

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

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

31 **1. INTRODUCTION**

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

37 In marine benthic ecosystems, the role of bioturbating species as EES is well established
38 (e.g., Krantzberg 1985; Levinton 1995; Lohrer et al. 2004; Mermillod-Blondin & Rosenberg
39 2006; Meysman et al. 2006). The process of bioturbation is described as any modification of the
40 sediment matrix, including interstitial waters, due to the activities of organisms living mainly in
41 or on the substratum (Kristensen et al. 2012). The locomotion, feeding and burrowing activities
42 of bioturbators substantially displace sediment particles. These sediment reworking activities
43 strongly affect the physical properties and geomorphology of sediments (e.g., Jones & Jago 1993;
44 Rhoads & Young 1970; Volkenborn et al. 2007a). Bioturbators also significantly enhance the
45 transport of water in sediments. This water input stimulates movements of solutes between pore-
46 and overlying waters, a process named bioirrigation (Kristensen et al. 2012). In particular,
47 sediment-dwelling organisms largely stimulate hydrological fluxes (Aller 1988; Volkenborn et al.
48 2012), since (1) biogenic structures, such as burrows, increase the surface of solute exchanges
49 between the sediment and the overlying and porewaters and (2) the ventilation of the burrow
50 stimulates advective irrigation. Thus, bioturbators play a key role in the biogeochemistry of
51 sediments (e.g., Aller 1982; Webb & Eyre 2004; Volkenborn, Hedtkamp, et al. 2007; Volkenborn
52 et al. 2012).

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

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

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

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

91 **2. DEFINITIONS**

92 **2.1. Type of bioturbators**

93 In this study, bioturbating species were restricted to epi- or endobenthic faunal organisms
94 influencing the physical structure (i.e. grain size, porosity, organic matter content, etc.) and/or
95 biogeochemical properties (i.e. nutrient and solute contents, redox status, etc.) of sediments. In
96 addition, this literature review was limited to invertebrates occurring in coastal environments,
97 including mangrove forests. Taking these restrictions into account, publications were searched in
98 Scopus using the terms “bioturbation”, “sediment reworking” and “bioirrigation”. Because of the
99 very high number of related papers, the search was further constrained to publications belonging
100 to the “environmental science” subject area for the items “sediment reworking” and
101 “bioirrigation”. A list of 4912, 732 and 296 publications for the terms “bioturbation”, “sediment
102 reworking” and “bioirrigation” were gathered (May 11th, 2018), respectively. Bioturbators were
103 taxonomically classified based on the World Register of Marine Species (WoRMS Editorial
104 Board 2018). Our search found a total of 176 bioturbating species studied in coastal environments
105 worldwide (Fig. 1; see ESM 1 for a full list of the bioturbators). Species belonging to the phyla
106 Arthropoda, Annelida and Mollusca were the most extensively studied, representing 37, 27 and
107 23 % of the total number of bioturbator species richness, respectively (Fig. 1).

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
111 unicellular organisms) and macroparasites (mainly helminths and arthropods) of bioturbating
112 species (Anderson & May 1979). For each of the bioturbating species identified in our first
113 search, a second search for publications mentioning parasites occurring in these organisms was
114 made by using the name of the bioturbating species in combination with the terms “parasite”,

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

122 **3. PARASITE SPECIES INFECTING BIOTURBATING ORGANISMS**

123 Of the 176 species of bioturbators identified, 55 species (i.e. 31 %) were reputed as being
124 parasitized with at least one macro- or microparasite species (Fig. 1). More specifically, 27 (i.e.
125 15 %) and 11 (i.e. 6 %) bioturbating species are infected with at least one macro- or microparasite
126 species only, respectively and 17 bioturbators (i.e 10 %) with both macro- and microparasites
127 (Fig. 1; see ESMs 2 and 3, respectively, for a full list of macro- and microparasites of
128 bioturbating species). There is an important disparity regarding the distribution of parasites across
129 the phyla of bioturbators, with highly parasitized, such as molluscs (51 % of the species
130 harbouring at least one parasite species), and others apparently less parasitized, for example
131 echinoderms (22 %) and arthropods (23 %) (Fig. 1). Similarly, the number of parasite species
132 identified per bioturbating host strongly differed among phyla (Fig. 2). Numerous studies were
133 devoted to bioturbating molluscs and highlighted that they were diversely parasitized, with on
134 average (\pm SE) 8.2 ± 2.9 macroparasite species (Fig. 2A) and 8.6 ± 2.8 microparasite species
135 (Fig. 2B) identified per individual species. To the contrary, only a few parasites species have
136 been documented in annelids, with on average 1.4 ± 0.3 macroparasite species (Fig. 2A) and 1.8
137 ± 0.4 microparasite species (Fig. 2B) identified per annelid species. Finally, there was also a large

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).

