

REVIEW

Influence of parasitism on bioturbation: from host to ecosystem functioning

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

KEY WORDS: Bioturbation · Parasitism · Ecosystem functioning · Behaviour modifications · Cascade effects

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1. INTRODUCTION

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

In marine benthic ecosystems, the role of bioturbating species as EES is well established (e.g. Krantzberg 1985, Levinton 1995, Lohrer et al. 2004,

Mermillod-Blondin & Rosenberg 2006, Meysman et al. 2006). The process of bioturbation is described as any modification of the sediment matrix, including interstitial waters, due to the activities of organisms living mainly in or on the substratum (Kristensen et al. 2012). The locomotion, feeding and burrowing activities of bioturbators substantially displace sediment particles. These sediment-reworking activities strongly affect the physical properties and geomorphology of sediments (e.g. Rhoads & Young 1970, Jones & Jago 1993, Volkenborn et al. 2007). Bioturbators also significantly enhance the transport of water in sediments. This water input stimulates movements of solutes between pore- and overlying waters, a pro-

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cess named bioirrigation (Kristensen et al. 2012). In particular, sediment-dwelling organisms largely stimulate hydrological fluxes (Aller 1988, Volkenborn et al. 2012) because (1) biogenic structures, such as burrows, increase the surface area for solute exchanges between the sediment and the overlying and porewaters and (2) the ventilation of the burrow stimulates advective irrigation. Thus, bioturbators play a key role in the biogeochemistry of sediments (e.g. Aller 1982, Webb & Eyre 2004, Volkenborn et al. 2007, 2012).

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

Among biotic factors influencing faunal EES, one major concern is the role played by parasites and associated infectious diseases. In the context of global climate change, it has been suggested that warmer conditions could increase the frequency and intensity of disease events (Marcogliese 2001, Harvell et al. 2002). For example, increase in seawater temperature enhances infection success of the trematode *Maritrema novaezealandense* in the amphipod host *Paracalliope novizealandiae*. A larger parasite burden is associated with a higher mortality rate of amphipods (Studer & Poulin 2013). Although many parasites and associated infectious diseases can produce mass mortality events in host populations (e.g. Jensen & Mouritsen 1992, Jonsson & Andé 1992, Fredensborg et al. 2004), parasites can also have a wide range of sub-lethal effects, especially on the physiological status and behaviour of infected organisms. For example, the health of parasitized organisms is often impaired as reflected in reduced growth rate and condition index (e.g. Thielgtes 2006, Dang et al. 2013, O'Connell-Milne et al. 2016). This pattern could be due to parasites directly interfering with food uptake (Flye-Sainte-Marie et al. 2007, Stier et

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

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

2. DEFINITIONS

2.1. Type of bioturbators

In this study, bioturbating species were restricted to epi- or endobenthic faunal organisms influencing the physical structure (i.e. grain size, porosity, organic matter content, etc.) and/or biogeochemical properties (i.e. nutrient and solute contents, redox status, etc.) of sediments. In addition, this literature review was limited to invertebrates occurring in coastal environments, including mangrove forests. Taking these restrictions into account, publications were searched in Scopus using the terms 'bioturbation', 'sediment reworking' and 'bioirrigation'. Because of the very high number of related papers, the search was further constrained to publications belonging to the 'environmental science' subject area for the items 'sediment reworking' and 'bioirrigation'. A list of 4912, 732 and 296 publications for the terms 'bioturbation', 'sediment reworking' and 'bioirrigation', respectively, were gathered (on 11 May 2018). Bioturbators were taxonomically classified based on the World Register of Marine Species (WoRMS Editorial Board 2018). Our search found a

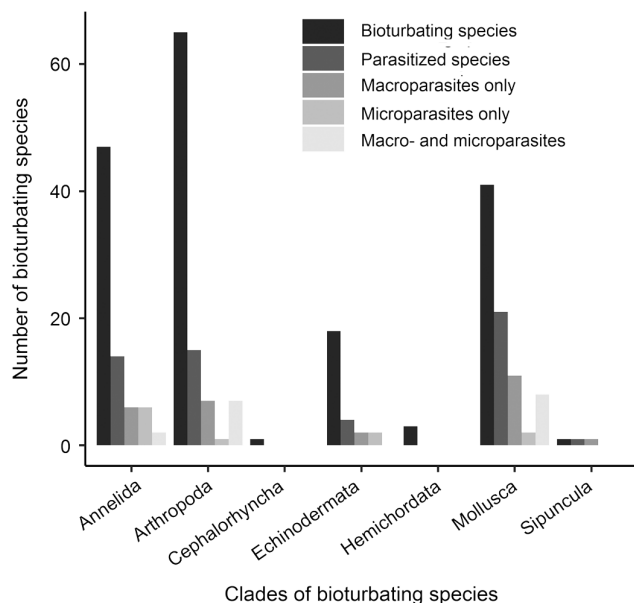


Fig. 1. Number of coastal bioturbating species commonly studied and number of parasitized bioturbators per taxonomic clade. Parasitized bioturbators are categorized as being infected with macroparasites only, microparasites only or both groups of parasites

total of 176 bioturbating species studied in coastal environments worldwide (Fig. 1; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m619p201_supp.pdf for a full list of the bioturbators). Species belonging to the phyla Arthropoda, Annelida and Mollusca were the most extensively studied, representing 37, 27 and 23% of the total number of bioturbator species richness, respectively (Fig. 1).

