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1 The use of multiple biological traits in marine community ecology 2 and its potential in ecological indicator development

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15

16 Abstract

17

18 Biological traits offer valuable approaches to understand species distributions and underlying mechanisms.
19 Their use has received a growing interest in marine community ecology, for both fundamental and applied
20 purposes. The need of ecological indicators as part of marine directives and conservation programmes has
21 promoted the use of multiple traits for indicator development, but in a questionable context regarding the
22 state of fundamental developments. Biological Trait Analysis (BTA) is a complex research field,
23 characterised by flexible concepts and applications. In order to enhance the development of relevant marine
24 ecological indicators, this review provides baselines for better theoretical and applied BTA. A compilation of
25 the existing literature reveals that specific topics have dominated the use of multiple traits in marine ecology
26 unlike in freshwater and terrestrial ecology where tests of theories and uses of evolutionary concepts
27 consistently preceded BTA applications. Availability of data sets and analytical techniques seemed to have
28 driven the growing use of marine BTA rather than fundamental questions regarding life history theories in
29 marine ecosystem components and the functional nature of traits. It is therefore suggested that greater focus
30 on life history ecology and on the links between marine species traits and ecosystem functioning are still
31 needed to support trait-based indicator development. Life history strategy understanding is put forward as a
32 theoretically-sound basis and fundamental pre-requisite for trait-based marine indicator development.

33

34 Keywords: biological traits; ecological indicators; marine environment

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36

37 1. Introduction

38

39 Biological traits are characteristics of species life history and are generally used to understand the structure
40 and dynamics of ecological communities (Dray et al., 2014). Until fifteen years ago, ecologists were still
41 debating the fundamental and applied research potentialities of community ecology (Lawton, 1999;
42 Simberloff, 2004). The complexity of biotic interactions and biology among species in communities were
43 thought to be major obstacles to generate ecological laws. Although analytical techniques were sufficiently
44 sophisticated to detect multiple gradients in ecosystems (Dolédec and Chessel, 1991; Gauch, 1982),
45 correlations between species distributions and habitat characteristics had limited potential for mechanistic
46 understanding of ecological patterns since analyses based on taxonomic grounds alone do not provide
47 confirmation of assembly rules independent of species biology (Fleishman et al., 2006; Statzner et al., 1994).
48 Species assemblage distributions are only patterns, and patterns are phenomena arising from unknown
49 mechanisms, a mechanism being a comprehensive interplays between variables (Rosenzweig and Ziv, 1999).
50 Biological traits can be used to understand why different taxonomic entities (e.g. species, genera) occur in
51 similar habitats (Dolédec et al., 1996; Dray and Legendre, 2008; Keddy, 1992; Legendre et al., 1997), as
52 organism performances result from common adaptations to environmental forces (Greenslade, 1983;
53 Southwood, 1988). Hence, the use of multiple traits, as variables describing species performances, enable to
54 generate laws, patterns with mechanisms, and consequently can support the development of theoretically-

55 sound applications.

56 Incorporation of biological traits in community ecology gained momentum in terrestrial and freshwater
57 research (Bonada et al., 2006; Statzner and Bêche, 2010). Increased biological knowledge and better
58 computational tools have since triggered the development of trait-based frameworks that were used both in
59 theoretical studies (Statzner et al. 1994) and for practical monitoring requirements (WFD, 2000; Bonada et
60 al., 2006; Furse et al., 2006; Dolédec and Statzner, 2008). The growing success of Biological Trait Analysis
61 (hereafter “BTA”) has given a new impetus to community ecology, and it has even been suggested to rebuild
62 the discipline based on BTA when studying large sets of species (McGill et al., 2006). Currently, the use of
63 biological traits to understand natural community assembly patterns has become standard practice, as well as
64 to support management tools in ecosystems undergoing adverse effects of human impacts (de Bello et al.,
65 2010; Resh and Rosenberg, 2010; Statzner and Bêche, 2010).

66 More recently, traits have been used in the development of functional diversity indices, enabling the
67 description of the dynamics of ecological niches (Mason et al., 2005). Although such indices have been
68 shown to be a potentially promising tool to identify ecological impacts of disturbances (Mouillot et al.,
69 2013b), their use will not be discussed in this review as traits are not directly expressed in the procedure,
70 which rather uses traits to indirectly separate the different facets of ecological niches. For a complete review
71 on this topic, see Mason et al. (2005), Villéger et al. (2008), Mouchet et al. (2010), and Mouillot et al.
72 (2013b).

73 These last years, the use of biological traits has received a growing interest in marine ecology as a means
74 to improve the understanding of marine ecosystem functioning, which is still relatively limited relative to
75 that in terrestrial ecosystems (Heip, 2003). In parallel, multiple human pressures are exerted on the marine
76 environment so that growing demands from marine directives and conservation programmes are enhancing
77 the need of ecosystem understanding and reliable indicators of environmental health (Bremner, 2008). To
78 this end, the use of multiple traits in the marine environment has been claimed to have many application
79 potentials (Bolam, 2013; Bremner, 2008; King and McFarlain, 2003; Rijnsdorp et al., 2016; Tillin et al.,
80 2006), but a theoretically-sound basis for this needs further development (Kershner et al., 2011). Using
81 biological traits to this end requires firstly an understanding of life history in marine habitats. In other words,
82 this means that empirical models validated in given areas can be generalized to other areas if the identified
83 mechanistic relationships between environmental conditions and subsequent species adaptations are
84 conserved (i.e. absence of biogeographic contingencies). The debate in terrestrial and freshwater ecology has
85 significantly advanced as has the understanding of habitat-species and community relationships in a way able
86 to guide environmental management (de Bello et al., 2010; Menezes et al., 2010; Resh and Rosenberg,
87 2010). In the marine environment, greater challenges to sampling, observation and manipulation of natural
88 assemblages' means, from first principles, that our stride has been shorter, and the present understanding of
89 the mechanisms driving marine habitat-community relationships, as derived from biological traits, lags
90 behind.

91 Monitoring environmental health is constrained by ecosystem complexity (e.g. several tens of species),
92 whereas only a reduced set of variables can be technically handled for assessment. Ecological indicators, by
93 relaying and/or summarising complex fluxes of information, aim to provide a more practical and economical
94 way to track the state of the environment. Though they have been more frequently explored in the academic
95 community, there is at present almost no concrete multivariate application of biological traits to support
96 environmental policies. In this domain, most uses are limited to individual (Bolam et al., 2014; Greenstreet et
97 al., 2012), or few traits, such as feeding and bioturbation (Rijnsdorp et al., 2016; Jennigns et al., 1999).
98 Though these are important traits mediating specific ecosystem processes (e.g. benthic-pelagic coupling,
99 trophic linkage), we have a limited understanding of underlying pressure impact and recovery mechanisms
100 on the biota. As traits represent the link between life-history and habitat, there is clearly potential to explore
101 multiple trait approaches in support of marine management and policies aimed at curbing human impact on
102 the marine environment.

103 The literature in marine ecology has been largely enriched with BTA these last years; synthesis is
104 presently lacking, both assessing the present state of the art and to guide future research. The aims of this
105 review are (1) to provide an explicit description of the nature of biological species traits to support the
106 conceptualisation of fundamental and applied uses; (2) to list key developments to assess current knowledge
107 gaps among the different ecosystem components; (3) to review the technical uses in order to (4) provide a
108 framework toward the development of sound, multiple trait-based marine indicators.

109

110 2. The nature of traits

111

112 There has been some confusion in the use of the term “trait” in the literature. Violle et al. (2007) discussed
113 the semantic aspects of this use and define several categories of traits corresponding to specific
114 organizational levels from individual organism to ecosystem. Here, we consider a biological trait at species
115 and community levels and as any measurable biological characteristic observed in all sampled species from a
116 same location (species community), as traditionally considered in BTA.

117 The expression “functional trait” is used in a large majority of studies on community ecology using
118 multiple traits. This denomination can be subtle to define (Calow, 1987), but Violle et al. (2007) formalised
119 it as “*any trait which impacts fitness indirectly via its effects on growth, reproduction and survival*”. Rather
120 than shedding troubles on what could or could not be functional in a species community, a broad distinction
121 can be made among types of traits so that traits be relevantly selected to describe species or considered
122 according to research questions. In this respect, four main natures of traits are found in the literature (Chown
123 et al., 2004; Costello et al., 2015; Díaz and Cabido, 2001; Lavorel and Garnier, 2002): (1) taxonomic traits,
124 (2) ecological traits, (3) response traits and (4) effect traits.

125 (1) Taxonomic traits simply refer to taxonomic levels of any species from phylum to genus. Taxonomic
126 traits are shaped over evolution through taxonomic radiation resulting from vicariance, intra-specific
127 competition or other types of evolutionary processes. Although taxonomic traits have recently been
128 considered in combination with usual BTA for evolutionary development (Pavoine et al., 2011), the use of
129 these traits will not be discussed here as evolutionary aspects are far beyond the scope of this review.

130 (2) Ecological traits (environmental requirements) have been used in fundamental studies in a theoretical
131 way to highlight differences among biological strategies across spatio-temporal variations (Statzner et al.,
132 1997; Usseglio-Polatera et al., 2000). In practice, ecological traits are not relevant to causally explain
133 empirical species occurrences among habitats because leading to circular arguments; simplistically,
134 ecological traits are measured where species are found. Species biology results from evolutionary
135 adaptations to habitats in which the abiotic and biotic components vary over time, so that other traits
136 responding to this variability are more relevant.

