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Protecting the Commons: the use of Subtidal Ecosystem Engineers in Marine Management

ULRIKE BRAECKMAN[a,*], MARIJN RABAUT[a], JAN VANAVERBEKE[a], STEVEN DEGRAER[b,a] and MAGDA VINCX[a]
[a] *Ghent University, Department of Biology, Marine Biology Research Group, Krijgslaan 281/S8, 9000 Ghent, Belgium*
[b] *Royal Belgian Institute of Natural Sciences, Operational Directorate Nature, Gulledelle 100, 1200 Brussels, Belgium*

ABSTRACT

1. Biodiversity conservation often focuses on threatened or rare species. While this structural asset of biodiversity is indeed important, the functional diversity aspect has to be considered as an even more important criterion for marine management and conservation. This paper explores the use of functionally important ecosystem engineers in North Sea management approaches.

2. An overview of several North Sea ecosystem engineering species shows that ecosystem engineers such as bulldozing echinoderms and burrowing shrimps as well as bio-irrigating polychaetes are bound to receive more attention in the management of marine areas than they do now, given their important structuring aspect in associated fauna and implications for seafloor ecosystem functioning.

3. The use of ecosystem engineers could contribute considerably to the concept of Ecosystem-Based Management in the marine realm. This is clearly illustrated in the present case study of the bio-irrigating polychaete *Lanice conchilega*. Since this species manifests both autogenic and allogenic ecosystem engineering properties, the management of human activities that affect common species such as *L. conchilega* reefs can enhance protection of the entire local ecosystem. In the North Sea, some commonly occurring ecosystem engineers and their engineered habitat can be protected under the European Habitats Directive and the EU Marine Strategy Framework Directive.
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ECOSYSTEM ENGINEERS AND MARINE MANAGEMENT

In recent decades, much debate has been devoted to the relationship between biodiversity and ecosystem functioning (Naeem *et al*., 1994, 2009; Tilman, 1999; Emmerson *et al*., 2001; Loreau *et al*., 2001). While most ecologists now agree that it is functional biodiversity that matters for ecosystem functioning (Naeem *et al*., 2012), nature conservation is still lagging somewhat behind in the sense that the focus is often laid upon protection of

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*Correspondence to: U. Braeckman, Ghent University, Department of Biology, Marine Biology Research Group, Krijgslaan 281/S8, 9000 Ghent, Belgium. E-mail: Ulrike.Braeckman@UGent.be

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threatened or rare species (Grenyer *et al*., 2006). Nevertheless, there is an increasing amount of evidence that more common species, including ecosystem engineers (Jones *et al*., 1994, 1997; Wright and Jones, 2006), have disproportionate effects on the functioning of the ecosystem and on the provision of services.

An ecosystem engineer is defined as an organism that directly or indirectly modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials (Jones *et al*., 1994). In doing so, it modifies, maintains and creates habitats. Autogenic engineers (e.g. corals or trees) change the environment via their own physical structures (i.e. their living and dead tissues), while allogenic engineers (e.g. woodpeckers, beavers, earth worms) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means.

The ecological engineering concept has been widely discussed for terrestrial environments (see examples in Hastings *et al*., 2007). Moreover, there is substantial evidence that the concept is as important in marine environments. In soft bottom marine environments, allogenic ecosystem engineering is often performed by macrobenthic (benthic organisms > 1 mm) bioturbators (*sensu* Kristensen *et al*., 2012). Through redistribution of high quality organic matter (Graf, 1989; Levin *et al*., 1997), oxygen and toxic metabolites in the sediment (Kristensen and Kostka, 2005), bioturbation may influence the distribution of macrofauna (Zühlke *et al*., 1998; Volkenborn and Reise, 2007) and nematodes (Reise, 1985), and the sediments surrounding burrows support microbial communities that differ from those in the surficial sediments (Kristensen and Kostka, 2005; Papaspyrou *et al*., 2005; Laverock *et al*., 2010). In addition, bioturbators stimulate biogeochemical processes along the burrow walls resulting in an increase of nutrient fluxes to the water column (Stief, 2013). At the same time, higher coupled nitrification–denitrification rates along burrow walls give rise to an important release of dinitrogen gas from the sedimentary nitrogen cycle (Stief, 2013), thereby counteracting nitrogen eutrophication (Seitzinger, 1988). Common burrow-ventilating ecosystem engineers such as *Arenicola marina* and *Hediste diversicolor* might even control the entire nutrient budget in Danish fjords (E. Kristensen pers. comm., 2013). Examples of common allogenic ecosystem engineers in the subtidal North Sea are the burrowing brittlestar *Amphiura filiformis* (Figure 1(a)) (Solan and Kennedy, 2002; Gilbert *et al*., 2003; Vopel *et al*., 2003), burrowing shrimps such as *Callianassa*