2.2. Type of parasites

Parasites were broadly defined as organisms exploiting other organisms (the hosts) and can include viruses (Combes 1995). This study investigated both microparasites (viruses and unicellular organisms) and macroparasites (mainly helminths and arthropods) of bioturbating species (Anderson & May 1979). For each of the bioturbating species identified in our first search, a second search for publications mentioning parasites occurring in these organisms was made by using the name of the bioturbating species in combination with the terms 'parasite', 'infection', 'bacteria' and 'virus'. In addition, we collected data related to prevalence, intensity and/or abundance of parasitic infections when available. In a sampled population, prevalence is defined as the

percentage of infected individuals, intensity of infection as the mean number of parasites per parasitized hosts, and abundance as the mean number of parasites per potential host (including both parasite-infected and uninfected) (Margolis et al. 1982). Furthermore, the influence of parasites on the physiological state, behaviour and bioturbating activity of their host was also recorded.

3. PARASITE SPECIES INFECTING BIOTURBATING ORGANISMS

Of the 176 species of bioturbators identified, 55 species (i.e. 31%) were reputed as being parasitized with at least 1 macro- or microparasite species (Fig. 1). More specifically, 27 (i.e. 15%) and 11 (i.e. 6%) bioturbating species are infected with at least 1 macro- or microparasite species only, respectively, and 17 bioturbators (i.e. 10%) are infected with both macro- and microparasites (Fig. 1; see Tables S2 & S3 for a full list of macro- and microparasites, respectively, of bioturbating species). There is an important disparity regarding the distribution of parasites across the phyla of bioturbators, with some phyla highly parasitized, such as molluscs (51% of the species harbouring at least 1 parasite species), and others apparently less parasitized, for example echinoderms (22%) and arthropods (23%) (Fig. 1). Similarly, the number of parasite species identified per bioturbating host strongly differed among phyla (Fig. 2). Numerous studies were devoted to bioturbating molluscs and highlighted that they were diversely parasitized, with on average (\pm SE) 8.2 ± 2.9 macroparasite species (Fig. 2A) and 8.6 ± 2.8 microparasite species (Fig. 2B) identified per individual mollusc species. In contrast, only a few parasite species have been documented in annelids, with on average 1.4 ± 0.3 macroparasite species (Fig. 2A) and 1.8 ± 0.4 microparasite species (Fig. 2B) identified per annelid species. Finally, there was also a large variability in parasite species richness per bioturbating species within a given phylum (Fig. 2). For example, the number of macro- and microparasites identified in molluscan bioturbators ranged from 1–55 and 1–26, respectively (Tables S2 & S3).

Several factors explain the discrepancy in parasite species richness recorded among and within the phyla of bioturbators. First, through a large meta-analysis, Kamiya et al. (2014) highlighted a positive association between parasite species richness and host body size, population density and geographical range. Second, differences in sensitivity and sus-