137 (3) Response traits characterize species performance under different kind of natural environmental
138 variability such as stability, stress and favourableness (Díaz and Cabido, 2001). Complex combinations of
139 reproductive traits and/or resistance forms can translate species ability to survive in specific conditions:
140 resistant species adapted to physical stress may provide strong reproductive allocation (e.g. continuous
141 reproduction to warrant reproductive success), other species may remain resilient to disturbance (e.g.
142 dispersal capability for re-colonisation), whereas some others from stable environment may be more adapted
143 to biotic interactions (e.g. predation, competition). These traits adequately document size, motility, trophy,
144 resistance forms, reproduction and dispersal. Formally, these traits indirectly characterize growth, survival
145 and reproduction at the individual level (fitness) which result in habitat occupancy patterns across species
146 distributions and at the community level (Violle et al., 2007). Hence, response traits can be a priori
147 considered as those that explain why a community is found in a certain habitat and not in another one.

148 (4) Effect traits describe the consequences of the activity of organisms on their environment, also called
149 “ecosystem engineering”, operating at different degrees of magnitude, depending on individual or biomass
150 density, body size and metabolic rate. The expression of these traits can ensure functions within habitats or
151 ecosystems, as services from one ecological entity to another one such as habitat creation, food provision and
152 nutrient cycling. Species can contribute to ecosystem processes directly (e.g. predatory regulation, habitat
153 creation) or indirectly through cascading effects on energy fluxes through food-webs or decomposition. As
154 an example, the sea-floor is an ecological compartment particularly rich in functions where benthic
155 organisms exhibit important effect traits. This is especially the case in sedimentary habitats where the
156 benthic fauna mediates many biogeochemical pathways via enhanced mixing of particulates (i.e.
157 bioturbation) and solutes (i.e. irrigation and advection) through general ecological processes such as feeding,
158 burrow construction and ventilation (Queirós et al., 2013; Woodin et al., 1995).

159 Table 1 displays a list of important traits related to response and effect, and encountered in the literature
160 (see Table A1, supplementary material); the column “Functions and processes” underlines the complexity of
161 traits which can act in concert through covariances such as body length, very exemplary in this respect: this
162 trait does not provide a clear primary function, but when increasing, it conditions the expression of diverse
163 physiological, reproductive and ecological functions and performances. Table 1 also help to understand the
164 possible double nature of some traits expressing both response and effect. For instance, trophic mode

165 expresses the feeding aspects of a species in terms of diet and mechanical acquisition, expressing growth
166 requirement driven by environmental drivers (response) and the effect of that species on the food web
167 through e.g. predator-prey relation (effect). Also, burrowing depth (in sediment) is considered as an
168 evolutionary consequence of a survival adaptation as a response to surface sediment predation (Meysman et
169 al., 2006), but the burrowing life style also strongly impacts sediment biogeochemistry and contributes to
170 niche creation as an effect trait (Kristensen, 1988). In Table 1, an emphasis is placed on fundamental traits
171 for the study of life history of marine organisms. However, this list is not fully comprehensive and it is not
172 meant to imply that other traits are not deserving of interest for other purposes. Taxonomy and external
173 aspects of organisms might be mechanistically meaningful in some specific research cases: for instance,
174 calcareous skeletons, shells, cell walls or protective tubes may be of importance regarding environmental
175 influences like acidification (Costello et al., 2015).

176 Choosing traits and modalities is flexible, but it depends on their relevance to research objectives and
177 independence of trait expressions. In Table 1, redundancy among traits was minimized. Redundant traits can
178 be found in studies and may lead to spurious results or numerical noise. For instance, both feeding mode and
179 diet can be found in a same study, but most of their respective modalities have high correspondence (e.g.
180 suspension feeding corresponds to a diet composed of plankton and/or suspended particulate matter;
181 carnivory corresponds to a diet of animals; deposit feeding corresponds to a diet of detritus, etc.) and some
182 dietary seasonal changes may occur (e.g. switch from a specific diet to omnivory) with possible discordance
183 in the sampling season depending on food availability. Regarding reproduction, Reproductive frequency
184 (seasonal or continuous) and annual fecundity are fundamental traits. However, hermaphroditism, very often
185 encountered in fishes and frequently used in studies, is not considered here as when it is protandrous (switch
186 from male to female in ageing individuals), the function consists in increasing female fecundity (number of
187 ovules correlated to body mass whereas number of spermatozoa is always in excess) which is expressed in
188 Table 1 by annual fecundity; the reverse, protogyny, occurs mainly as a result of intraspecific competition
189 where larger males can out-compete smaller ones. Hermaphroditism might express adaptations to habitat
190 conditions, but the role of this trait (or modality) may not be relevant in studies of large species communities
191 where it is mainly intraspecific (Avisé, 2011), its use never discussed and its nature (synchrony, protandry or
192 protogyny) rarely specified in BTA studies. By contrast, asexuality (e.g. fragmentation in annelids,
193 fissiparity in sea stars and brittle stars) can provide independent reproductive information since it can
194 modulate recruitment and habitat colonisation (Mladenov and Emson, 1984), and can minimize cost
195 associated with parasitism (McCurdy, 2001).

196 Trait relevance can also be affected by modality expressiveness, in other words, the meaningfulness of a
197 modality in translating a biological process. “Egg/Propagule size”, when documented (MarLIN BIOTIC,
198 2006; Garcia, 2010), is a typical example whereby modality expressiveness may fail to translate the process
199 of interest: usually, modalities are limited to egg diameter classes, even in the case of direct development
200 when an offspring is released as a miniature adult with much higher survival rate than an egg released into
201 the water column. Although direct development can include an egg stage during internal incubation in a
202 brood pouch or in a uterus (e.g. in amphipods and sharks), consideration of how an organism is released from
203 the parent may be a more meaningful means to express life history strategy than egg size, and better express
204 reproductive effort, size of offspring at birth and consequent juvenile survival rate.

205
206 **Table 1.** Fundamental traits for the study of life history of marine organisms (mostly metazoans) and encountered in the literature at
207 various degrees of frequency. In the last two columns, “+” indicates when the trait expresses fitness (“Response”) and/or the
208 consequences of this expression on the environment, including both abiotic and biotic components (“Effect”). Presented in this way,
209 traits and associated modalities can be used in both qualitative (complete disjunction 0/1) and quantitative way (continuous or fuzzy
210 coding); see Figure 3.
211

Traits	Modalities	Functions and processes	Response	Effect
Motility	Attached/Sessile	Foraging mode, ability to escape predation, migratory requirements, dispersal	+	
	Tubicolous			
	Crawler			
	Crawler-Swimmer			
	Swimmer			
	Flyer			
Body length	Length classes	Sensitivity (small) or resistance (large) to predation, thermal resistance, fecundity increase, metabolic oxygen consumption rate	+	+
Trophic mode	Deposit feeding	Food acquisition, growth requirements, demographic control (predation), nutrient cycling	+	+
	Deposit-Suspension feeding			
	Suspension feeding			
	Carnivory			
	Omnivory			
Lifespan	Age classes	Longevity increases reproductive successes over time	+	
Age at sexual maturity	Age classes	Early age at maturity increases demographic resilience in adverse environmental conditions	+	
Annual fecundity	Number of eggs/propagules classes	Dispersal, resource to higher trophic levels	+	+
Egg/Propagule size	Size classes	Juvenile survival and recruitment success	+	
Reproductive frequency	Seasonal	Continuous reproduction can support demographic resilience in adverse conditions	+	
	Continuous			
Assexuality	None	Most of time, auxiliary advantage to sexual reproduction (heterogamy) to ensure demographic resilience in adversity or temporary dispersals	+	
	Assexual seasonal			
	Assexual continuous			
Early development	Direct development	Juvenile survival, dispersal potential	+	
	Larval pelagic stage duration classes			
Egg Propagule protection	None	Juvenile survival and recruitment success	+	
	Brooding/Bearing			
	Capsule			
	Gel			
Structural robustness	Fragile	Sensitivity to physical damage (e.g. storm, predatory aggression)	+	
	Intermediate			
	Robust			
Burrowing depth	Sediment depth classes	Foraging mode, protection against epibenthic and benthopelagic predators, biogeochemical impacts	+	+
Resistance form	None	Survival against abiotic damages and biotic aggressions	+	
	Body regeneration			
	Poison			
Habitat creation ability	None	Biogeochemical requirements, niche creation, refuge, nursery, below sediment oxygenisation	+	+
	Below sediment 3D structures			
	Above sediment 3D structures			
	Both			
Sediment mixing	None	Food acquisition, impact on biogeochemistry, organic matter re-distribution, habitat provision	+	+
	Diffusion			
	Advection			
	Regeneration			
Irrigation	None	Food acquisition, survival against hypoxia, organic matter re-distribution, impacts on biogeochemistry	+	+
	Water flushing			

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Overlapping roles of response and effect traits in ecosystem processes have already been considered before (Lavorel and Garnier, 2002). Correlation between the response and effect is not always observed, given that the traits that enable a species to persist in given conditions are not necessarily the same that support the performance of a particular process of interest (Solan et al., 2004). The simultaneous use of multiple traits should therefore be undertaken with great care for the nature of traits studied. Compiling a

219 trait data set requires parsimony, and that the consideration of the life history hypotheses underlying
220 individual or collective roles of traits within typologies is also taken into account. Conversely, a “Darwinian
221 soup” is never constructive, and blind data compilations simply because the biological information is
222 available may lead to irrelevance. Compiling a data set with many heterogeneous traits without such
223 considerations can create numerical noise whereby the potential responses of relevant and covariant traits
224 could be blurred among many gradients without objective biological meaning. Finally, within the common
225 goal of predicting species survival in ecosystems under human pressure, response traits might be better
226 candidates for indicator development than effect traits since they directly translate demographical responses
227 to causal effect (survival, damage or death).

