized  
701 bioturbators per taxonomic clade. Parasitized bioturbators are categorized as being infected with  
702 macroparasites only, microparasites only or both groups of parasites.

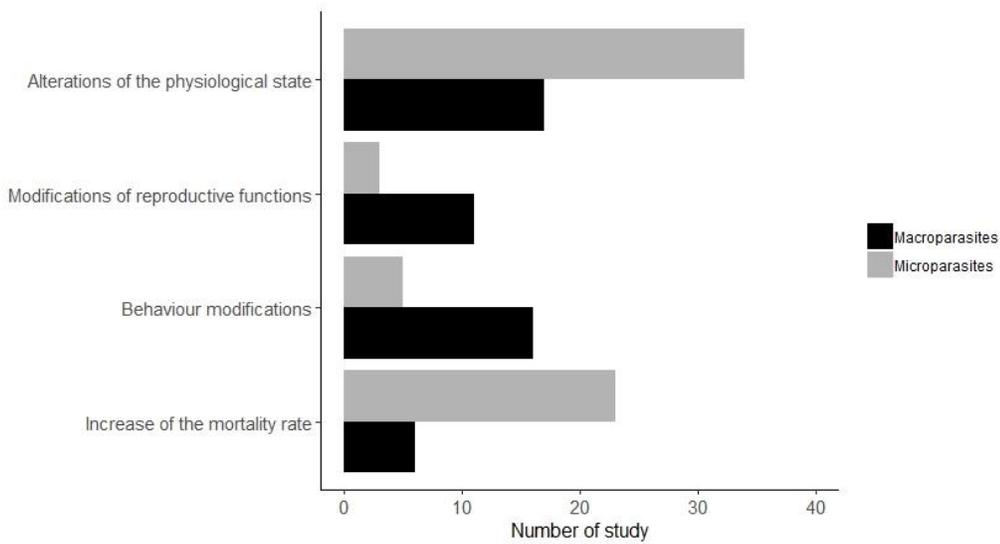
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704  
 705 **Fig. 2** Number (log scale axis) of (A) macroparasite and (B) microparasite species identified per  
 706 bioturbating host species. Bioturbators are classified according to their taxonomic clade. The  
 707 boxes represent the interquartile range, the black lines the median and the red dots the mean  
 708 number of parasites species in each clade of bioturbators.

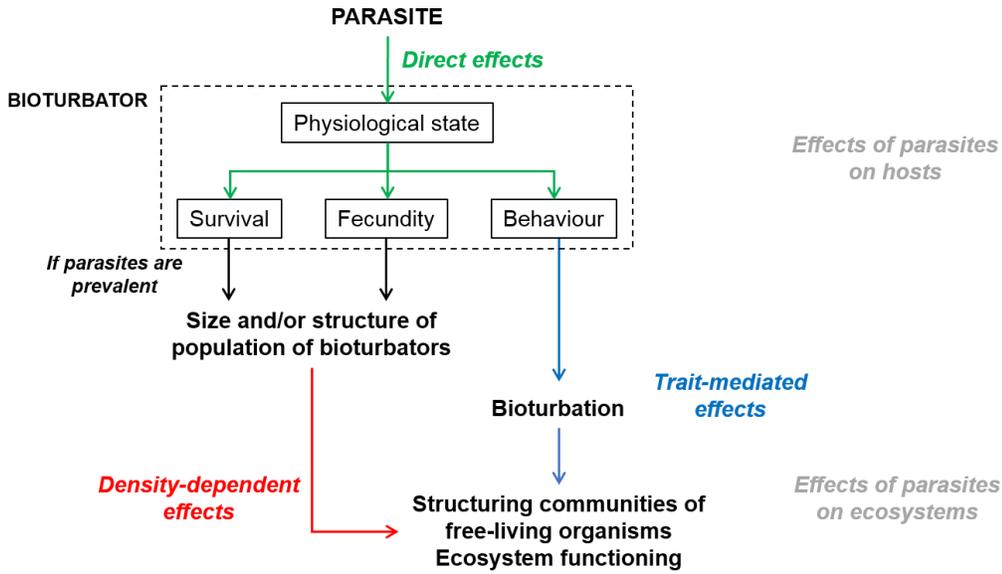


710  
 711 **Fig. 3** Taxonomic types of (A) macroparasites and (B) microparasites reported in clades of  
 712 bioturbating species. The total number of parasite species identified per clade of bioturbators is  
 713 given (N).



714

715 **Fig. 4** Impacts of macro- and microparasites on bioturbating organisms. Alterations of  
 716 physiological state: parasites influencing gene expression, cellular functions, physical integrity,  
 717 growth rates of the host, etc. Modifications of reproductive functions: parasites reducing or  
 718 increasing their host's fecundity, causing total or partial castration, etc. Modifications of  
 719 behaviour: parasites reducing their host's activity levels, inducing abnormal behaviours, etc.  
 720 Increase of the mortality rate: changes in survival. Total number of studies  $N = 85$ , of which  $N =$   
 721 35 studies on macroparasites and  $N = 47$  studies on microparasites.