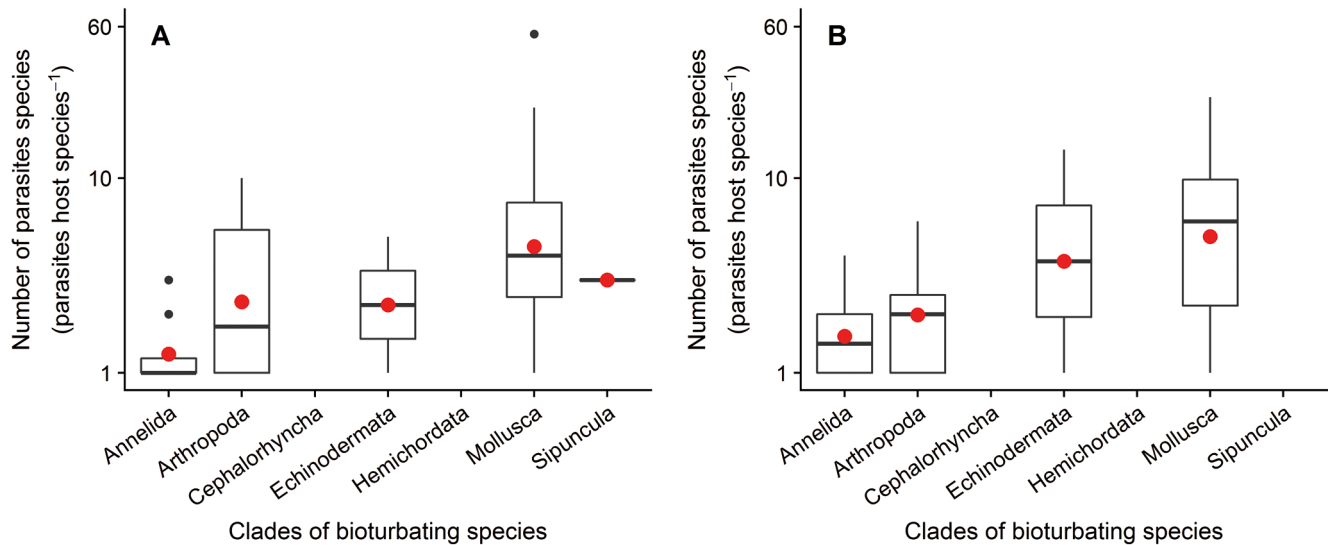


Fig. 2. Number (log-scale axis) of (A) macroparasite and (B) microparasite species identified per bioturbating host species. Bioturbators are classified according to their taxonomic clade. Boxes: interquartile range, black lines: median, and red dots: mean number of parasite species in each clade of bioturbators

ceptibility of bioturbating species to parasites could also explain interspecific variation in parasite species richness (Dang et al. 2009). However, we suggest that the large disparity in parasite species richness we observed among and within phyla of bioturbators is more likely related to a bias in research effort on parasites occurring in these organisms. Notably, the higher the economic value of a species, the more intensive are the research efforts to identify any potential pathogens or other stressors that could influence the sustainability of the production and/or the quality of the resource. For instance, numerous studies have been conducted in molluscs, a phylum of broad interest for fisheries and aquaculture, with the common cockle *Cerastoderma edule* and the Manila clam *Ruditapes philippinarum* being 2 important species. Although a small proportion of echinoderms have been described as being parasitized so far, there is a proportionally extensive literature on parasites infecting bioturbating species with commercial value, such as the sea cucumber *Apostichopus (Stichopus) japonicus*. In the same pattern, annelids are poorly exploited and have rarely been studied with regard to parasites and associated infectious diseases.

Bioturbators harbour a large diversity of macro- and microparasite species with large differences in the relative frequency among parasite phyla (Fig. 3, Tables S2 & S3). Platyhelminthes are the most common macroparasites infecting bioturbators, with 75% of the reported parasites species belonging to this phylum. Platyhelminthes infect molluscs, echinoderms and annelids, and to a lesser extent arthropods

(Fig. 3A). Platyhelminthes includes ~30000 species (Caira & Littlewood 2013), of which many are parasites (Dobson et al. 2008), such as members of the Trematoda or Cestoda. Moreover, it is one of the most important groups of marine parasites (Rohde 2005), which makes it unsurprising that infections with Platyhelminthes have been noted in bioturbators to such extent. In contrast, only a few studies highlighted the occurrence of parasitic annelids or nemertean in bioturbators. As these 2 groups mainly consist of free-living organisms, they represent minor parasite groups in marine environments (Rohde 2005). Regarding microparasites, 53% of the species identified are eukaryotes, and 36% are bacteria. Eukaryotic microparasites encompass a large diversity of phyla, while bacteria are mainly represented by Proteobacteria (Fig. 3B). Finally, a few viral syndromes and infectious diseases for which the etiological agent has not yet been fully characterized (e.g. various neoplasias, viscera ejection syndrome, brown muscle disease; Table S3) have been noted in bioturbating organisms as well.

4. DIRECT EFFECTS OF PARASITES ON BIOTURBATING SPECIES

Parasites have direct effects on their host, i.e. pathological impacts on individuals. The literature is limited concerning bioturbating species. Our literature survey documented that 376 macroparasites (N = 108 studies) and 188 microparasites and asso-

ciated infectious diseases (N = 132 studies) parasitize 55 coastal bioturbating species. Among these parasites, impacts on the host were recognized in 32% and 36% of the studies highlighting the occurrence of macro- and microparasites (and associated infectious diseases) in bioturbating species, respectively. These direct effects included alterations of physiological state (i.e. modulation of gene expression and cellular functions, initiation of inflammatory responses, tissue damages, etc.), modifications of reproductive functions (i.e. partial or total castration, changes in reproductive success,

etc.), increase of the mortality rate of the host and modifications of host behaviour (reduced activity levels, abnormal behaviours, etc.) (Fig. 4, Tables S2 & S3). More than 82% of the known impacts of macroparasites are due to Platyhelminthes (see Table S2). Most studies on microparasites focused on Proteobacteria (36%) and Myzozoa (30%) (Table S3). These patterns are in accordance with those showing that Platyhelminthes, Proteobacteria and Myzozoa are the most commonly described macro- and microparasites in bioturbating species (Fig. 3).