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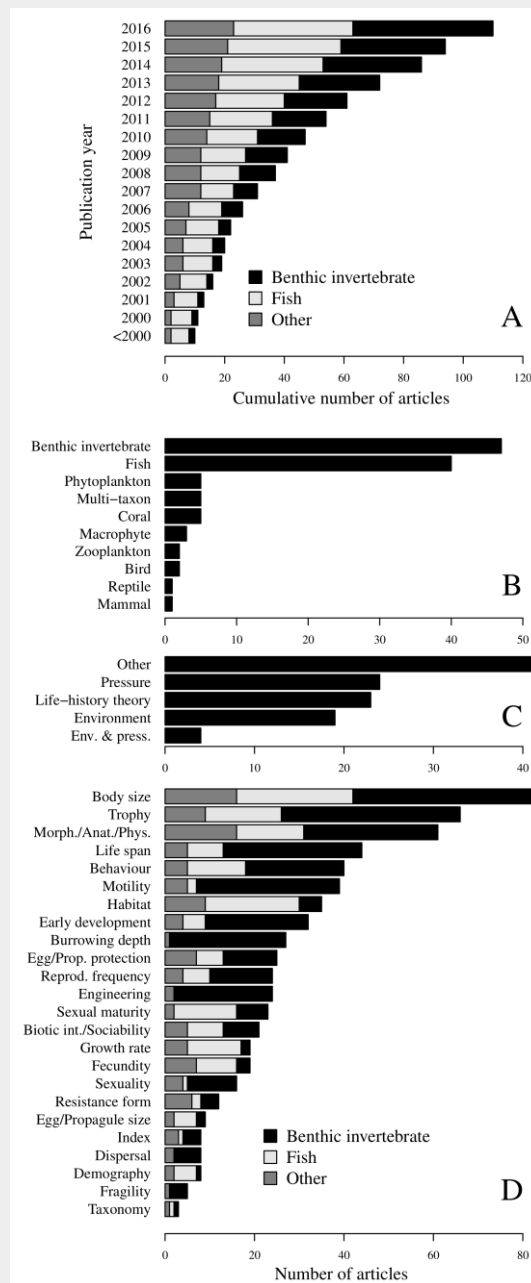
230 **3. BTA in the marine environment**

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232 Although BTA in terrestrial and freshwater ecosystems has been applied for a long time, their regular use in
233 the marine environment is relatively more recent (Bremner, 2008). Important theoretical developments in the
234 marine benthos relating species traits to habitats appeared as early as the 1970’s (Pearson and Rosenberg,
235 1978; Rhoads, 1974). However, this early development, focusing specifically on the relations between
236 feeding types and ecological preferences for different sediment types, may have limited broader
237 developments on biological traits (Bremner et al., 2003). Since then, and to the time of this study, 111 peer-
238 reviewed articles were found through a Google Scholar search based on four terms: “marine waters”,
239 “species”, “communities” and “traits” (≥ 2). We present here the results of this search, which should be read
240 with consideration for the working of this particular search algorithm (Beel and Gipp, 2009) and the fact that
241 we were unable to use other search engines due to resource constrains. The resulting list is available as
242 supplementary materials (Table A1). A graphical summary of the topics covered by marine BTA studies
243 returned by this search is displayed in Figure 1.

244 Figure 1A represent the cumulated number of articles per year; since 2006, the publication rate has
245 increased and was particularly high in 2016 ($n = 17$ articles). A wide range of ecosystem components is
246 represented but benthic invertebrate and fish studies largely dominate the literature (Fig. 1B). Studies
247 preliminary to indicator development (traits as part of life history theory and their relationships with
248 environment) and relationships between traits and pressure are also numerous (Fig. 1B). Studies
249 investigating life history theory and fundamental concepts to trait applications are poorly represented ($n =$
250 23).

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Fig. 1. Graphical summary of peer-reviewed studies on marine communities based on multiple traits ($n = 111$ articles). **A.** Cumulative number of articles per dominant ecosystem components; the category “Other” includes everything else than “Benthic invertebrate” and “Fish” in **B**. **B.** Number of articles per ecosystem component. **C.** Number of articles per research theme; “Env. & press.” for “Environment & pressure”. **D.** Number of articles per trait and per dominant ecosystem component; “Morph./Anat./Phys.” for “Morphology/Anatomy/Physiology”, “Reprod. Frequency” for “Reproductive frequency”, “Egg/Prop. protection” for “Egg or Propagule protection” and “Biotic int./Sociability” for “Biotic interaction or Sociability”.

Benthic invertebrate communities are the most frequently studied marine ecosystem component in BTA ($n = 47$). These communities are composed of many different species exhibiting a large diversity of living modes specific to the complex structures of sea-floor habitats in space and time. The potential suitability of these communities as indicators of environmental change lies in their reflection of local environmental conditions, because most of species (at least when adults) have limited mobility compared to other faunal groups such as fish, and have relatively shorter life spans. These aspects probably explains why benthic invertebrate traits, environment and pressures are the themes more frequently documented in the search results ($n = 29$ articles within the category Benthic invertebrate). Some studies provided evidence of basic relations between traits and habitats (Bremner et al., 2006a; Paganelli et al., 2012). Studies focusing on pressures investigated mostly physical impacts such as those from dredging (Cooper et al., 2008) and beam-

271 trawling (Bolam et al., 2014; Tillin et al., 2006); studies on other pressures included organic enrichment
272 (Gusmao et al., 2016; Oug et al., 2012) and coastal and infrastructure management (Fraschetti et al., 2016;
273 Munari, 2013). Since 2006, the publication rate on benthic invertebrate BTA has increased as displayed in
274 Figure 1A (cumulative number of articles), and this area of research has been particularly prolific since the
275 beginning of 2016 ($n = 12$).

276 Fish studies represented a comparable amount of articles and this likely reflects a historical interest on
277 this topic (two thirds of the studies occurred prior to 2000). Since 2010, the publication rate has also
278 increased, but the research themes contrast with those from benthic invertebrates due to a growing interest on
279 functional diversity indices (15 articles on this specific theme since 2008 out of a total of 40 fish studies).
280 Most of time, these works consider poorly diversified traits (e.g. limited to size, trophy, habitat and/or
281 morphology) and usually disregard reproductive aspects, or consider uniquely morphology (Albouy et al.,
282 2011; Mouchet et al., 2012; Mouillot et al., 2008; Villéger et al., 2010). Such data are comparatively easier to
283 compile in a taxonomic group like fish, which is well documented, and enables very broad scale studies
284 (Mouillot et al., 2014; Stuart-Smith et al., 2013; Wiedmann et al., 2014) relative to other groups such as
285 invertebrates. Fishes are the best documented organisms in BTA studies concerning life-history theory ($n =$
286 10), ranging from pioneer works (Jennings et al., 1999; Winemiller and Rose, 1992) to the most recent
287 indicator developments (Greenstreet et al., 2012).

288 Seventeen studies on other specific groups of organisms were found, and five others were found focusing
289 on several taxa (multi-taxon, mainly combining fish and benthic invertebrate). Half of these studies are
290 related to specific themes, whereas very fundamental works dealing with life-history were found for other
291 marine groups: reptiles (Van Buskirk and Crowder, 1994), birds (Hamer et al., 2002), a recent analysis on
292 copepods (Benedetti et al., 2015) and a broad scale documentation of tropical corals (Darling et al., 2010).
293 The rest of this literature comprises studies investigating the roles of limited numbers of traits. Cleary and
294 Renema (2007) documented the relation between foraminifera traits and their environmental gradients; in
295 this case, considered traits referred to anatomy and presence of symbionts; Edwards et al. (2011, 2013)
296 analysed trade-offs in phytoplankton communities, but limited their investigation to nutrient uptake ability in
297 competitive processes; Nyberg and Wallentinus (2005) provided a ranking of macrophyte species traits that
298 facilitate dispersal and establishment of introduced species. By contrast, Spitz et al. (2014) recently provided
299 a remarkable analysis on marine mammals with a large number of traits, but limited their investigation to
300 trophic aspects between mammals and their preys; Litchman et al. (2010) advocated for an electronic trait
301 data base and proposed a set of traits covering many aspects of phytoplankton biology, but such an initiative
302 may be too recent to find subsequent applications.

303 Globally, marine community ecology based on multiple biological traits is still poorly studied for most of
304 ecosystem components. Fish has been the most explored one in terms of life history theory (Winemiller and
305 Rose, 1992) with relatively early attempts for deriving ecological indicators (Jennings et al., 1999). Besides,
306 benthic invertebrates studies, although the most numerous, have poorly focused on general life history (only
307 four articles), and common adaptations to habitats among species of similar traits performances were never
308 discussed. A lack of consideration for trait functionality might explain the lack of theoretical studies as
309 underlined by Figure 1D, displaying the number of articles per trait, based on a standardisation of twenty-
310 four main traits to cope with variable degrees of heterogeneity (e.g. body size comprises adult body mass and
311 adult body length). The use of traits easy to document (typically, describing external features of organisms)
312 has been dominant: body size, trophy, morphology/anatomy/physiology (mainly morphology), behaviour,
313 motility and habitat. Among these traits, comparatively less efforts have aimed to document reproductive
314 traits, marginally represented among the remaining traits, except, to a lesser extent, body size and life span
315 which can partially express a reproductive aspect, yet their uses may not always provide objective proxies
316 (Table 1). Moreover, important reproductive traits like age at sexual maturity, fecundity and egg/propagule
317 size were documented mainly for fish when documented. Despite the aforementioned limitations of this
318 search exercise, the observations suggest two general themes in marine BTA research: in general, that
319 authors do not attribute much importance to reproduction, and/or that reproduction traits are difficult to
320 document. Because reproduction is a crucial component of fitness, this gap poses important limitations in the
321 understanding of how the ecological traits expressed by marine species relate to single species ecology, as
322 noted by others (Tyler et al., 2012). Costello et al. (2015) proposed to document certain traits for a maximum
323 of marine species as some traits are easy to document. In this context, documentation is always laudable, but
324 quantity against quality remains a dilemma.