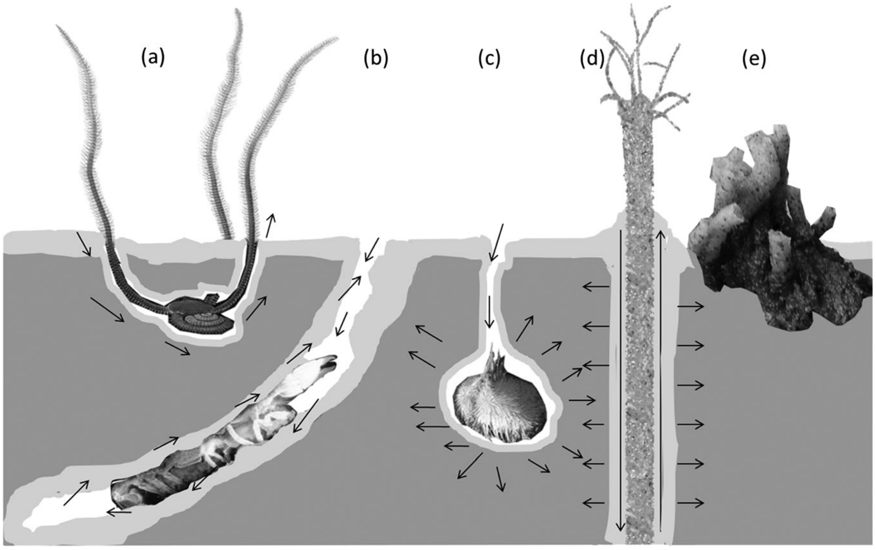

Figure 1. Common ecosystem engineer species in North Sea bottom: (a) *Amphiura filiformis* (photo courtesy Michigan Science Art); (b) *Callianassa subterranea* (photo courtesy www.blueanimalbio.com); (c) *Echinocardium cordatum* (photo courtesy D. Busti); (d) *Lanice conchilega*; and (e) *Sabellaria spinulosa* (photo courtesy SAMS). Arrows indicate the directions in which the ecosystem engineer affects porewater flow.

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spp. (Figure 1(b)) and *Upogebia* spp. (Forster and Graf, 1995) and the bulldozing sea urchin *Echinocardium cordatum* (Figure 1(c)) (Osinga *et al*., 1995; Sandnes *et al*., 2000; Caradec *et al*., 2004) (Table 1).

Macrobenthic autogenic ecosystem engineers may interact positively with the surrounding infauna (Zühlke *et al*., 1998) and with post-settlement juveniles of commercially important fish species (Watling and Norse, 1998), through the construction of physical structures (e.g. polychaete tubes) that provide shelter from predation. In addition, these structures modify the hydrodynamic flow regime near the sea floor, with potentially significant ecological effects on sedimentation patterns, food availability, larval and/or juvenile recruitment, growth, and survival. A good example of an autogenic ecosystem engineer is *Sabellaria spinulosa* (Figure 1(e), Table 1), a filter-feeding tube-building polychaete commonly occurring along the European coasts (Holt *et al*., 1998). Dense aggregations of this species can reach up to 60 cm high (Holt *et al*., 1998), and reefs can considerably influence the benthic community structure (Holt *et al*. (1998) and references therein).