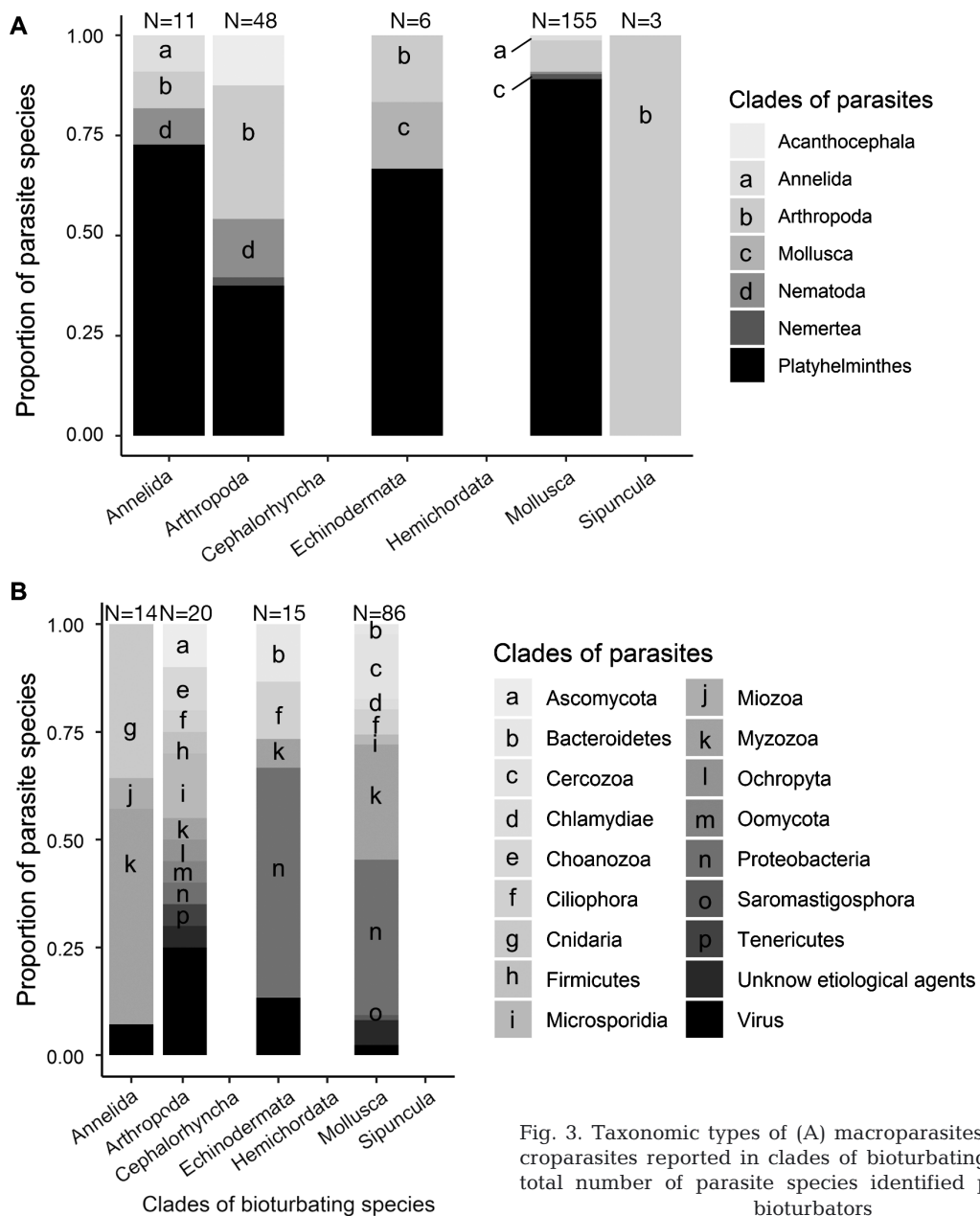


Fig. 3. Taxonomic types of (A) macroparasites and (B) microparasites reported in clades of bioturbating species. N: total number of parasite species identified per clade of bioturbators

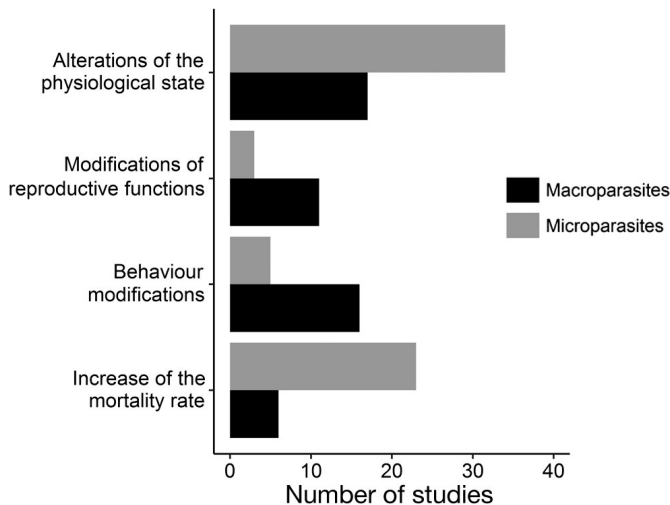


Fig. 4. Observed impacts of macro- and microparasites on bioturbating organisms. Alterations of physiological state: parasites influencing gene expression, cellular functions, physical integrity, growth rates of the host, etc. Modifications of reproductive functions: parasites reducing or increasing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

