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This paper reviews the utility and availability of biological and ecological traits for marine species so as to prioritise the development of a world database on marine species traits. In addition, the 'status' of species for conservation, that is, whether they are introduced or invasive, of fishery or aquaculture interest, harmful, or used as an ecological indicator, were reviewed because these attributes are of particular interest to society. Whereas traits are an enduring characteristic of a species and/or population, a species status may vary geographically and over time. Criteria for selecting traits were that they could be applied to most taxa, were easily available, and their inclusion would result in new research and/or management applications. Numerical traits were favoured over categorical. Habitat was excluded as it can be derived from a selection of these traits. Ten traits were prioritized for inclusion in the most comprehensive open access database on marine species (World Register of Marine Species), namely taxonomic classification, environment, geography, depth, substratum, mobility, skeleton, diet, body size and reproduction. These traits and statuses are being added to the database and new use cases may further subdivide and expand upon them.

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Mark John Costello[1], Simon Claus[2], Stefanie Dekeyzer[2], Leen Vandepitte[2], Éamonn Ó Tuama[3], Dan Lear[4], Harvey Tyler-Waters[4]

[1] Institute of Marine Science, University of Auckland, New Zealand 1142.
[2] Vlaams Instituut voor de Zee, VLIZ – InnovOcean site, Wandelaarkaai 7, 8400 Oostende, Belgium.
[3] Global biodiversity Information Facility, Copenhagen, Denmark
[4] Marine Biological Association, Plymouth, Devon, UK.

ABSTRACT

This paper reviews the utility and availability of biological and ecological traits for marine species so as to prioritise the development of a world database on marine species traits. In addition, the 'status' of species for conservation, that is, whether they are introduced or invasive, of fishery or aquaculture interest, harmful, or used as an ecological indicator, were reviewed because these attributes are of particular interest to society. Whereas traits are an enduring characteristic of a species and/or population, a species status may vary geographically and over time. Criteria for selecting traits were that they could be applied to most taxa, were easily available, and their inclusion would result in new research and/or management applications. Numerical traits were favoured over categorical. Habitat was excluded as it can be derived from a selection of these traits. Ten traits were prioritized for inclusion in the most comprehensive open access database on marine species (World Register of Marine Species), namely taxonomic classification, environment, geography, depth, substratum, mobility, skeleton, diet, body size and reproduction. These traits and statuses are being added to the database and new use cases may further subdivide and expand upon them.

INTRODUCTION

World databases of marine species have now been published but are limited to taxonomic (e.g., WoRMS) and distribution (e.g., Ocean Biogeographic Information System, OBIS) data (Costello *et al.* 2007). The benefits of these databases could be multiplied by associating species with richer ecological and biological information. Classification of species provides hypotheses for the evolution, organisation, and ecological interactions of biodiversity from genes to ecosystems. Initially, newly discovered species are classified by their taxonomic relationships, which are intended to indicate their evolutionary lineages and origins. New research challenges this classification, resulting in changes to species genera and even changes in higher taxonomic classification (Costello *et al.* 2013a). Species are readily classified by their geography, for example what region, country or locality they occur in, and within that, by environment (e.g., freshwater, terrestrial, marine, soils or sediments). Ecological classification is more complex, and may refer to their habitat, a concept combining the physical environment and associated species with which the species typically occurs (Costello 2009). Species may be associated with a guild of co-occurring species similar in distribution and habit; such as benthos, plankton, sessile epifauna, or ectoparasites. Biological classification includes attributes of life stages, reproduction, body size, behaviour, feeding method, and diet. However, data on such attributes or species traits are widely scattered in the literature and are time consuming to gather (Naeem and Bunker 2009, Tyler *et al.* 2012). To solve this, databases of traits for (a) 21,000 species of freshwater plants, invertebrates and fish in Europe (Schmidt-Kloiber and Hering 2015), and (b) terrestrial plants (Naeem and Bunker 2009, Kattge *et al.* 2011), have been established.