The influence of ecosystem engineers might also be negative, by depleting food resources (Ólafsson *et al*., 1993) or by direct physical disturbance due to regular bioturbation (Austen and Widdicombe, 1998; Schratzberger and Warwick, 1999).

The above mentioned relatively long-lived ecosystem engineers are all sensitive to mechanical disturbance (e.g. bottom trawling) and/or pollution (Bergman *et al*., 2004; Eggleton *et al*., 2007). The consequences of disturbance of ecosystem engineers have far-reaching impacts on the ecosystem (Solan *et al*., 2004). Through alteration of their densities, not only may biodiversity associated with these ecosystem engineers decline (Bergman *et al*., 2004; Widdicombe *et al*., 2004), but also biogeochemical processes can be affected (Duplisea *et al*., 2001; Allen and Clarke, 2007; Olsgard *et al*., 2008). Loss of allogenic ecosystem engineers will possibly have consequences for oxygenation and metabolite removal that result in a decrease in favourable niches for other infauna (Austen and Widdicombe, 1998; Austen *et al*., 1998, 2003; Widdicombe and Austen, 1998, 1999; Widdicombe *et al*., 2004).

Thus, by reshaping the landscape, ecosystem engineers change the abiotic context upon which biotic interactions heavily depend (Byers *et al*., 2006). Owing to their functional characteristics, ecosystem engineers can exert a strong influence on ecosystem properties that exceeds what may be expected based on their relative abundance alone (Hooper *et al*., 2005). The value of the ecosystem engineering concept therefore lies in its ability to formalize (1) interactions among organisms that are mediated by the physical environment (Wilby, 2002), and (2) the relationship between biodiversity and ecosystem functioning, rendering it an important contribution to Ecosystem-Based Management (EBM). Indeed, EBM is defined as an environmental management approach that recognizes the full array of interactions within an ecosystem, including humans, rather than considering single issues, species, or ecosystem services in isolation (Christensen *et al*., 1996; McLeod *et al*., 2005). Because of the cascading effects of ecosystem engineers on the wider ecosystem, it is important to consider this group of common, but functionally important species (Godet *et al*., 2008) as conservation targets (Crain and Bertness, 2006), complementary to the larger, epibenthic and rarer species that traditionally receive more attention in conservation.

In what follows, we will discuss the potential use of ecosystem engineers in EBM of the North Sea floor, with special emphasis on Natura 2000 and the European Marine Strategy Framework Directive. The specific example of the conservation status of the tube-building polychaete *Lanice conchilega* is elaborated as a case study, since this species manifests both autogenic and allogenic ecosystem engineer characteristics.

LEGISLATIVE TOOLS TO PROTECT ECOSYSTEM ENGINEERED HABITATS

Currently, two key legal instruments of the European Union exist for the protection of (common) marine functionally important species. First, the Interpretation Manual (EUR 27; European Commission DG Environment 2003, 2006, 2007) to the EU Habitats Directive allows protection of aggregating ecosystem engineered habitats as reefs (Habitat Type 1170).

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Table 1. Overview of ecosystem engineering properties of common ecosystem engineers in the North Sea, with ´+´, ´-´ and ´?´ indicating, respectively, a positive, negative and unknown effect