4.1. Impacts of parasites on bioturbator physiology

Numerous parasites are documented to impact the physiological state of their bioturbating host (Fig. 4). At the molecular scale, parasites interfere with gene regulation, thereby either up- or down-regulating their expression. For example, the trematode *Himasthla elongata* up-regulates the expression of several genes related to mitochondrial metabolism and oxidative responses in infected cockles *Cerastoderma edule*, a reputed bioturbator. These modulations in gene expression are considered to be a molecular response to parasites causing energetic losses and oxidative stress in cockles (Paul-Pont et al. 2010). Parasites can also impair the host's physical integrity if physiological alterations are concomitant with physical injuries. While developing and residing inside their host, parasites cause significant histopathological damages to host tissue (Lauckner 1980, Robaldo et al. 1999, Dang et al. 2008). For instance, the protozoan parasites *Perkinsus* spp. induce histological lesions in gills, digestive gland and gonad gland of the sand gaper clam *Mya arenaria* (McLaughlin & Faisal 1998). As the gills and the digestive gland play a key role in nutrient absorption, such tissue alterations are expected to be energetically costly for the host and may

have direct repercussions on its growth. In fact, a caging experiment conducted at 2 sites affected by perkinsosis along the northeast Atlantic coast of France demonstrated that growth rates of the bioturbators *Ruditapes decussatus* and *R. philippinarum* are significantly compromised as a result of *Perkinsus* spp. infections (Dang et al. 2013). Macroparasites impacting the growth of their bioturbating host have also been broadly documented (e.g. Mouritsen & Jensen 1994, Smith et al. 2008, Pascal et al. 2016). The mud shrimp *Upogebia* cf. *pusilla* displays reduced size when infected with the epicaridean isopod *Gyge branchialis* (Pascal et al. 2016). The negative effect of the parasite is probably not related to histological lesions but to the parasite directly feeding at the expense of its host (Tucker 1930). By doing so, the parasite strongly affects host energetics (Hughes 1940) and consequently its physiological state (Williams & Boyko 2012). Parasites do not always diminish their host's growth rate. The bioturbators *Peringia (Hydrobia) ulvae* infected with trematodes grow to larger sizes than their unparasitized conspecifics (Mouritsen & Jensen 1994). Such cases of gigantism have been reported in several host-parasite association involving parasitic castrators (Pearre 1976, Sluiter et al. 1980, de Montaudouin et al. 2003).

4.2. Impacts of parasites on bioturbator reproduction

Evidence for alterations to host fecundity are common and has been found in 31% and 6% of the studies on effects of macro- and microparasites, respectively (Fig. 4). Macroparasites, and especially digenean trematodes (Platyhelminthes), are often associated with impairment of the host reproductive function (Table S2). Digenean trematodes have complex life cycles. One of the stages, called sporocyst or rediae according to digenean species, is fundamentally damaging for the fecundity of the host (Lauckner 1980, 1983). Digenean trematodes infect the digestive gland and/or the gonad of their host (Probst & Kube 1999), causing partial or complete castration via mechanical or chemical damages to host reproductive tissue (Hurd 1990). For instance, infection with trematodes leads to an important reduction of the penis size of the mud snail *Peringia (Hydrobia) ulvae* and to almost non-existent oviposition in females (Mouritsen & Jensen 1994). Castration is not only caused by digenean trematodes; crustacean parasites like epicaridean isopods also have strong influences on the fecundity of their bioturbator hosts

(Tucker 1930, Dumbauld et al. 2011). However, castration of hosts by isopods seems to be related to the parasite lowering the condition index of the host and/or interfering with the secretion of host reproductive hormones (Reinhard 1956, Williams & Boyko 2012). In sharp contrast, some parasites such as microsporidians can enhance the fecundity of their bioturbating host (Mautner et al. 2007), but these examples are more rare.

4.3. Impacts of parasites on host mortality

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

Among macroparasites, digenean trematodes have been recognized to deeply affect the survival of their hosts, at time causing collapses of natural populations. For instance, the trematodes *Microphallus claviformis* and *Maritrema subdolum* are considered to be the main cause of the 40% population decline of the bioturbating mud snail *P. ulvae* observed in the Danish Wadden Sea during spring 1990 (Jensen & Mouritsen 1992). Digenean trematodes can also modulate the population size structure of their bioturbating hosts because of differential susceptibility to parasitism of small and large organisms. An extensive field survey conducted in Arcachon Bay, France, over the years 1998–1999 indicated an important decline of the largest mud snails *P. ulvae* during the winter 1998–1999, which were also the most parasitized (up to 100%). A laboratory experiment conducted in parallel highlighted higher mortality rates of parasitized organisms compared to unparasitized individuals. Together, these results demonstrate that digenean parasites substantially influence the population size structure of the bioturbator *P. ulvae* (de Montaudouin et al. 2003).