Commentaire [XdM1]: Mais est-il parasité ?

Commentaire [AD2]: Pas dans cette étude. Données sur microparasites ailleurs. Mais on met juste en relation, on a un effet bioturbateur density dependant qui pourrait être impacter par des parasites qui...

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_c) and community bioirrigation potential (BIP_c) 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_c 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_c

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_c 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_c and the BIP_c 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.

444 **Acknowledgments**

445 A.D. was supported by a doctoral grant of the French “Ministère de l’Enseignement Supérieur et de la
446 Recherche” (Université de Bordeaux - 2015/AUN/25). The authors are grateful to Dr. M.A. Goedknecht for
447 interesting comments on an earlier draft of the manuscript. Many thanks to Dr. R.B. Carnegie (Virginia
448 Institute of Marine Science) for editing the manuscript.

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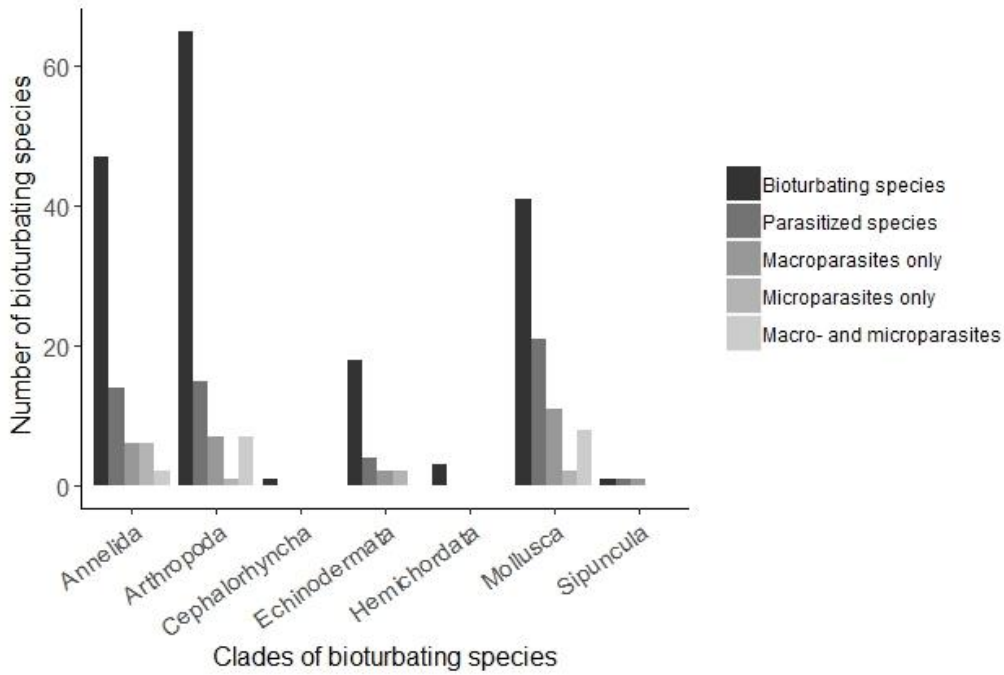
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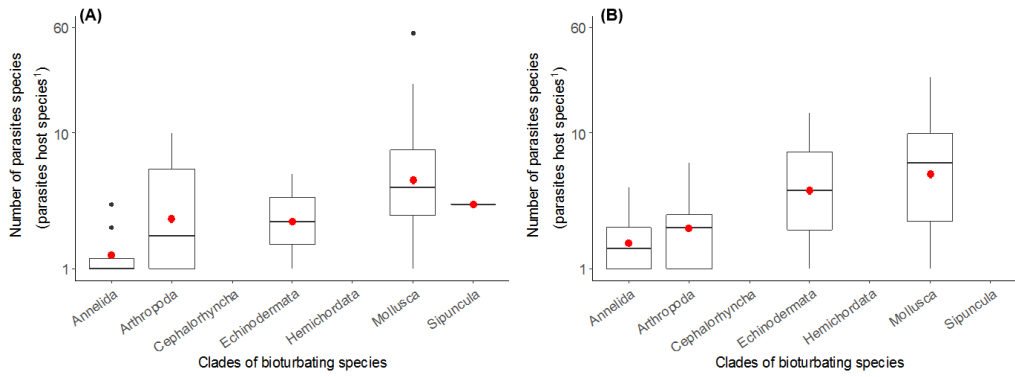
698 **Figure**