A rich terminology surrounds descriptions of a species biology and ecology, with sometimes different definitions for the same terms, synonymous terms, and context dependent (e.g., habitat) terms (e.g., Lepczyk *et al.* 2008, Hernandez-Perez *et al.* 2014). This terminology has developed over several hundred years of natural history, in different languages, and often terms have multiple meanings in common use. For example, "littoral" habitat can be the marine zone between the low and high tide marks, extend to the continental shelf and include coastal river catchments, and refer to the edge of freshwater lakes (Aquatic

51 Sciences and Fisheries Abstracts 2014). The lack of standard use of terms can compromise the bringing
52 together of this knowledge from different sources, and thus limit understanding of patterns beyond local
53 scale, context specific studies (Lepczyk *et al.* 2008). Hence the publication of a glossary particular to the
54 marine biology community (Costello *et al.* 2010) that followed a popular biology and ecology dictionary
55 (Lincoln *et al.* 1998). That glossary provided the starting point for a standard vocabulary to be used in the
56 World Register of Marine Species (WoRMS) database (Costello *et al.* 2013a).
57   In this paper we review and classify traits so as to decide which should be prioritised to apply to
58 marine species in WoRMS. In parallel, we are developing a wider vocabulary and classification of traits
59 that would provide the basis for expanding the traits in WoRMS in the longer-term. Thus scientists
60 interested in more detailed trait classifications for a particular taxon or ecological function could build on
61 the more general primary traits proposed here.
62
63 **Biodiversity databases**
64   Global databases that integrate information on species force the development of standard
65 classifications (Costello and Vanden Berghe 2006). This process then enables analyses across many species
66 and datasets previously compromised by inconsistent terminologies. The World Register of Marine Species
67 (WoRMS) is such a database (Costello *et al.* 2013a, Boxshall *et al.* 2014). It contains the names of almost
68 all known marine species and classifies them (1) taxonomically, (2) by environment (e.g. marine,
69 freshwater, terrestrial), and (3) by geographic distribution. Each additional field in the database may have
70 a multiplier effect on how useful the database may be to researchers, educators and other users. For example,
71 the availability of the author and year of description of each species, and their synonyms, has facilitated
72 research into the rate of discovery of marine species (Costello and Wilson 2011, Mora *et al.* 2011, Appeltans
73 *et al.* 2012, Costello *et al.* 2012, 2013b, c, d, 2014 a, b, 2015).
74   Several databases already include information on marine species traits, namely WoRMS, BIOTIC
75 (Marshall *et al.* 2006), FishBase (Froese and Pauly 2014), and SeaLifeBase. The SeaLifeBase data fields
76 are a subset of those in FishBase. These databases have already applied some traits to marine species and
77 it can be preferable to build on these applications than start anew. However, they contain hundreds of traits
78 which would take considerable effort and resources to apply to all marine species. Thus, in this paper we
79 present a rationale for the prioritisation of traits for immediate inclusion in WoRMS.
80
81 **User needs**
82   Particular groups of users have begun to develop thematic databases within WoRMS. For example,
83 species involved in Harmful micro-Algal Blooms (HAB) (Moestrup *et al.* 2013), occurring in the deep sea
84 (WoRDSS, Glover *et al.* 2013), and that have been introduced by human activities (Pagad *et al.* 2015).
85 Biological traits may also be used to help predict a species sensitivity to toxic substances (Baird and Van
86 der Brink 2007), but may be a poor predictor of its likelihood of going extinct, becoming invasive, and/or
87 its reaction to climate change (Angert *et al.* 2011). However, a failure to detect which traits affect a species'
88 ecology at a global level may be because traits are operational within a local and regional context (Vermeij
89 and Leighton 2003). That is, the importance of traits is relative to the ecological and environmental factors
90 acting on individuals of a species at any time.
91   Traits that determine ecological function can be better predictors of invasiveness of marine fouling
92 communities (e.g.**,** Atalah *et al.* 2007a, b, Wahl *et al.* 2011) and be less sensitive to sampling effort for
93 sediment macrobenthos (Törnroos and Bonsdorff 2012) than taxonomic richness. The richness of traits in
94 an assemblage of species is positively correlated with species richness but not necessarily linearly (e.g.**,**
95 Cumming and Child 2009, Törnroos and Bonsdorff 2012**)**. Other users of marine species data include
96 ecologists studying the functional role of species in ecosystems (e.g.**,** Naeem and Bunker 2009, Bostrom *et*
97 *al.* 2010). They may wish to know a species' place in the food web and body size. The value of biodiversity
98 to society is being quantified in terms of ecosystem goods and services, with the species' importance being
99 dependent on their functional role in the ecosystems. Conservation biologists conduct species extinction
100 risk assessments using standard criteria based on species biological (e.g.**,** population size and trends,
101 generation time, age at maturity, longevity, fecundity, natural mortality) and geographic (e.g.**,** range size)

102 traits (IUCN 2012, Grave *et al.* 2015). Invasive species are an increasing concern. So information on which
103 species have been introduced beyond their native range by human activities and have become invasive is
104 in demand (Blackburn *et al.* 2014, Jeschke *et al.* 2014). Whether a species is likely to be transported by
105 human activities, such as in ballast water, fouling on a ship-hull or aquaculture equipment, may depend on
106 its habitat, habit and modes of dispersal (Brine *et al.* 2013). Gallien *et al.* (2014) proposed phenotypic
107 similarity, based on taxonomic and functional traits, can predict invasiveness in communities.