4.4. Impacts of parasites on bioturbator behaviour

Parasites can have more subtle effects on their hosts such as behaviour alteration. Such effects have been reported in 46% and 11% of the studies evaluating the influence of macro- and microparasites on their bioturbating hosts, respectively (Fig. 4, Tables S2 & S3).

Modifications of the behaviour of the host can be a side effect of parasitism, that is, phenotypic alterations with no adaptive value for either the parasite or the host (Ewald 1980). Few examples report how parasites impair the behaviour of bioturbators and their activities (Fig. 4, Tables S2 & S3). For instance, mud snails *P. ulvae* infected with trematode parasites experience modifications of locomotory behaviour, with parasitized snails moving slower and crawling over shorter distances compared to uninfected organisms (Mouritsen & Jensen 1994). This behavioural modification could be a side effect of parasites interfering with the host energy allocation. Indeed, mud snails exhibited increased growth rates ('gigantism'). Since locomotory activity is a highly costly behaviour, it has been suggested that parasites stimulating host growth reduce the energy available for the host to crawl (Mouritsen & Jensen 1994).

Regarding the impacts of microparasites on host behaviour, the literature is even more scarce, with altered behaviour recognized in only 11% of the studies documenting the occurrence of microparasites or infectious diseases in bioturbators (Fig. 4, Table S3). Given the large influence of microparasites on the physiological status of their hosts (Table S3), it is likely that microparasites have side effects on host behaviour as well. For instance, brown muscle disease causes a serious atrophy of the posterior adductor muscle of the Manila clam *R. philippinarum* (Dang et al. 2008). Any alterations to this muscle are expected to disturb clam feeding and respiration, as well as locomotion. Such modifications of locomotory activity were observed in Manila clams infected with the protozoan *Perkinus olseni*. This parasite promotes the emergence of *R. philippinaum* at the sediment surface and limits its ability to re-burrow in thermally stressful conditions (Nam et al. 2018).

Modifications of the behaviour of the host can also be adaptive manipulations. This typically involves parasites with complex life cycles as host behaviour modifications are expected to enhance the transmission success of parasites (Combes 1991, Lafferty 1999, Moore 2002). One of the most detailed examples of adaptive manipulation in bioturbators involves the New Zealand cockle *Austrovenus stutchburyi*, which

is commonly found at the sediment surface of tidal flats, with organisms showing difficulty in burrowing (Thomas & Poulin 1998). Surfacing cockles (i.e. in abnormal position) are heavily infected with the trematode *Curtuteria australis*, compared to buried cockles (i.e. in normal position) (Thomas & Poulin 1998). The trematode needs the cockle to be eaten by marine birds to complete its life cycle, which is facilitated by its altered behaviour at the surface of the sediment. Together, these results suggest that the parasite alters the cockle phenotype to enhance its own transmission success (Thomas & Poulin 1998).

5. INFLUENCE OF PARASITES ON BIOTURBATION ACTIVITY AND ECOSYSTEM FUNCTIONING

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

5.1. Trait-mediated effects

Of the 215 studies evidencing the occurrence of 376 macro- and 188 microparasites in 55 bioturbating species over 176 bioturbators commonly studied in coastal environments, 82 studies showed that parasites can impair the physiological state, reproductive capacity, behaviour and/or the mortality of their bioturbating hosts. Of these studies, only 21 studies depicted effects of parasites on the behaviour of their bioturbating host. Within these 21 studies, just 7 focused on the link between the occurrence of parasites and their role in modulating the bioturbating activity of their hosts, with potential outputs on the community of free-living organisms and ecosystem functioning, the so-called trait-mediated effects (Table 1). Nevertheless, these few papers strongly support the idea that parasites can act as EES themselves by modifying functional traits of their host involved in bioturbation activities (Thomas et al.

1999) (Table 1, Fig. 5). For instance, Pascal (2017) monitored the influence of the epicaridean parasite *G. branchialis* on the behaviour of the mud shrimp *U. cf. pusilla* through video recording. Pascal (2017) defined 4 main behavioural states for the mud shrimp species as 'resting', 'burrowing', 'ventilating' and 'walking'. 'Burrowing' and 'ventilating' are the 2 behaviours associated with bioturbation activities of the mud shrimp. Pascal (2017) demonstrated that parasitized mud shrimp spend 1.8- and 2.3-fold less time 'burrowing' and 'ventilating' than healthy organisms. These behavioural modifications are associated with negative impacts on the intensity of the bioturbating activity: the sediment-reworking rate of parasitized organisms is 4.6-fold lower and the bioirrigation rate 2.9-fold lower compared to unparasitized organisms. As a result, biogeochemical fluxes are also strongly modified. The total oxygen and nitrate uptake are reduced, and there is a diminished release of ammonium at the sediment-water interface. These results suggest that parasitized mud shrimp have a much lower influence on organic matter mineralization and nutrient turnover than uninfected organisms (Pascal 2017). At the ecosystem level, these findings can be highly relevant (Fig. 5) as (1) mud shrimp can attain high densities (e.g. Nates & Felder 1998) and (2) epicarideans are widespread in natural populations of mud shrimp (Smith et al. 2008, Pascal et al. 2016).