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326 **4. Applicability of biological traits in community analysis**

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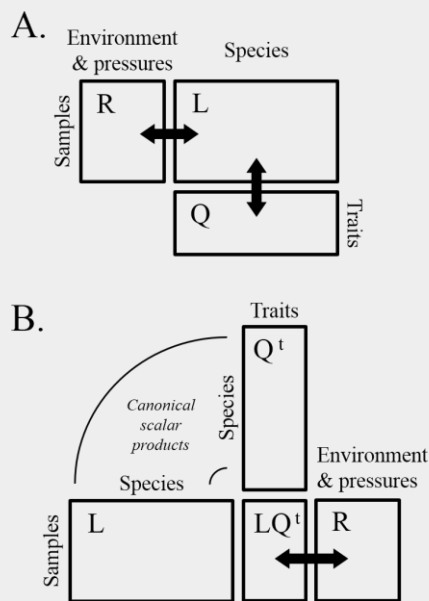
328 **4.1. Methodological considerations**

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330 BTA explores potential relationships between community biology and environmental characteristics, the
 331 latter including human activities. Although the literature includes several studies analysing traits through
 332 bivariate approach or multiple regression, we will focus here on multivariate ordination techniques and tests
 333 which deserve special attention given the large diversity of analytical contexts and the growing need of such
 334 applications in marine community ecology the last fifteen years. Of this kind, the earliest studies found fall
 335 within the framework of freshwater bioindication (Statzner and Bêche, 2010) and this context is still
 336 predominant in current applications as part of biomonitoring studies. In practical terms, BTA proceeds with
 337 three different tables (Dolédec et al., 1996; Legendre et al., 1997): Table R (samples \times environment and
 338 pressures variables; depending on the purpose, Table R can be composed exclusively of environmental
 339 variables or exclusively of human pressure variables or both; hereafter called “environment & pressures”),
 340 Table L (samples \times species) and Table Q (species \times traits). Whereas Table R and Table L are also used in
 341 more classical species-based approaches, Table Q is at the heart of BTA. In Table Q, measurements of
 342 species biological traits can be recorded and used in different ways, depending mainly on research questions
 343 and data availability. In terms of possible research question specific to BTA, a primary methodological
 344 distinction is then made between studies at the species level (Fig. 2A) or the community level (Fig. 2B)
 345 (Kleyer et al., 2012). In essence, in the species level approach (1.), the statistical units are the species
 346 whereas in the community level approach (2.), the community is considered as the observation unit:

- 347 1. Determining specific biological trait combinations requires the explicit use of species trait data (Fig. 2A);
 348 this approach enables the identification of species ensuring key-roles in the functional identity of
 349 communities, the quantification of sample functional amplitudes, but it can also enable to identify the
 350 distribution of species playing any particular role along a gradient.
- 351 2. A community-level approach responds to a narrower range of questions and proceeds simply through a
 352 samples \times traits matrix (Fig. 2B). This approach assumes a certain homogeneity of trait performances
 353 within communities and is most relevant when environmental gradients are strong enough to mask local
 354 biological disparities among species. By simple matrix multiplication, a community level analysis can be
 355 undertaken based on the full information at species level when available, but the reverse is not true: when
 356 trait information is available as a samples \times traits table, patterns of species functional differences cannot
 357 be investigated.

358



359

360

361 **Fig. 2.** Illustration of data sets to undertake biological trait analysis (BTA); rectangles represent data matrices containing either
 362 quantitative or qualitative data; arrows indicate that tables match each other by rows or columns, enabling the investigation of
 363 relationships between them. A. Complete data set enabling BTA at both species and community levels; different questions can be

364 investigated such as the relationships between environment (Table R) and organisms communities (Table L), between organisms
 365 (Table L) and biological traits (Table Q), but also between environment (Table R) and traits (Table Q) through RLQ analysis (see
 366 text for details). B. Matrix multiplication enabling BTA at the community level only; “Canonical scalar product” shows the sum of
 367 multiplications between species abundances in Table L and trait scores in the transposed Table Q (Table Q^t), for each sample with
 368 each trait, and resulting in Table LQ^t, for Community Weighted Means approach (CWM, see text for details). “Environment &
 369 pressures” are variables measured at the sample level and describe environmental information (e.g. depth, water velocity, sediment
 370 type,...) and human pressures (e.g. xenobiotic concentrations, fishing intensity, dredging frequency,...).

371
 372 **4.2. Data and analytical potential**
 373

374 Defining which type of biological trait information to consider is the first step of BTA. As in the case of
 375 environmental data (Table R), biological traits in Table Q can be recorded either in a quantitative or
 376 qualitative way. The simplest use of quantitative data consists in compiling average or median trait values
 377 from bibliographical sources so that species are ascribed a single (averaged) score for each trait in the
 378 resulting Table Q. When sufficient information is available, fuzzy coding (Chevenet et al., 1994) enables a
 379 more sophisticated approach by distributing values among several modalities of a same trait (Fig. 3A); this
 380 approach has the advantage of taking within-species variability into account and to assess the variance of a
 381 trait, a necessary development in the framework of Statzner et al. (1994). Qualitative coding remains a last
 382 option when biological information is scarce for quantitative traits so that only coarse categories within traits
 383 can be defined (Fig. 3B). All these data formats differ in terms of analytical potential; nevertheless, each
 384 format enables different analytical approaches, at species level, community level or both.
 385

A. Fuzzy coding

	Life span				Frequency distribution by taxon →		Life span			
	<2years	2-4years	5-10years	>10years			<2 years	2-4 years	5-10 years	>10 years
<i>Acanthocardia echinata</i>	0	0	1	3		<i>Acanthocardia echinata</i>	0.00	0.00	0.25	0.75
<i>Actinauge richardi</i>	0	0	0	4		<i>Actinauge richardi</i>	0.00	0.00	0.00	1.00
<i>Adamsia carciniopados</i>	0	1	3	0		<i>Adamsia carciniopados</i>	0.00	0.25	0.75	0.00
<i>Aequipecten opercularis</i>	0	0	4	0		<i>Aequipecten opercularis</i>	0.00	0.00	1.00	0.00
<i>Alcyonidium</i>	0	0	4	0		<i>Alcyonidium</i>	0.00	0.00	1.00	0.00
<i>Alcyonium digitatum</i>	0	0	0	4		<i>Alcyonium digitatum</i>	0.00	0.00	0.00	1.00
<i>Amphiura</i>	0	1	3	2		<i>Amphiura</i>	0.00	0.17	0.50	0.33
<i>Anapagurus laevis</i>	1	3	0	0		<i>Anapagurus laevis</i>	0.25	0.75	0.00	0.00

B. Qualitative data

	Size	Motility	Complete disjunctive table →		Size				Motility		
					<1cm	1-3cm	3-10cm	>10cm	Attached	Tubicolous	Crawler
<i>Abra alba</i>	1-3cm	Crawler		<i>Abra alba</i>	0	1	0	0	0	0	1
<i>Balanus crenatus</i>	1-3cm	Attached		<i>Balanus crenatus</i>	0	1	0	0	1	0	0
<i>Ensis</i>	>10cm	Crawler		<i>Ensis</i>	0	0	0	1	0	0	1
<i>Spio filicornis</i>	3-10cm	Tubicolous		<i>Spio filicornis</i>	0	0	1	0	0	1	0
<i>Kellia suborbicularis</i>	<1cm	Crawler		<i>Kellia suborbicularis</i>	1	0	0	0	0	0	1

386
 387
 388 **Fig. 3.** Illustration of data transformations of taxa × traits matrices (Table Q) prior to analysis. A. Fuzzy coding, one trait as an
 389 example (Life span, four modalities); for each taxon, affinity scores for life span modalities (left) are transformed in frequency
 390 profiles (right). B. Qualitative data, two traits as an example (left); for each taxon, “1” is ascribed to the dominant modality, “0”
 391 elsewhere (right).
 392

393 **4.3. Most common BTA approaches for investigation of biological gradients**
 394

395 For analyses of large communities, multivariate ordinations have become preferred tools to highlight
 396 taxonomic and biological gradients. Specific techniques have been developed for the analysis of the interplay
 397 of environmental descriptors, species occurrences and traits. A first review of technical advants was provided
 398 by Dolédec and Chessel (1991); crucial complements and ways to adapt analyses to research objectives were
 399 illustrated in Dray et al. (2003a). Here, we summarize the most commonly used techniques for biological
 400 trait ordinations; this list is nevertheless not exhaustive, other methods using different kind of metrics being
 401 also applicable. For simplicity, we group these techniques in: 4.3.1. Table Q ordinations – where we include
 402 those methods often used to investigate trait and species ordinations; and, 4.3.2. Relationships between

403 environment & pressures and biological traits – where methods for linking traits to habitat are summarized.