Species	***Amphiura filiformis***	***Echinocardium cordatum***	***Callianassa* spp.**	***Lanice conchilega***	***Sabellaria spinulosa***
densities in North Sea	up to 3500 ind. m^{-2}[a]	up to 340 ind. m^{-2}[b]	up to 180 ind. m^{-2}[b]	up to 43 000 ind. m^{-2}[b]	up to 3500 ind. m^{-2}[c]
affected sediment depth (cm)	4[a]	6.5–20[d]	25- >90[e]	± 10, max. 80[f]	no (epibenthic)
sediment reworking mode	bioturbation incl. bio-irrigation	bioturbation incl. bio-irrigation	bioturbation incl. bio-irrigation	sedentary, mostly bio-irrigation	no bioturbation
effect on sediment stability	-[g]	-[h]	-[g]	+[i]	+[c]
stimulation of O_2 flux into bottom	180% (natural populations)[j]	109% (per ind.)[k]	117-240% (natural populations)[l]	200% (per ind.)[m]	?
stimulation of nitrogen cycling	yes[n]	yes[k]	3-4x (natural populations)[o]	2x (per ind.)[m]	?
effect on infauna	?	+ nematodes[p], no[k] or –[h] effect on macrofauna	- meiofauna and macrofauna[q]	+ nematodes[r] macrofauna[s]	?
effect on epifauna	?	?	?	+ macrofauna[s], juvenile flatfish[t]	+ epifauna and crevice infauna[c]
ecosystem engineering effect	allogenic	allogenic	allogenic	allogenic + autogenic	autogenic

[a] Eggleton *et al*. (2007);
[b] Rees *et al*. (2007);
[c] Hendrick and Foster-Smith (2006);
[d] Van Noort and Kraay (1992); Degraer *et al*. (2006);
[e] Riisgaard and Larsen (2005);
[f] Carey (1987); Holt *et al*. (1998);
[g] Amaro *et al*. (2007);
[h] Lohrer *et al*. (2008);
[i] Rabaut *et al*. (2009);
[j] Vopel *et al*. (2003);
[k] Lohrer *et al*. (2004);
[l] De Wilde *et al*. (1984); Witbaard and Duineveld (1989); Forster and Graf (1995); Webb and Eyre (2004);
[m] Braeckman *et al*. (2010);
[n] Lindqvist *et al*. (2009); Wood *et al*. (2009);
[o] Howe *et al*. (2004); Webb and Eyre (2004); D'Andrea and DeWitt (2009);
[p] Dashfield *et al*. (2008);
[q] Pillay *et al*. (2007) and references therein;
[r] Zühlke *et al*. (1998); Braeckman *et al*. (2011a, b);
[s] Rabaut *et al*. (2007, 2008); Van Hoey *et al*. (2008);
[t] Rabaut *et al*. (2010, 2013);

Second, the EU Marine Strategy Framework Directive (2008/56/EC) ('MSFD') specifically refers to Sea-Floor Integrity (Descriptor 6 of the Directive). According to the MSFD, 'Sea-floor' includes the physical and chemical parameters of the seabed and the biotic composition of the benthic community. 'Integrity' covers spatial connectedness so that the habitats are not artificially fragmented, and having the natural ecosystem processes functioning in characteristic ways. The Sea-Floor Integrity descriptor includes amongst the eight attributes that describe the physico-chemical properties of the sediment and the biological communities living in it, also a 'bio-engineer' attribute. Allogenic ecosystem engineers such as bulldozing echinoderms and burrowing shrimps as well as bio-irrigating polychaetes do classify as 'bio-engineer' attribute within Sea-Floor Integrity (Rice *et al*., 2012).

With respect to the Sea-Floor Integrity attributes related to species diversity and size composition, monitoring indicators of Good Environmental Status (GES) of soft-sediment Sea-Floor Integrity should, next to structural benthic indicators such as BEQI and AMBI (Van Hoey *et al*., 2013) also involve *functional* sediment reworking features. This may be accomplished by Biological Traits Analysis (Bremner, 2008), but also by means of the Bioturbation Potential Index (Solan *et al*., 2004; Queirós *et al*., 2013). This functional trait-based index involves quantitative measures of species abundance and biomass on the one hand, and qualitative measures for sediment reworking mode and intensity on the other hand. Bioturbation Potential of the community (BPc) was demonstrated as an appropriate tool for highlighting the importance of allogenic ecosystem engineers in benthic ecosystem functioning: it has been linked directly to sediment chlorophyll a and organic carbon content (Solan *et al*., 2012), depth of the redox layer (Birchenough *et al*., 2012) and carbon and nitrogen cycling (Van Colen *et al*., 2012; Braeckman *et al*., in press). In fact, BPc encompasses five out of eight attributes of Sea-Floor Integrity: it is correlated with bio-engineer biodiversity (attribute 2), species (attribute 5) and size (biomass) (attribute 6) composition of the community, and life history traits (attribute 8). Bioturbating organisms also increase sediment oxygen content, hence BPc also relates to oxygen concentration in the sediment (attribute 3). The BPc metric shows that it is not necessarily rare species that contribute to high bioturbation potential. Species with high density or biomass (i.e. common species) can also strongly influence ecosystem functioning.