Mouritsen & Poulin (2005, 2010) addressed the influence of parasitism on animal community structure (Table 1). Over a long-term field experiment, they highlighted a positive relationship between macrozoobenthic species richness (and density) and the presence of parasitized cockles *Austrovenus stutchburyi* (Mouritsen & Poulin 2005). A similar pattern was reported at a larger spatial scale (Mouritsen & Poulin 2010). The bivalve *A. stutchburyi* harbours multiple parasites, some of which can manipulate the behaviour of cockles to facilitate transmission. These behaviour modifications can also change the role of cockles as EES. Heavily parasitized organisms are more likely found at the sediment surface than buried in the sediment and show reduced ability to rebury in the sediment (Thomas & Poulin 1998). Moreover, heavily parasitized cockles exhibit reduced crawling activity compared to moderately infected conspecifics (Mouritsen & Poulin 2005). Cockles exhibit important reworking activity in subsurface sediments, where they also strongly impact nutrient cycling and the production of primary producers (Sandwell et al. 2009). Mouritsen & Poulin (2005, 2010) suggested that the positive association

Table 1. Summary of the literature evaluating the influence of parasitism on the activity and the role as ecosystem engineer of bioturbating species. TOU: total oxygen uptake, dSi: dissolved silicate

Bioturbator	Parasite	Type of parasite	Effects of parasitism	Type of effect	Source
<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 hypothesize that the parasite interferes with the ability of cockles to burrow (Thomas & Poulin 1998), modifying their role as autogenic 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 hypothesize 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 > Reduced burrowing capability > Changes in the structure of the intertidal benthic community: increase of the density of certain macroinvertebrates, modification of the taxonomic composition of the benthic community > Changes in sediment characteristics and seabed elevation	Direct effects leading to trait-mediated effects	Mouritsen & Poulin (2005)
<i>Peringia (Hydrobia) ulvae</i>	<i>Cryptocotyle concave</i> , <i>Himasthla</i> spp., <i>Mari-trema</i> spp. or <i>Microphallus claviformis</i>	Macroparasite: Trematoda	No effect on sediment characteristics (organic content, median particle diameter, sorting coefficient, etc.) Decrease of the chlorophyll <i>a</i> content of the sediment Changes in the diatom community structure (epipellic and epipsammic diatoms) Changes in the structure of the intertidal benthic community: increased abundances of some invertebrates, while the abundances of others decreased > The authors hypothesize 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 with a decrease of the diversity of some primary producers and an increase in diversity of few secondary producers	Trait-mediated effects	Mouritsen & Haun (2008)
<i>Ruditapes decussatus</i>	<i>Perkinsus olseni</i>	Microparasite: Myxozoa	Reduced impact on iron mobilization (but this appears to depend on the clam density). > The authors hypothesize that the infection affects the physiology of clams, with infected organisms being lethargic	Trait-mediated effects	Simão et al. (2010)

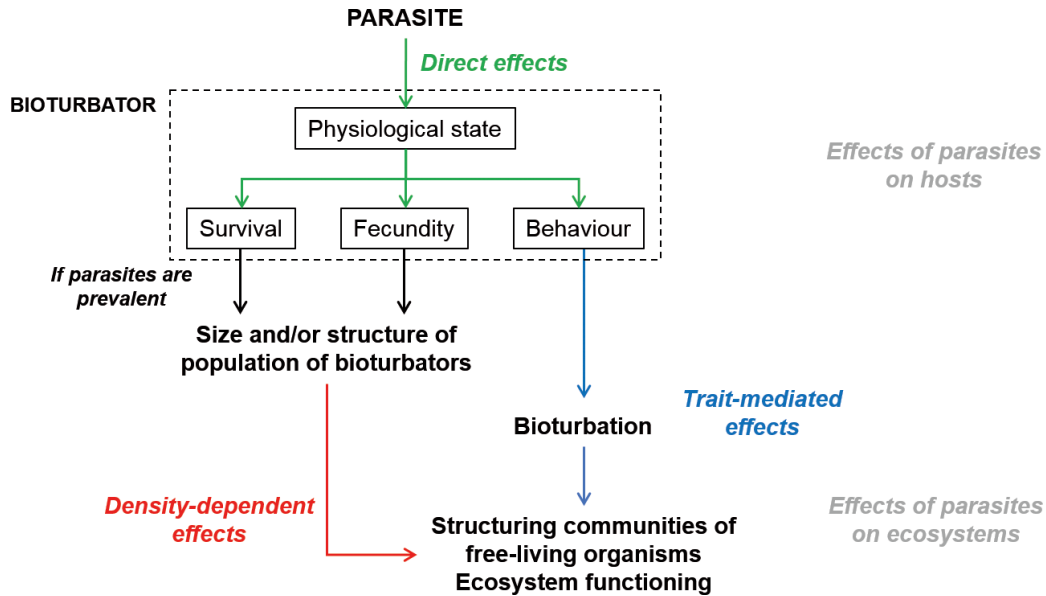


Fig. 5. Impacts of parasites on bioturbating organisms and on their influence as ecosystem engineer species (EES). The behaviour of bioturbating organisms conditions the intensity of their bioturbation and their role as EES when they are abundant. Parasites can significantly alter the physiological state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

between macrozoobenthic species richness and parasitized cockles could be related to (1) a lower disturbance of the sediment via parasites reducing bioturbating activities of cockles and (2) surfacing cockles acting as physical ecosystem engineers (Jones et al. 1997, Thomas et al. 1998).