108 We propose that the traits that users need should be prioritised for inclusion in databases. Ideally,
109 this should result in users publishing new analyses resulting from the inclusion of traits in the database,
110 which in turn would drive improvements in the quality and quantity of trait information. For the purpose of
111 this paper, we identify two main classes of users, scientists (usually ecologists) and wider society.
112 Ecologists require traits that identify a species' role in an ecosystem. These traits provide the basis for
113 understanding and assessment of species socio-economic importance. Society is interested in species by
114 virtue of their importance as food (e.g., fisheries, aquaculture), threat to human and animal health (e.g.,
115 toxic algae and other species, sharks), pests (e.g., invasive), and likelihood of extinction.

116 It must also be recognised that most traits are not available in the literature for most species. For
117 British North Sea macrobenthos, body size was the most available trait (Webb *et al.* 2009). Tyler *et al.*
118 (2012) found there was no trait data available for about a quarter of the North Sea macrobenthic species,
119 and most traits were only available for about another quarter. They found that adult mobility, feeding
120 method, development mode, sociability, migration and life span were available for only 30-40% of the
121 species with body size data. The most valuable traits for end users wishing to compare traits across taxa
122 will be those available for most species.

123

Data

125 Data related to species may be of numerical, continuous and categorical form (Törnroos and
126 Bonsdorff 2012). Most traits are categorical, that is they are a concept described in a word that may or may
127 not apply to a species, such as whether a species is a parasite or not. Törnroos and Bonsdorff (2012) show
128 the utility of categorical traits for marine benthos because a wider variety of concepts and traits can be
129 applied to species than if limited to numerical measures. However, some traits can be described by
130 numerical data, such as body size and depth distribution, and geographic distributions by continuous
131 variables such as contours on maps. Numerical and continuous trait data are preferable because they can be
132 converted into categorical (concept-based) data but not the reverse. Thus, an actual depth range would be
133 preferred to 'bathyal' or 'mesopelagic' because the latter categories cannot be converted to a depth range.

134 Most traits will need to be applied to a particular life stage, probably the adult stage in the first
135 instance. In some cases traits may vary between sexes and populations (e.g., body size). Population level
136 traits would require each trait to be placed in the context of the sampled location, and it may be unclear as
137 to how representative they may be of the species.

138

Aims

140 In this paper, we review traits assigned to marine species in existing biodiversity databases, and
141 evaluate which would be most useful to users to prioritise for inclusion in WoRMS. The criteria for
142 prioritisation were that (1) the trait could (in theory) be applied across most taxa, (2) that information on
143 the trait existed for most taxa, and (3) it was likely that the availability of the trait would result in new uses
144 of the databases in the short-term. As there are arguments for more and fewer traits depending on user
145 needs, we created a top-10 shortlist. If a trait could be applied at a higher taxon level (e.g., family, order,
146 phylum) this would make it easier to apply across many species. Where possible, we favoured numerical
147 and continuous traits over categorical. Thus, although traits peculiar to populations rather than a species,
148 and secondary traits derived from others, were not prioritized for inclusion in WoRMS, these are included
149 in a wider classification and vocabulary for discussion by users.