723

724 **Fig. 5** Impacts of parasites on bioturbating organisms and on their influence as ecosystem  
725 engineer species (EES). The behaviour of bioturbating organisms conditions the intensity of their  
726 bioturbation and their role as EES when they are abundant. Parasites can significantly alter the  
727 physiological state of organisms with consequences on their behaviour, fecundity and survival.  
728 By doing so, parasites can regulate the density of their host population or altered their functional  
729 traits. Both density- and trait mediated effects of parasites on bioturbators would modify the  
730 functional roles of these organisms as EES.

731 **Table 1** Summary of the literature evaluating the influence of parasitism on the activity and the role as ecosystem engineer species of  
 732 bioturbating species.

<b>Bioturbator</b>	<b>Parasite</b>	<b>Type of parasite</b>	<b>Effects of parasitism</b>	<b>Type of effect</b>	<b>References</b>
<i>Upogebia cf. pusilla</i>	<i>Gyge branchialis</i>	Macroparasite: Isopoda	Moribund organisms ➤ 4.5-fold lower sediment reworking rate 2.9-fold lower bioirrigation rate Reduced influence on nutrient exchanges (TOU, NH <sub>4</sub> <sup>+</sup> , NO <sub>3</sub> <sup>-</sup> , dSi)	Direct effects leading to trait-mediated effects	(Pascal 2017)
<i>Austrovenus stutchburyi</i>	<i>Curtuteria australis</i>	Macroparasite: Trematoda	Changes in the epibiont community of cockles ➤ The authors hypothesizing that the parasite interfering with the ability of cockles to burrow (Thomas & Poulin 1998) modifies their role as autogene engineers.	Trait-mediated effects	(Thomas et al. 1998)
<i>Austrovenus stutchburyi</i>	<i>Curtuteria australis</i>	Macroparasite: Trematoda	Reduced crawling activity (mean distance travelled) of highly infected cockles (the cockles' crawling activity considered to be a measure of their bioturbation potential)	Direct effect	(Mouritsen 2004)
<i>Austrovenus stutchburyi</i>	<i>Curtuteria australis</i>	Macroparasite: Trematoda	Changes in the structure of the intertidal benthic community: increased abundances of some macroinvertebrates, modifications of the biomass of certain taxonomic groups, increased species diversity. ➤ The authors hypothesizing that parasitism reduces the mobility of cockles (1) lowering the sediment disturbance and (2) providing new colonisable substrate (see Thomas et al. 1998)	Trait-mediated effects	(Mouritsen & Poulin 2010)
<i>Austrovenus stutchburyi</i>	Echinostome trematodes (genera <i>Curtuteria</i> + <i>Acanthoparyphium</i> )	Macroparasite: Trematoda	Reduced crawling activity (mean distance travelled) of highly infected cockles, meaning the disturbance of the upper sediment layer is relaxed ➤ Changes in the structure of the intertidal benthic community: increase of the total abundance of macroinvertebrates and of the species richness	Direct effects leading to trait-mediated effects	(Mouritsen & Poulin 2005)

			<p>Reduced burrowing capability</p> <ul style="list-style-type: none"> <li>➤ Changes in the structure of the intertidal benthic community: increase of the density of certain macroinvertebrates, modification of the taxonomical composition of the benthic community.</li> <li>➤ Changes in sediment characteristics and seabed elevation.</li> </ul>		
<b><i>Peringia (Hydrobia) ulvae</i></b>	<i>Cryptocotyle concave</i> or <i>Himasthla</i> spp. or <i>Maritrema</i> spp. Or <i>Microphallus claviformis</i>	Macroparasite: Trematoda	<p>No effect on sediment characteristics (organic content, median particle diameter, sorting coefficient, ...)</p> <p>Decrease of the chlorophyll-a content of the sediment</p> <p>Changes in the diatom community structure (epipelagic and epipsammic diatoms)</p> <p>Changes in the structure of the intertidal benthic community: increased abundances of some invertebrates while the abundances of others decreased</p> <ul style="list-style-type: none"> <li>➤ The authors hypothesizing that parasitism reduces the mobility of snails (Mouritsen &amp; Jensen 1994), lowering the sediment disturbance. Thus, there is a decrease of the release of nutrients leading to a decline in the microphytobenthos biomass. This is associated to a decrease of the diversity of some primary producers and an increase diversity of few secondary producers.</li> </ul>	Trait-mediated effects	(Mouritsen & Haun 2008)
<b><i>Ruditapes decussatus</i></b>	<i>Perkinsus olseni</i>	Microparasite: Myzozoa	<p>Reduced impact on iron mobilization (but this appears to depend on the clam density).</p> <ul style="list-style-type: none"> <li>➤ The authors hypothesizing that the infection impacts the physiology of clams with organisms being lethargic.</li> </ul>	Trait-mediated effects	(Simão et al. 2010)