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

5.2. Density-mediated effects

The effect of bioturbators as EES relies on their activities but also on their abundance. Therefore, para-

sites can affect ecosystem functioning via density effects on major EES (Poulin 1999, Mouritsen & Poulin 2002) as bioturbators (Fig. 5). We reported several examples of parasites reducing the fecundity and/or the survival of their host (see Tables S2 & S3). The intensity of the bioturbation activity can vary according to population biomass and bioturbator density (e.g. Dupont et al. 2006, Sandwell et al. 2009, Braeckman et al. 2010), with potential impacts on ecosystem functioning (Fig. 5). As an illustration, Lohrer et al. (2004) evaluated the influence of a declining density of the irregular urchin *Echinocardium* sp. on nutrient cycling. They highlighted a positive influence of density of urchins on ammonium efflux and on oxygen, nitrite and nitrate and phosphorus influxes at the sediment-water interface. These nutrients being of fundamental importance for primary production, the microphytobenthic primary production increased with the *Echinocardium* sp. density. Considering the intricate link between bioturbators and microphytobenthos, one would expect that the reduction of the abundance of bioturbators related to parasitic infection could be ecologically relevant (Fig. 5).

Parasites can also interfere with the engineering role of their bioturbating hosts by shaping the size structure of their host populations. Concomitantly, the magnitude of the bioturbation activities of organisms depends on their individual size (Bachteram et al. 2005, Bosch et al. 2015). In a laboratory experi-

ment, Bosch et al. (2015) evaluated the influence of the nereid polychaete *Alitta (Neanthes) succinea* biomass on nitrogen cycling by manipulating the density and size of worms. They found that at similar density, large polychaetes (high biomass) stimulated nitrogen solute fluxes at the sediment-water interface to a greater extent than small worms (low biomass). Moreover, large organisms enhanced solute diffusion in deeper horizons of the sediment column compared to small worms. This pattern is probably the result of larger organisms building larger and deeper burrows than small organisms (Davey 1994), which would boost bioirrigation processes (Mermillod-Blondin et al. 2004, Bosch et al. 2015). These examples suggest that parasites could also theoretically interfere with the role of bioturbators in nutrient cycling and/or in shaping benthic environments (via reduction of sediment reworking) by modifying the size structure of the population of their bioturbating hosts (Fig. 5).

Finally, it should be considered that parasites can have both trait-mediated and density effects on their bioturbating host. In particular, we documented that the bioturbators identified in this review host a large variety of parasites with complex life cycles (Tables S2 & S3), many of which need to be trophically transmitted (i.e. Platyhelminthes or Acanthocephala) to definitive hosts to reproduce. To facilitate their trophic transmission, parasites can drive significant modifications of behaviour, similar to those reported previously for the cockle *A. stutchburyi* (i.e. reduced ability to bury and lower crawling activity). Therefore, such parasite species induce changes in bioturbating host traits and density, altering the functional role of the bioturbator host and ecosystem properties.

5.3. What next?

Over the last years, there has been a growing interest in developing indices providing estimations of the impact of the benthic community on the functioning of marine ecosystems. Among them, community bioturbation potential (BP_c) and community bioirrigation potential (BIP_c) are 2 metrics estimating the influence of benthic organisms on sediment mixing and solute exchanges, respectively (Solan et al. 2004, Renz et al. 2018, Wrede et al. 2018). Both of these scoring systems rely on a classification of marine infauna based on the (1) abundance, (2) biomass and (3) functional traits of organisms. For instance, the BIP_c categorized species according to their feeding type, burrow type

and burrowing depth. Our literature review highlights that parasites modulate the abundance, biomass and functional traits of their bioturbating hosts. For instance, mud shrimp *U. cf. pusilla* parasitized with the bopyrid *G. branchialis* show reduced ventilation rates and built smaller burrows than uninfected organisms. These changes have consequences on the influence of mud shrimp in driving solute exchanges at the sediment-water interface (Pascal 2017). Thus, one would expect that the application of the BIP_c on macrofaunal communities dominated by the mud shrimp *U. cf. pusilla* without taking into account the presence of this parasite results in overestimation of the BIP_c of such communities, with potential biases in the comparison of ecosystems. In our opinion, a successful application of trait-based indices such as the BP_c and the BIP_c would benefit by taking into account (1) the impact of parasites on their bioturbating hosts and (2) the prevalence of parasites in the community of bioturbators.

6. CONCLUSION

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

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

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