Although there are several assumptions and drawbacks associated with BPc (Queirós *et al*., 2013; Braeckman *et al*., in press), monitoring of Sea-Floor Integrity has to be time- and cost-efficient and for the time being, this inexpensive, rapid indicator is probably the one that best integrates the several attributes of Sea-Floor Integrity.

Belgium mentions an increased occurrence of ecosystem engineering species as a target within Sea-Floor Integrity and foresees incorporating the Bioturbation Potential Index in its monitoring of the GES of Sea-Floor Integrity. More specifically, for a GES the median BPc of the *Abra alba* – *Kurtiella bidentata* community in spring should be 100 per surface of 0.1 m^2 (Belgische Staat, 2012).

THE CASE OF THE SAND MASON *LANICE CONCHILEGA*

Lanice conchilega is a tube building terebellid polychaete (Figure 1(d), Figure 2), present throughout the North Sea, with the highest densities found in the German Bight, east of the Dogger Bank in the central part of the North Sea and along the French, Belgian (Figure 2(C)) and Dutch coasts (Van Hoey *et al*., 2008). The structuring effects of *L. conchilega* occur when densities are high and so-called reefs (Rabaut *et al*., 2009) are formed (Figure 2(A)). Its ecosystem engineering effects in the North Sea are well documented (Table 1). The autogenic engineering effects involve an increased sediment compaction explaining the formation of the biogenic concretions, leading to a significant increase in bed stability (Rabaut *et al*., 2009) and a significant elevation (generally ± 10 cm (Degraer *et al*., 2008)). These physical changes are reflected in important biological alterations, as the species provides new habitat. The presence of *L. conchilega* reefs in the Belgian part of the North

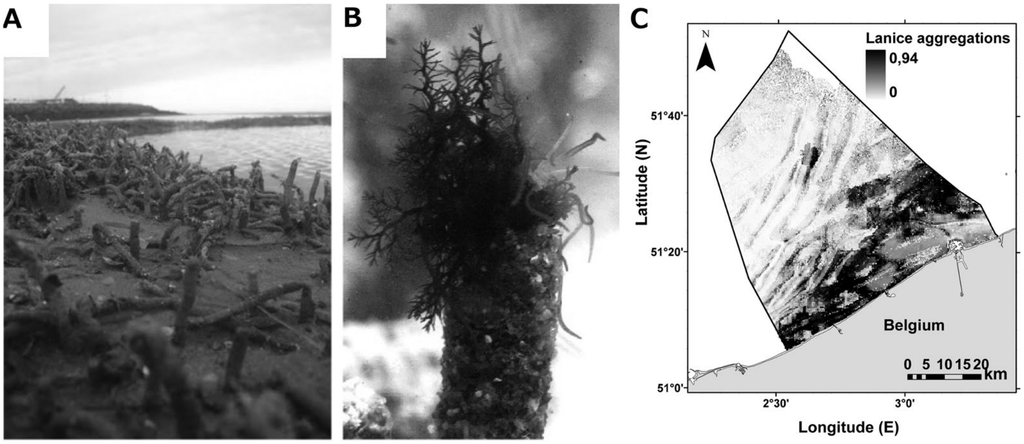

Figure 2. *Lanice conchilega* reef in the intertidal (A), and individual polychaete (B); Habitat Suitability Model predicting the occurrence (probability between 0 and 1) of *Lanice conchilega* aggregations (reefs) with > 500 ind. m^{-2} in the Belgian part of the North Sea (Merckx, 2011).