404

405 **4.3.1. Table Q ordinations**

406

407 Ordinations of simple quantitative traits (a single value per species and per trait) can be easily achieved with
408 the most common techniques. Normalised Principal Component Analysis (PCA; Hotelling, 1933), applied to
409 a correlation matrix, is relevant when different measurement units occur among traits (Ihde et al., 2011;
410 Pease et al., 2012). On the other hand, Centred PCA (Pearson, 1901), which is applied on a covariance
411 matrix, can be performed when traits have common measurement units (e.g. ordinal integer performance
412 score from 0 to 5); this procedure gives more importance to the variables (here traits) of higher variances and
413 scores compared to normalised PCA where all variances are equal to one.

414 A major development in BTA was brought by Chevenet et al. (1994) through Fuzzy Correspondence
415 Analysis (FCA); some practical examples can be found in Chevenet et al. (1994) and Usseglio-Polatera et al.
416 (2000). This technique was specifically designed to ordinate fuzzy coded data (Table Q, Fig. 3A); FCA axes
417 are constructed so that they maximize correlation ratios of traits (variance of modality scores divided by axis
418 variance). FCA incorporates properties inherent to simple correspondence analysis (Thioulouse and Chessel,
419 1992), a species (line) being positioned close to trait modalities (columns) for which it has the most
420 affinities, and reciprocally a modality being positioned around the species using it the most. This operation
421 depends on an initial chi-squared transformation of Table Q, sensitive to the diversity of associations
422 between species and traits modalities, and therefore tends to increase the number of axes to keep in the
423 analysis (i.e. high eigenvalues for several axes). FCA is thus relevant if the aim is to highlight precise
424 independent life history strategies reflected in modality groupings (many rare associations between one or a
425 few species and one or a few modalities). However, this dramatically increases the number of trade-offs as
426 the more diverse the assemblage included, the greater the chance that particular groups of species live in a
427 particular habitat (Statzner et al., 1997). Another version of a fuzzy coding analysis is the Fuzzy Principal
428 Component Analysis (FPCA; Chessel et al., 2004), less sensitive to rarity, and is simply a PCA centred in
429 columns and column-weighted per block (i.e. per trait) so that trait variances on axes are not influenced by
430 the number of categories per trait. In marine studies, fuzzy coding has been used to identify combinations of
431 trait modalities along biological gradients, but, very often, either graphical outputs are not conformed to a
432 proper use as illustrated in Statzner et al. (1994) or column-weighting prior to ordination is omitted, hence
433 cancelling the properties of fuzzy coded data.

434 The use of qualitative traits is also common in the literature (Beauchard et al., 2013; Benedetti et al.,
435 2015; Cleary and Renema, 2007; Dolédec et al., 1996; Ernst et al. 2012; Rachello-Dolmen and Cleary, 2007;
436 Ribera et al., 2001). Qualitative data ordination is possible through Multiple Correspondence Analysis
437 (ACM; Tenenhaus and Young, 1985). As in FCA, axis variance is also maximized by correlation ratios, but
438 column-weighting differs so that MCA is rather an equivalent to PCA on qualitative data; the data
439 transformation prior to ordination is illustrated in Figure 2B. Other procedures based on a dissimilarity
440 matrix processed by Principal Coordinate Analysis (PCoA) are also possible (Gower, 1971); see Darling et
441 al. (2012) for an application example.

442

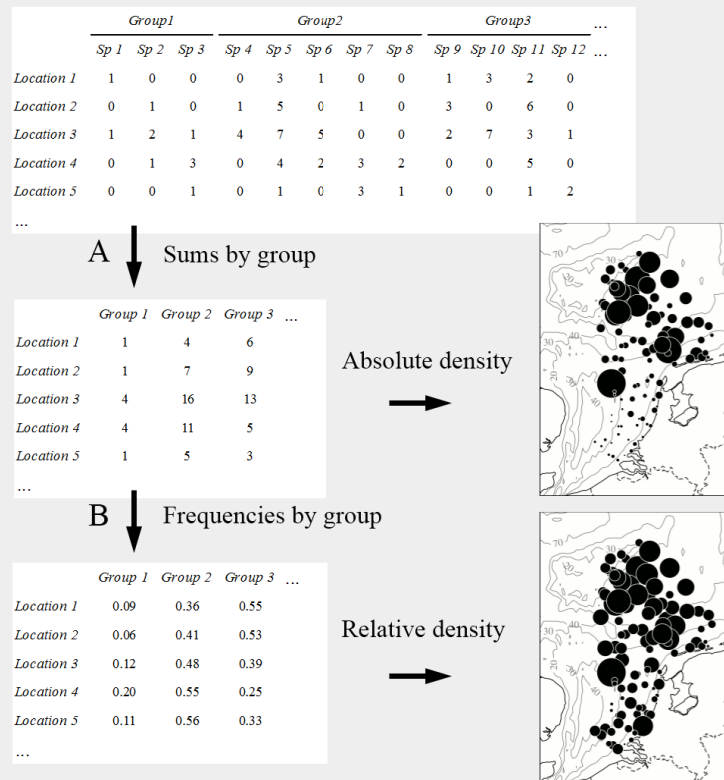
443 **4.3.2. Relationships between environment & pressures and biological traits**

444

445 Causality is a central question when studying pressures and gradients in community structure in the context
446 of ecological indicators. Analysis of Table Q can highlight the major gradients in the biological
447 characteristics of species in a community. Subsequent analyses can be undertaken to investigate how these
448 gradients may be linked to environmental factors, either natural, caused by human pressures, or both (Fig. 2).
449 A criterion to consider when using traits in BTA is their functional significance. A trait can be considered
450 “functionally significant” if it is significantly correlated to an environmental/pressure gradient and, of course,
451 if this relationship can be objectively interpreted; this can be easily done in the context of Figure 2B. The
452 context of Figure 2A illustrates the most advanced BTA, RLQ analysis, initially developed by Dolédec et al.
453 (1996). This method generates axes maximizing covariances between environment & pressures and traits,
454 and enabling the simultaneous representation of samples, environment/pressure descriptors, species and
455 biological traits. A critical factor in the interpretation of such an analysis is the significance of the
456 correlations measured between environment & pressures and traits. The analysis will always result in the
457 delineation the dominant correlations, but this does not preclude that these correlations should be stronger

458 than would be expected based on random allocations of species occurrences among samples and species
 459 performances among traits. In 1997, Legendre et al. proposed a first version of the “Fourth-corner method”.
 460 Independently of any kind of ordination technique, they developed a way to test the significance of
 461 environmental descriptors vs. biological traits relationships under a null hypothesis and based on a
 462 permutation procedure of columns and lines among the R, L and Q tables. Later, another version of the
 463 procedure was improved by Dray and Legendre (2008) to minimize type I error through a modified version
 464 of the permutation procedure delineating a suitable rejection zone of the null hypothesis. A correction of p -
 465 value assessment was proposed by ter Braak et al. (2012). More recently, Dray et al. (2014) developed a
 466 unified approach combining RLQ ordination and a testing procedure to assess the statistical significance of
 467 environment/pressure descriptors and traits correlations on RLQ axes in order to take into account multi-
 468 colinearity, which was not the case in the previous versions of the Fourth-corner method. The combination of
 469 RLQ and Fourth-corner method is now considered as the most powerful method for BTA (see Kleyer et al.,
 470 2012, for a comparative review of methods and extensions at both species and community levels) as it
 471 associates graphical interpretation and inferential statistics, this latter being determinant for biological trait
 472 selections.

473 Community Weighted Means (CWM; Garnier et al., 2007) is another approach used to relate traits to
 474 environment & pressures when objectives are limited to the community level as illustrated in Figure 2B. It
 475 involves building a samples \times traits table in which the lines match those of a samples \times environment &
 476 pressures table (Table R). From these tables, the absolute or relative mean value of a trait (or modality) is
 477 calculated per location, and subsequently these averages are spatially plotted or correlated with
 478 environmental factors. The choice between absolute and relative means can lead to different results, and this
 479 choice should be carefully based upon the research question (Schmera et al., 2014). Figure 4 exemplifies this
 480 problem, using the distribution of a typological group of benthic macroinvertebrate species (derived from a
 481 species \times traits ordination) in the Dutch sector of the North Sea where total individual density and species
 482 richness increase to the North (typical individual and biomass production gradient; Duineveld et al., 1992).
 483 Whereas the absolute density of this group follows this same pattern, its relative density provides weaker
 484 spatial contrasts, showing that functional identity (i.e. species of similar trait performances) can differ from
 485 production (i.e. common response of all species, of both similar and dissimilar trait performances).
 486



487
 488 **Fig. 4.** Computation of community weighted means matrix of a typological group resulting from a species \times traits ordination
 489 (clustering from Table Q ordination in Fig. 2). Species densities from Table L (samples \times species in Fig. 2) are first summed by
 490

491 group (A). The ratio of density of each group to site total (B) is necessary if research objectives are related to functional identity of
492 communities independently of production gradients. Maps: example of a same benthic macroinvertebrates typological group (12 life
493 history traits in Table Q; O. Beauchard, unpublished data), increasing in absolute individual density (proportional to circle diameter,
494 values standardised to their respective maximum) from South to North over the Dutch exclusive economic zone (southern North
495 Sea), as reported for the whole fauna (Duineveld et al., 1992); although the pattern of relative density shows a dominant habitat
496 preference in the North, contrasting values in southern locations demonstrate the possibility of independence between production and
497 functional identity. Faunal density data: Daan and Mulder (2009).
498