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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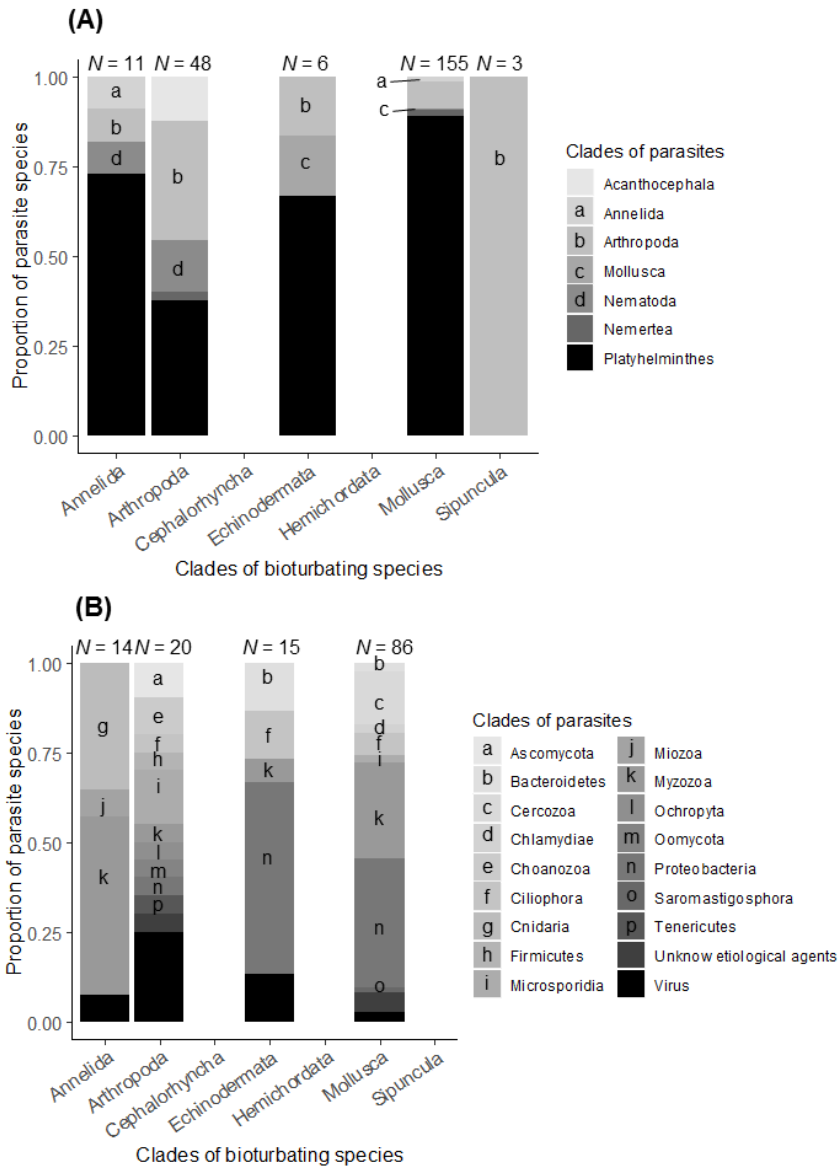
705 **Fig. 2** Number (log scale axis) of (A) macroparasite and (B) microparasite species identified per

706 bioturbating host species. Bioturbators are classified according to their taxonomic clade. The