Sea (Figure 2(C)) can result in a doubling of the biodiversity in the richest soft-sediment macrobenthic habitat in this region (Van Hoey *et al.*, 2008), and positive effects on biodiversity are also described for other North Sea areas (Carey, 1987; Féral, 1989; Dittmann, 1996; Zühlke *et al.*, 1998; Callaway, 2006; Rabaut *et al.*, 2007; Van Hoey *et al.*, 2008). The tubes provide shelter (Rabaut *et al.*, 2010) and feeding ground to juvenile flatfish (Rabaut *et al.*, 2013), waders (De Smet *et al.*, 2013) and diving birds such as the common scoter (e.g. through increased bivalve abundance in the reefs) (Petersen and Exo, 1999). Not only the altered physical habitat structure but also biogeochemical changes (Forster and Graf, 1995; Braeckman *et al.*, 2010) contribute to changes in species composition of smaller interstitial organisms (Zühlke *et al.*, 1998; Braeckman *et al.*, 2011a, b). *Lanice conchilega* bio-irrigates its tube (i.e. 'piston-pumping'), thereby introducing oxygen-rich water deep into the sediment (Forster and Graf, 1995). This intermittent ventilation pattern has pronounced effects on benthic respiration, nutrient release and denitrification (Braeckman *et al.*, 2010). Thus, apart from being an autogenic ecosystem engineer *sensu* Jones *et al.* (1994), *L. conchilega* has also proven to be an allogenic ecosystem engineer (Godet *et al.*, 2008; Rabaut, 2009).

It is clear that the importance of *Lanice*-engineered habitats largely exceeds the local scale where the species is actually present, i.e. the effect of one individual on its surroundings is geographically limited whereas the effect of the habitats created by dense aggregations are important at a much larger scale. Therefore, *L. conchilega* must be considered an important ecosystem engineer that does not need to be protected as a species *per se* but because of its value in the functioning of the ecosystem. The same accounts for other North Sea ecosystem engineers (Table 1), although not studied in as much detail as *L. conchilega*. As such, ecosystem engineered habitats such as created by *L. conchilega* become crucial when designing areas that deserve protection, as these habitats not only represent high structural biodiversity, but they are also biogeochemical hotspots that affect the full local marine ecosystem and maintain the delivery of valuable ecosystem services.

Aggregating tube-dwelling polychaetes *S. spinulosa* and *L. conchilega* classify as biogenic reefs under the Natura 2000 umbrella (Hendrick and Foster-Smith, 2006; Rabaut *et al.*, 2009). Although they build elevated and relatively stable bioconstructions and change the sedimentary environment, they can appear and disappear (Holt *et al.*, 1998; Pearce *et al.*, 2011), but also recolonize the area again within 1–3 years (e.g. *Sabellaria spinulosa*: Jones, 1998; *Lanice conchilega*: Ropert and Dauvin, 2000; Strasser and Pieloth, 2001; Zühlke, 2001). It is clear, however, that the occurrence of an opportunistic tube-building polychaete should not always lead to conservation measures. Where high density aggregations contribute to the local ecosystem's integrity, however, conservation measures will effectively contribute to the functioning of a substantial part of the ecosystem. The Belgian Natura 2000 site 'Flemish Banks' has been designated to protect shallow sandbank ecosystems and associated reef habitats. Reef habitats (1170) in this specific case are both biogenic and geogenic reefs (biodiverse gravel beds rich in unique epibenthic species). In the coastal zone, the area was designated because of the association with the biogenic *L. conchilega* reefs. The scientific advice on which this designation is based clearly refers to the ecosystem engineering aspects of this habitat. Thirty percent of the *L. conchilega* aggregation areas (see Figure 2(C) for aggregation distribution) are situated in the Special Area for Conservation. Targeted measures to reduce bottom disturbance are now being taken in front of the coast, specifically because of this ecosystem engineered habitat. The measures are incorporated in the Belgian marine spatial plan and include restrictions on commercial fisheries, gear adaptations and restrictions on use of bottom trawling gear for non-commercial fisheries.