499 Although community-level analyses have more limited application potentials than the RLQ method,
500 correlations between environment/pressure descriptors and traits or typological groups can be more intuitive
501 and can be easily conducted through simple bivariate or multivariate correlations depending on the research
502 question (case of Fig. 2B). Classical multivariate approaches include ordinations on instrumental variables
503 such as Redundancy Analysis (PCA on instrumental variables, PCAIV; Rao, 1964), Canonical
504 Correspondence Analysis (CCA; ter Braak, 1986) or Co-inertia Analysis (Dolédec and Chessel, 1994; Dray
505 et al., 2003a). A relevant choice among these two approaches depends on theoretical objectives and data
506 table dimensions (i.e. number of lines relative to number of columns and the nature of interplays among
507 predictors); see Dray et al. (2003a) for details. See Kleyer et al. (2012) for a synthesis of possible table
508 couplings when correlating biological traits and environment & pressures by using different ordinations
509 methods.
510

511 **4.4. Remarks on technical uses in marine studies**

512
513 Technical issues in the marine literature are worthy of further scrutiny. The hereto reviewed ordination
514 techniques (4.3.1. and 4.3.2.) belong to a group of techniques called “eigenanalysis”, widely used in marine
515 studies. A separate group of techniques called “non-metric multidimensional scaling” (NMDS) is also
516 encountered in the literature, but a correct application requires a more complex procedure in several runs to
517 find an optimal number of significant axes (Legendre and Legendre, 2012). Uses of both techniques in the
518 literature are found systematically omitting the dimensionality of the analysed patterns, which could in turn
519 be provided to support scrutiny of the analysis undertaken: as a simple table or by a bar diagram of axis
520 eigenvalues (eigenanalysis), or by display of the stress function in the case of NMDS. Such omissions can
521 lead to incomplete result reporting and inability to truly scrutinise result interpretation.

522 Other points worthy of review concern the use of fuzzy coding. Frequently, graphical reporting of
523 ordination based on fuzzy coding is not conform with the originally described procedure (Chevenet et al.,
524 1994), with no justification provided for this contrast. Whilst the graphical display may be of secondary
525 importance, trait correlation ratios along ordination axes (ranging from 0 to 1), expressing trait significance,
526 are often missing. Sometimes, when provided, values are surprisingly low (close to 0), rendering the
527 robustness of the pattern very questionable. Also, in several cases, fuzzy coding was used under CWM
528 (Community Weighted Means, Fig. 2B) where trait modalities are weighted by species abundances.
529 Although there is no incompatibility in this approach, a certain order should be respected in the steps of the
530 procedure: first, matrix multiplication of raw data tables (Fig. 3A), after which fuzzy coding should be
531 applied according to Figure 3A. Then, the ordination of the fuzzy coded table should be processed by a
532 column-weighting operation ensured in FCA (Correspondence Analysis) and FPCA (Fuzzy Principal
533 Correspondence Analysis), techniques specifically designed for this data format (Chevenet et al., 1994).
534 Further to this, the strength of the interpretation of ordination in reviewed studies in which NMDS was used
535 on fuzzy coded data is not warranted as no information of this aspect is provided, and it also holds when
536 PCoA (Principal Coordinate Analysis) was used. The weighting procedure ensures that traits with different
537 numbers of modalities have a similar numerical importance in the analysis; otherwise, sites (CWM) or
538 species (Table Q), traits and modalities can be artificially positioned on factorial planes without truly
539 reflecting their biological or ecological meaning.

540 Lastly, marine studies can cover very large spatial extents such as entire shelves, and this might condition
541 the choice of analytical approaches, especially regarding RLQ or CCA (Canonical Correspondence Analysis)
542 ordination. Correspondence analysis of Table L (Fig. 2) is central in these methods, but its optimal use
543 requires unimodal species responses along environmental gradients (ter Braak C.J.F., 1985; Thioulouse and
544 Chessel, 1992). However, at the regional scale, multimodal responses of species can occur due to the
545 presence of natural vicariances in population structure, due to biogeographic features. More generally, at
546 different spatial scales, multimodal responses may also result from local depletions in specific habitat

547 requirements caused by the impacts of human activities. In such contexts, RLQ and CCA may have limited
548 technical applications. Users should thus be mindful of this potential issue and, in such cases, consider
549 alternative analytical approaches.

550

551 **5. Relevance and limitations of BTA in marine studies**

552

553 **5.1. Phylogenetic groups**

554

555 BTA of benthic macroinvertebrates is most frequently carried out in impact assessment studies due to the
556 relevance of these organisms which account for a large part of sea-floor integrity and functioning (Van Hoey
557 et al., 2010), and which are directly exposed to the damaging effects of intense human activities such as
558 dredging and beam-trawling (Clark et al., 2016). However, other activities (e.g. degassing along ship traffic
559 routes) have consequences on other marine compartments (e.g. water surface and column) where other
560 ecosystem components may be more exposed than the benthos. Further focus on pelagic organisms could
561 therefore help improve the development of complementary indicators and broaden the spectrum of ecological
562 indicators over the whole marine system. This could also enable the development of indicators of optimized
563 temporal accuracy. For instance, phytoplankton provides an ideal group to apply trait-based approaches
564 because of their relative simplicity and the well-defined traits that determine their ecological niche (Litchman
565 and Klausmeier, 2008); due to a short generation time, phytoplankton can respond to environmental
566 changes over very short time periods (Litchman and Klausmeier, 2008; Edwards et al., 2013). Phytoplankton
567 trait studies have recently emerged and developments are currently ongoing (Litchman et al., 2010), and
568 compilation of their physiological and biophysical status could solve problems encountered since the 1990's
569 in finding causal phytoplankton model developments. Additionally, BTA on longer-living species such as
570 large pelagic vertebrates with complex development stages should be more relevant to assess long-term
571 marine ecosystem health. In this respect, mammals are relevant candidates and many mammal species are
572 widely distributed, enabling the development of indicators operational over very large areas (Davidson et al.,
573 2012).

574 The use of a multiplicity of phylogenetic groups is common in marine studies, particularly in benthic
575 studies, and important remarks on the relation between taxonomy and trait relevance deserve attention. The
576 essence of BTA is generally to mask taxonomic differences among communities in order to bring out their
577 mechanistic differences. Firstly, this enables relevant comparisons at both small and large scales, in the latter
578 case where historical processes engender strong taxonomic differences between regional biota whereas
579 similar habitats (e.g. similar stress and disturbance) from distant areas may conserve the same selection
580 forces of growth, survival and reproduction (i.e. habitat filtering; Webb et al., 2002). Secondly, there is no
581 technical limitation in BTA, even in broad extents when combining algae, invertebrates, fish, mammals, and
582 birds so long as every trait is measurable in all organisms (Dolédec and Statzner, 1994). For instance, within
583 the trait “Motility”, a polychaete cannot fly but simply its score for the modality “Flying” is null.
584 Additionally, there is no theoretical limitation to the number of traits to use, at least if a procedure justifies
585 the selection of a subset of traits significantly associated to habitats (Kleyer et al., 2012). BTA encompassing
586 such large diversity of organism types may be relevant at the ecosystem scale when taking all habitats and
587 processes into account is necessary (e.g. comparing ecosystems among biomes). However, depending on the
588 nature and the sensitivity of the required indicator development, some traits may affect the relevance of this
589 type of BTA. Traits convey information at divergent levels of requirement; a trait can express whether a fish
590 or a bird can fly whereas some others can express whether they share the same resource or not (e.g. preys). In
591 this sense, mechanism and taxonomy can converge or diverge depending on traits. For example, the use of
592 morphology can be questionable in many studies of marine benthic communities including several phyla
593 when the trait modalities are so closely linked to taxonomy that they become a proxy for the taxonomy of the
594 underlying community (Aarnio et al., 2011; Darr et al., 2014; de Juan et al., 2007; Paganelli et al., 2012; van
595 Son et al., 2013): a “Vermiform” morphology tends to cluster annelids together, a “Globose” morphology
596 tends to cluster echinoids, and “Laterally flat” or “Dorso-ventral compressed” or “Bivalved” tend more
597 simplistically to cluster bivalves. The main problem here is that such a trait is poorly related to fitness to
598 explain species occurrences among habitats, and possible roles of morphology along biological gradients are
599 poorly discussed. Morphology was constructively used in a determinant work on benthic communities from
600 running waters where hydrology strongly conditions the affinity of organisms to substratum (Townsend et
601 al., 1997). This might be an important distinction from marine soft bottoms where hydrological forces are

602 reduced and where burrowing living mode is enabled to a large diversity of morphologies. When working
603 within a clade (e.g. teleost fishes only) morphological characters may be more mechanistically expressive,
604 e.g. in terms of habitat adaptation, and identification of habitat degradation and feeding preferences (Villéger
605 et al., 2010; Farré et al., 2013).