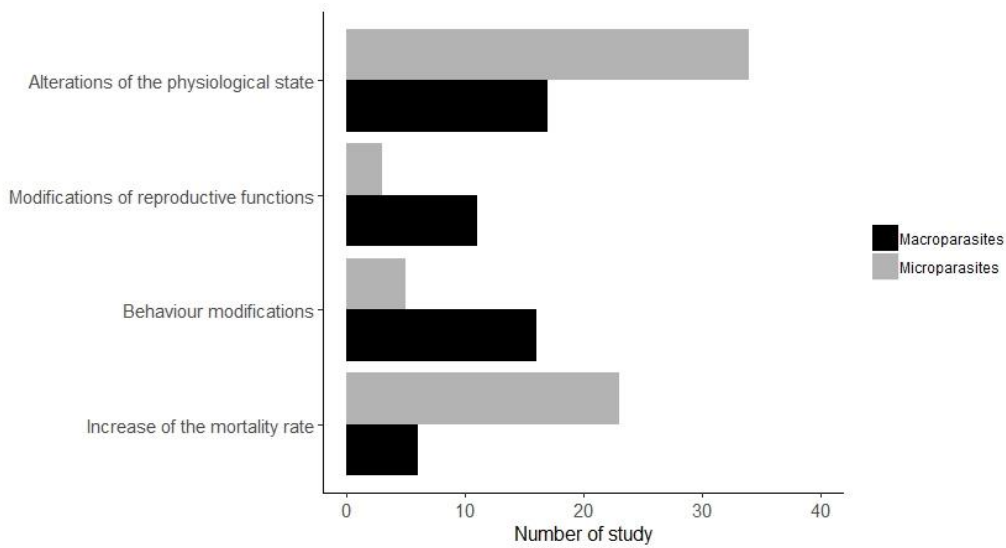
707 boxes represent the interquartile range, the black lines the median and the red dots the mean

708 number of parasites species in each clade of bioturbators.

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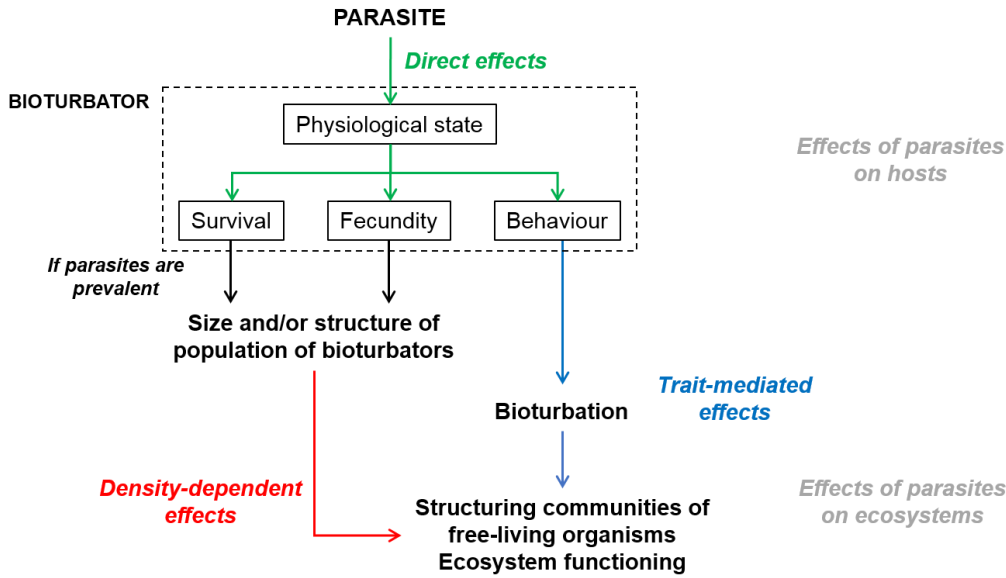
710
 711 **Fig. 3** Taxonomic types of (A) macroparasites and (B) microparasites reported in clades of
 712 bioturbating species. The total number of parasite species identified per clade of bioturbators is
 713 given (N).



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.

722



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.

Bioturbator	Parasite	Type of parasite	Effects of parasitism	Type of effect	References
<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 ₄ ⁺ , NO ₃ ⁻ , 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"> ➤ 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. ➤ Changes in sediment characteristics and seabed elevation. 		
<i>Peringia (Hydrobia) ulvae</i>	<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"> ➤ The authors hypothesizing that parasitism reduces the mobility of snails (Mouritsen & 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. 	Trait-mediated effects	(Mouritsen & Haun 2008)
<i>Ruditapes decussatus</i>	<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"> ➤ The authors hypothesizing that the infection impacts the physiology of clams with organisms being lethargic. 	Trait-mediated effects	(Simão et al. 2010)