In other European countries, SACs have been designated because of different autogenic reef-forming ecosystem engineers: *Sabellaria spinulosa* and cold water coral mounds of *Lophelia pertusa* in the UK (De Santo, 2013) intertidal *Sabellaria alveolata* reefs in France (Desroy *et al*., 2011), *Serpula vermicularis* tube worm reefs in Scotland (Moore *et al*., 2009) and horse mussel *Modiolus modiolus* beds in the Irish sea (Lindenbaum *et al*., 2008; Rees *et al*., 2008; Sanderson *et al*., 2008).

Species such as *L. conchilega* that are unique in having both autogenic and allogenic impacts can undoubtedly qualify as Marine Strategy Framework Directive attribute 'bio-engineer'. Several alternatives to annual extensive sampling schemes exist to monitor the GES of bio-engineer populations: habitat suitability modelling (Willems *et al*., 2008; Merckx, 2011, Figure 2(C)), very high resolution acoustics (Degraer *et al*., 2008; Van Lancker *et al*., 2011, 2013) and Sediment Profile Imaging (SPI) (Birchenough *et al*., 2006, 2012, 2013; Van Hoey *et al*., 2014). Applying BPc to *L. conchilega* populations is nonetheless inadequate since the metric does not appreciate stationary bio-irrigation, rendering it a low BPc qualification.

IDENTIFICATION OF IMPORTANT ECOSYSTEM ENGINEERS

According to Byers *et al*. (2006), identifying and preserving ecological engineering species and responsive ecosystems should be a key priority for conservation. When identifying ecosystem engineers it should be noticed that the ecosystem engineer concept is scale- and time- dependent (Hastings *et al*., 2007). Ecosystem engineering can be viewed as an ubiquitous process operating at all levels of the food web (Meadows *et al*., 2012). Organisms can have important ecosystem engineering characteristics, but owing to their limited presence (in space and/or time), their structural or functional effect on the environment is restricted. Nevertheless, their presence can be important for the local/temporal wider ecosystem. The tube-building polychaete *Pygospio elegans* for example, can occur in very high densities (> 20 000 ind. m^{-2}, Bolam and Fernandes, 2003), where it decreases sediment erodability (Brey, 1991; Montserrat *et al*., 2008) while increasing bivalve spat settlement and biodiversity in early succession stages (Bolam and Fernandes, 2003; Van Colen *et al*., 2008). In a later stage, enhanced bivalve competition leads to a rapid decrease in *P. elegans* densities, disappearance of the physical structure (Bolam and Fernandes, 2003; Montserrat *et al*., 2008; Van Colen *et al*., 2008) and its associated ecosystem engineer effect. Similarly, species can have context-dependent functionalities (Naeem, 2002; Rossi *et al*., 2008): a species that qualifies as an ecosystem engineer in a certain local ecosystem, does not necessarily do so in another. Therefore, we argue that the Jones *et al*. (1994) ecosystem engineer definition should be applied according to the ecosystem considered, ranking the effects of ecosystem engineer species by relative importance. The development of an ecosystem engineer index, involving assembled information on the species' allogenic and autogenic ecosystem engineering capacities (Table 1), can help to evaluate the strength of the effect of the ecosystem engineer on the local biotic and abiotic properties of the environment. In this respect, an ecosystem engineer index could be a broader version of the BPc index, extended with a measure for bio-irrigation, context-dependent activity (life stage, season, interaction with other organisms etc.), and evaluation of the effects on epifaunal and infaunal biodiversity and the sustainability of its populations in space and time. In this way, organisms that display both autogenic and allogenic properties are bound to receive a higher ecosystem engineer qualification. It is important to keep in mind that an ecosystem engineer should not be protected because of its intrinsic value as a species, but rather because its protection would result in the conservation of the entire local ecosystem. An ecosystem engineer index could then be applied as an indicator for the Good Environmental Status of Sea Floor Integrity or for identifying conservation targets within Natura 2000.

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