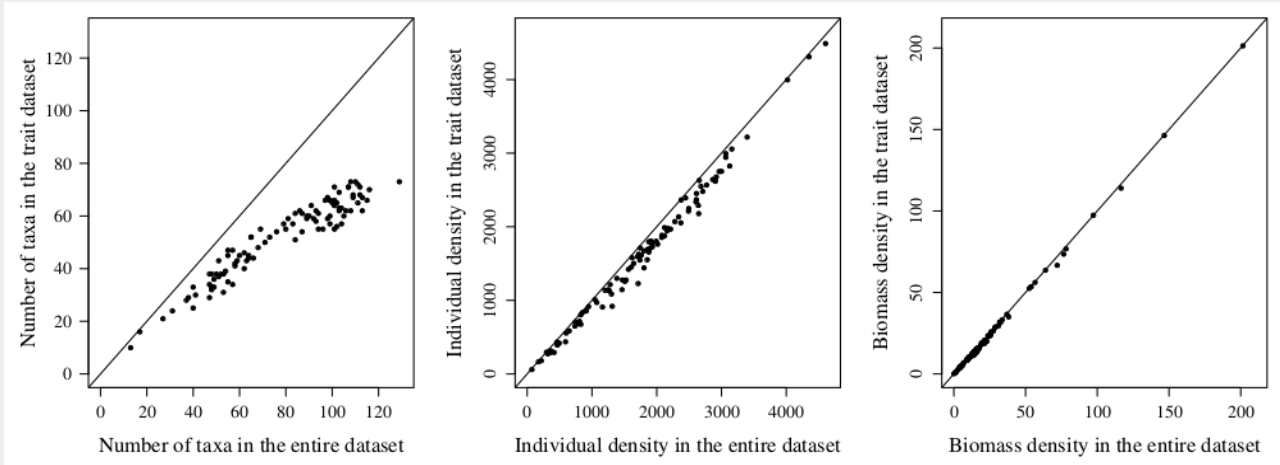
606 Although there is no technical limitation to multivariate BTA, the selection of some traits can be
607 irrelevant when considering several and very distinct phyla into account. This can be the case when building
608 a typology of indicator species groups (from a species \times traits table; Fig. 4) to compare different ecosystems
609 (i.e. ecosystem level indicators defined by an ecosystems \times groups table) whereby the use of some traits can
610 induce confounding effects. In a broad sense, motility acts as a taxonomic proxy separating benthos (e.g.
611 polychaete, modality “crawler”), pelagos (e.g. fish, modality “swimmer”) and avian component (modality
612 “flyer”) due to the three-dimensional nature of marine ecosystems. Consequently, at the ecosystem level,
613 taxonomy is confounded with the functional specificity of habitats such that biological gradients that would
614 ordinate these three modalities would express a basic habitat occupancy (i.e. bottom, water column and
615 surface); to a lesser extent, a trait “respiration type” (modalities “aquatic” vs. “aerial”) would induce a
616 similar effect. In other words, the resulting typology would simplistically show that fishes swim and birds
617 fly. By contrast, a meaningful typology should cluster species having similar degrees of sensitivity to
618 environmental variabilities in terms of abiotic forces or resource fluctuations. At least, in studies involving
619 different phylogenetic groups like in traditional benthology, traits affecting fitness (growth, survival and
620 reproduction) such as body size, sexual maturity, fecundity and reproductive frequency should be prioritized.
621 Avoiding taxonomically discriminant traits may better enable to highlight life history strategies common to
622 species from different phyla and of common mechanistic adaptations to habitat spatio-temporal variability,
623 hence evidencing their ability to resist to stress or their capability to recover from a disturbance. However, at
624 the level of the entire ecosystem, the use of such traits will fail in aiming at meaningful developments caused
625 by the strongly discriminant biologies of distant phyla (e.g. comparable annual fecundities between
626 macroinvertebrates and fishes, but not with birds or reptiles; similarly, body size between invertebrates and
627 mammals, etc.); see Cardeccia et al. (2016) as an illustrative example. In this respect, important
628 developments masking size effect have been done in life history ecology to explore differences and
629 similarities among taxonomically distant groups (Charnov, 1997; Charnov and Berrigan, 1991). It has been
630 shown with a few traits and dimensionless ratios that phylogenetic groups exhibit similar functionalities in
631 terms of energy allocation (life history invariants), whereas functional differences may explain
632 environmental adaptations; however, works in this direction are still necessary (Charnov, 2002; Economo et
633 al., 2005). In marine ecology, fish is by far the ecosystem component for which such achievements have
634 been the most elaborate (Greenstreet et al., 2012).

635 636 **5.2. Biological trait data availability and quality**

637 Although the publication rate of studies on biological traits in the marine environment is increasing, current
638 inventories of trait data remain limited for the vast majority of the large number of marine species, in many
639 taxonomical groups (Tyler et al., 2012), including phytoplankton (Litchman and Klausmeier, 2008) and
640 benthic macroinvertebrates (Bolam et al., 2014). Recent initiatives have therefore attempted to improve
641 public access to trait inventories, supporting the growth of trait data bases (Brey, 2001; Bremner et al.,
642 2006b; MarLIN, 2006; Bruggeman, 2011; Barton and Pershing, 2013; Queirós et al., 2013; Faulwetter et al.,
643 2014); see Costello et al. (2015) for a detailed overview. Stutzner and Bêche (2010) pointed the general
644 problem of retirement of ageing experts, limiting the extension of existing data bases. In the marine
645 community, Dayton (2003) evoked the basic ability of species identification which could be consequently
646 undermined. Currently, the analytical potential of traits has been severely limited by incomplete collection of
647 traits on a wide range of species, like in the phytoplankton (Litchman and Klausmeier, 2008) and in benthic
648 macroinvertebrates (Bolam et al., 2014). Despite the recent efforts to improve marine trait data availability,
649 the vast extent of marine ecosystems requires continued efforts in species autoecology, but financial support
650 to these types of fundamental science is often difficult to gather.

651 Is it important to document every species in every sample? It has been suggested that reductions of taxon
652 lists can be undertaken under the assumption that trait composition behaves in the same way as species
653 compositional structure in a random subset (Bremner, 2008). For instance, this is the traditional approach
654 implemented in meiofauna samples when the logistical difficulty of analysing a whole sample deem it
655 mandatory to that only a random subset of organisms in a sample are actually analysed. It follows therefore
656

657 that biological traits will be most documented for dominant species. However, whether or not this
 658 assumption is supported by evidence has not frequently been discussed in BTA. In the absence of a general
 659 rule, and when adequate data is available, basic verifications enable to assess the relevance of a taxonomic
 660 subset from a whole taxocenosis (Fig. 5). It is also possible to test whether community structure is indeed
 661 conserved from an entire data set to a random subset through multivariate concordance of sample locations
 662 (using locations \times species tables; sensu Dray et al., 2003a, 2003b). If the main features of species
 663 assemblage's subset are representative of the whole data set (i.e. concordant community structures between
 664 entire data set and subset), nothing prevents its use to derive resistance or resilience properties to stress and
 665 disturbance among the entire communities. As biological traits are most documented for dominant species,
 666 this may be less possible for specific purposes such as biological conservation when analyses require to
 667 consider many rare species (Mouillot et al., 2013a).
 668



669
 670 **Fig. 5.** Comparison between a whole taxocenosis of benthic macroinvertebrates ($n = 384$ taxa) and a subset ($n = 182$ taxa)
 671 documented for life history traits (12 traits; O. Beauchard, unpublished data). The three basic community descriptors (number of
 672 taxa, individual density (number of individuals/m²) and biomass density (AFDW g/m²)) were calculated for each sample (black dots,
 673 103 sampling stations). Despite a large number of undocumented taxa, the documented data set conserves the main features of
 674 community structure from the complete data set. Faunal density data: Daan and Mulder (2009).
 675

676 When sufficient biological information is available, fuzzy coding is usually employed in ordination
 677 analysis, and this fact deserved some considerations. Fuzzy coding can be a constraining approach as it
 678 requires a significant bibliographical research to support the application of trait variances within the coding,
 679 and this is not always available for a substantial amount of marine species. Documenting the biology of a
 680 widely distributed species based on the literature from its entire biogeographical range can lead to
 681 irrelevances if the research context is limited to a sub-regional scale. For instance, many species in the north-
 682 east Atlantic, distributed from Norway (sub-Arctic) to the Mediterranean Sea (temperate warm), and may
 683 often exhibit local differences in trait performance (e.g. body size, age at maturity, reproductive season). For
 684 a species, the variance of a trait at the biogeographic scale can result from other processes (e.g. history) than
 685 the variance between habitats in a local area characterized by smaller variations in trait or modality
 686 performances (e.g. local habitat heterogeneity). It is not sure that this issue was considered in existing marine
 687 studies where fuzzy coding was used. In principle, trait variance should reflect the consequences of species
 688 evolution and adaptation to spatio-temporal habitat heterogeneity. Statzner et al. (1997) evidenced this
 689 correlation in freshwater communities at a small scale, but they also showed that it did not hold at a larger
 690 scale with the variance consequent of their compiled data.

691 Recent efforts across the peer-review community to improve access to source data is also increasing the
 692 transparency and access to data inventories, and this is a welcome change in the marine literature.
 693 Frequently, citations for source literature in marine BTA studies we reviewed focused on a few key
 694 references (e.g. books and/or online data bases) whereas referencing individual assignments of trait
 695 modalities or scores within species (Tillin et al., 2006) could be seen as a basic requirement which would
 696 benefit, at least, to the quality of the peer-review, but would mostly benefit the progress of the field.
 697 However, when documentation of trait assignment is limited, qualitative coding is still possible (Fig. 3B) and
 698 can be seen as less dubious, particularly if biological gradients are relatively long. For instance, an error in

699 categorising the body length class of a species ranging in reality between 1 and 3cm, e.g. either <1cm or 3-
700 10cm by error, will be negligible in the final data set if body lengths of the different documented species
701 range sufficiently (e.g. from <1cm to >30cm) and if a sufficient number of classes are considered across the
702 trait, ensuring a meaningful variance expression of the trait across species (for these exemplified values in
703 benthic macroinvertebrates, typically five to six classes are found in the literature). In summary, the problem
704 of data availability can be solved but it implies a certain pragmatism: when information is scarce, it should
705 be recognized upfront, and a simple analytical approach with realistic data should be preferred against a
706 sophisticated one with improbable data.

707

708 **5.3. Uses in ecological indicator development**

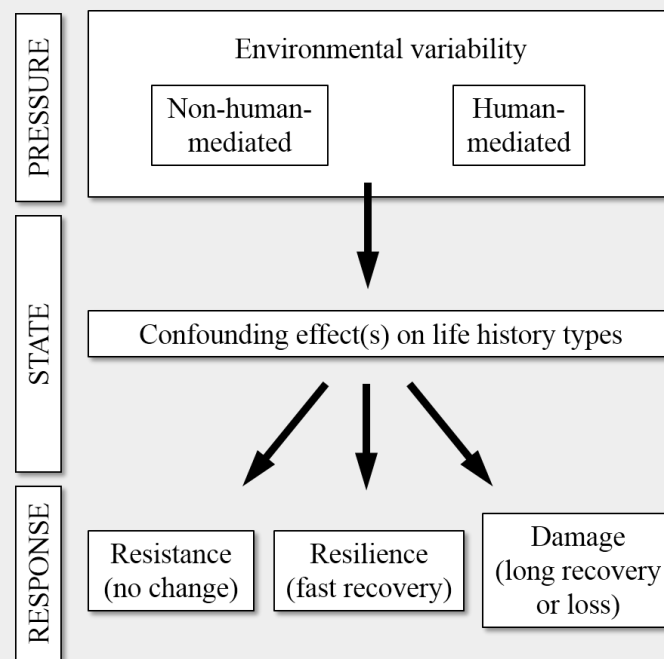
709

710 BTA provides great benefits when several traits are used and when the resulting multivariate pattern provides
711 few synthetic biological gradients along which traits positively and/or negatively covary. This reduction of
712 complexity can progressively pave the way for ecological indicators of pressures on the marine environment,
713 since an indicator should be a simplification of ecological complexity. Whilst indicator development in
714 entirety dictated by the research questions, it is possible that indicators based on single traits may fail to
715 represent co-evolutionary processes exhibited by natural communities, which lead to a filtering of life
716 histories at the local scale. Traits are expressed in concert, reflecting life history strategies (Greenlade,
717 1983; Southwood, 1988), and their synthetic use lowers uncertainties in correlation analyses that target
718 understanding or predicting community structure (Márquez and Knowles, 2007). In those cases, holistic
719 approaches investigating the implications of multiple and complementary traits reflecting species
720 occurrences may therefore be more relevant to evaluate the response of marine species communities to
721 pressures, than single trait approaches. The interest of marine ecologists for individual traits is still firmly
722 rooted on the aim of identifying “magic” indicator traits whereas such approaches can be poorly conclusive
723 as evidenced by Bolam et al. (2014).

724 Organism-based indicator development should aim to consider both traits that confer sensitivity and
725 recoverability in the face of pressures. Some traits are more easily coupled to sensitivity: for instance, many
726 benthic studies have reported the sensitivity of sessile organisms to beam-trawling. However, a sessile
727 species, whilst being indeed sensitive, may easily recover after a disturbance due to auxiliary advantages
728 such as meroplanktonic larval stage (dispersal advantage) or early age at sexual maturity (fast generational
729 dynamics). This can be illustrated by comparing sedentary tubicolous worms and some corals, both exposed
730 to physical damages, but with different recovering potential (some spionid worms mature at only a few
731 months of age whereas some coral species do not reproduce before reaching ten years of age). In this regard,
732 an approach less explored in empirical ecology, but used frequently in ecological modelling (Queirós et al.,
733 2015), is the elaboration of typological groups of species based on the simultaneous use of multiple traits.
734 This approach, considering groups of species with similar trait performances, was suggested by Stearns
735 (1992), hence solving the problem of the multiplicity of trade-offs (Statzner et al., 1997). Clustering species
736 scores from the main axes of a multivariate analysis may therefore be more relevant to indicator
737 development than many analyses of individual traits, as it considers simultaneously the multiple biological
738 facets of a species pool (interactions and covariations). This may lead to improved understanding of temporal
739 variations in species communities based on only a few consequent indicator variables as required for
740 management. The works of Winemiller and Rose (1992), Van Buskirk and Crowder (1994), Cortés (2000),
741 Darling et al. (2012) and Benedetti et al. (2016) are exemplary in this respect. They deal with different
742 taxonomic groups of marine organisms and derive biological gradients from multiple traits ordinations;
743 combinations of trait modalities are discussed as evolutionary determinants of life history strategies and
744 adaptations to habitats. However, empirical validations with field data are still needed to support the
745 development of operational indicators.

746 Since the 1970's, general theories on community and habitat relationships in which traits play a central
747 role have flourished (Grime, 1977; Hildrew and Townsend, 1987; Sibly and Calow, 1985; Reynolds, 1999;
748 Southwood, 1977). Most of them define axes opposing life history strategies, often in the number of three,
749 corresponding to specific environmental conditions (stress, disturbance and favourableness). Winemiller and
750 Rose (1992) pioneered the assessment of the relevance of such theories in marine fish communities; more
751 recently, Lawrence (2013) reviewed the potential applicability in sea urchins. From theory to indicator
752 development, a strong assumption made may be that human pressures mimic non-human-mediated forces,
753 inducing similar environmental variabilities. For example, eutrophication of habitats can occur without

754 human mediation (e.g. phytoplanktonic bloom caused by meteorological phenomena); comparatively, waste
 755 water discharges or aquaculture can drive local eutrophication, resulting in human-mediated change in
 756 primary producers and their surrounding food web (Pearson and Rosenberg, 1978). Similarly, physical
 757 damages (e.g. dredging, trawling) may engender the same effects on benthos than storms and strong bottom
 758 water currents (Kenchington et al., 2001; Lindegarth et al., 2000; Queirós et al., 2006). Hence, non-human-
 759 and human-mediated forces on ecosystems can drive similar types of changes in natural communities by
 760 selecting similar species trait expressions. Natural and human pressures gradients can be confounded, as
 761 observed in fisheries where fishing intensity can be driven by a gradient of biological productivity (Hinze et
 762 al., 2009; van Denderen et al., 2014). The sensitivity of communities can radically change along these
 763 gradients, so that a significant relationship between the density of vulnerable organisms and fishing intensity
 764 can be observed; neither by fishing only nor by environmental conditions only, but by both. In these cases,
 765 identifying causality between a human pressure and biological traits (or any derived indicator) in natural
 766 communities can be challenging, and requires that the effects of natural, environmental variables are
 767 removed, so that the effects of the pressure of interest can be isolated. Procedures to overcome confounding
 768 effects are increasingly used (Borcard et al., 1992; Legendre and Legendre, 2012), but are still rare in marine
 769 ecology. These procedures are, however, fundamental to assess reference conditions (European Community,
 770 2000) and good environmental status of marine waters (European Community, 2008; Queirós et al., 2016).
 771 As noted by others, understanding of natural variability already existent in a system determines the ability to
 772 accurately attribute impacts of a managed pressure (Queirós et al. 2016). If it can be assumed that human
 773 pressures mimic natural variabilities, the development of ecological indicators could be made possible in a
 774 very comprehensive way. Figure 6 summarizes how ecological indicators derived from multiple traits could
 775 be rendered understandable and operational.
 776



777
 778
 779 **Fig. 6.** Conceptual representation of trait-based ecological indication with life history strategy, derived from biological trait analysis,
 780 as a central component due to natural evolutionary adaptations to environmental variability: habitat conditions and human pressures
 781 can similarly impact a species community so that indicators based solely on response to pressure may be inadequate if the effect of
 782 habitat is not removed.
 783

784
 785 **6. Conclusion: Can the development of ecological indicators arise from BTA in marine systems?**
 786

787 The use of biological traits in marine ecology is a growing research field and could positively relaunch
 788 interest for natural history. The conservation of biodiversity requires factual knowledge of particular
 789 organisms whereas we know little or nothing of most marine species (Greene, 2005). This review provides
 790 additional evidence that trait understanding, and its links to life history of marine organisms, is poorly

791 documented for ecosystem components other than benthic macroinvertebrates and fishes. Two main
792 constraints curb a larger and better use of multiple traits to increase knowledge of marine ecosystems.
793 Firstly, high expertise is required in assigning trait performance to taxa and in designing and analysing data
794 sets, in a large diversity of numerical contexts. Secondly, biological trait data availability remains a critical
795 obstacle to applications in many biogeographic areas. Therefore, most of marine BTA studies have been so
796 far carried out for very specific purposes over well studied areas of limited spatial extent. Consequently,
797 ecological indicators derived from multiple traits, those with the greatest anchoring in ecological theory, are
798 still largely absent in marine monitoring. Further developments risk to be compromised without large-scale
799 projects involving fundamental trait data compilations and the maintenance of biological expertise within the
800 scientific community. Workshops and collaborative projects associated to current ones are necessary to
801 concrete achievements based on biological traits (Barton et al., 2016; Costello et al., 2015).

802 Fundamental research and marine ecological indicator development leading to sound applications for
803 maritime management will remain limited as long as they will not be well founded in theory and based on
804 complete sets of meaningful traits. For the time being, the vast majority of existing BTA studies are seen
805 here as exploratory, and more work is necessary to support their use as decision-making tools. Extensive sets
806 of biological traits may be needed to understand the functional nature of species communities, when this is
807 the aim, applications focused on individual traits separately may fall short as indicators. Life-history
808 typologies may provide a useful approach to derive meaningful marine ecological indicators expressing the
809 effects of environmental pressures and their variability.

810

811

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813

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