150
151   METHODS

152 The prioritization of traits for marine species involved a review of the use of traits in literature and related
153 databases, and asking experts in a range of taxa (including crustaceans, molluscs, fish, echinoderms, algae,
154 birds, nematodes, annelids), and benthic and pelagic ecology of coastal and deep sea environments (listed
155 in the Acknowledgements) their opinion on how to rank traits by importance and what uses they may make
156 of an enhanced marine species trait database. Initial capture of potential traits and trait values made use of
157 spreadsheets but as the development of a traits vocabulary is, of necessity, a community process involving
158 discussion and feedback leading to consensus, the suitability of the open source Semantic MediaWiki
159 (SMW) (https://semantic-mediawiki.org/) was investigated for building a hierarchical list of traits. SMW,
160 an extension to MediaWiki, the wiki engine underlying Wikipedia, allows the content within wiki pages to
161 be semantically marked up for subsequent processing and querying. It is well suited for capturing
162 hierarchical knowledge organisation systems such as thesauri or other taxonomies. SMW is receiving some
163 attention within biodiversity informatics having been adopted by Biowikifarm (http://biowikifarm.net/)
164 which hosts several installations, e.g., for the TDWG draft standard, Audubon Core
165 (http://terms.tdwg.org/wiki/Audubon_Core), with a dedication to long term sustainability through a
166 consortium providing service sponsorship. SMW provides a number of advantages. Each term (i.e., concept
167 or trait) can have its own web page where labels, definitions and examples can be presented. User friendly
168 web forms can be used in place of raw wiki mark-up by domain experts/scientists to add content including
169 translations to multiple languages. An associated discussion page allows capture of comments relating to a
170 term so they are all conveniently available for review and building consensus. Relationships between terms
171 can be established and the terms can be grouped into categories and collections. SMW can be scripted to
172 output collections of terms in standard formats such as Resource Description Framework (RDF)
173 (http://www.w3.org/standards/techs/rdf) and Simple Knowledge Organization System (SKOS)
174 (http://www.w3.org/TR/skos-reference/) thereby making them more easily usable by other applications.
175 Following best practices, SMW supports the issuing of resolvable identifiers for terms and the importing
176 of already existing terms from other vocabularies so they can be re-used rather than re-invented.
177   For the marine species traits vocabulary, a customised version of SMW was established within the
178 VLIZ hosted Coastal Wiki (http://www.coastalwiki.org). This wiki is an encyclopaedia providing up-to-
179 date high quality information for coastal and marine professionals, which is continuously improved,
180 complemented and updated by expert users. The wiki was implemented to allow collaborative writing by
181 authors who can add new terms or improve and update existing articles. The main difference between this
182 wiki and the online Wikipedia are the procedures to maintain the quality, consistency and
183 comprehensiveness of the information (Claus *et al.* 2008). Within the wiki, an additional namespace, '*traits*'
184 was created. The namespace name is a variable for searching in, and reporting on, sets of pages. It is also
185 used to apply features that configure the sets of pages in one namespace differently from another
186 namespace. So every trait name, value, concept and collection falls under the namespace 'traits' within the
187 Coastal and Marine Wiki, and is available under the same base URL as the World Register of Marine
188 Species at http://www.marinespecies.org/traits/wiki. It is intended that the wiki will provide further
189 functionality based on user feedback. Developing a hierarchy of traits, expressed formally in SKOS, will
190 provide the foundation for future, semantically richer ontologies where a marine species traits ontology
191 can draw on other published vocabularies and ontologies, including the Environment Ontology
192 (http://environmentontology.org)   and   the   Phenotypic   Quality   Ontology   (PATO)
193 (wiki.obofoundry.org/wiki/index.php/PATO).
194
195   RESULTS
196
197   TRAITS IN DATABASES
198 Most of the traits in BIOTIC (Table 1) and FishBase (Table 2) can be applied to most marine species. The
199 trait categories and descriptors used in BIOTIC were developed by the MarLIN project, with minor
200 amendments (Hiscock *et al.*,1999; Tyler-Walters *et al.*, 2001). They encompass distribution, biology,
201 phenotypic and genetic attributes, and importance to humans. FishBase has evolved over 20 years and is
202 the most comprehensive database on any global taxon. However, in both databases there can be overlap

203 between groups of traits, and some traits developed for particular use cases or projects at a level of detail
204 would be impractical to achieve for most marine species in the short-term. For example, BIOTIC has
205 separate classifications for habit, sociability, environmental position, growth form, mobility, dependency
206 and host, which contain overlapping and/or strongly inter-dependent traits, and include bioturbation and
207 fragility traits that are applicable to limited groups of species. Thus, it is necessary to review and select a
208 simpler classification of traits in the first instance. Other classes of traits in BIOTIC include 'Reproduction'
209 (regeneration, frequency, development mechanism, reproductive type), and 'Distribution and Habitat'. The
210 latter includes: Migration Pattern, Biological Zone (depth zone categories), Physiographic features,
211 Salinity, Substratum (includes biogenic habitats, crevices and sediment mixtures), Water Flow Rate, and
212 Wave Exposure. In BIOTIC, body size data was available for *ca* 96% of the 685 species covered, but only
213 half of the traits were complete for 60% of the species (Table 3).
214   Taxon-specialist databases tend to contain traits that are difficult to apply to other taxa. For
215 example, the TRY plant-trait database focuses on 52 groups of 681 traits characterizing the vegetative and
216 regeneration stages of the plant life cycle, including growth, reproduction, dispersal, establishment and
217 persistence (Kattge *et al.* 2011). These groups of traits were collectively agreed to be the most relevant for
218 plant life history strategies, vegetation modelling and global change responses on the basis of existing
219 shortlists and consultation with vegetation modellers and plant ecologists. Traits were summarized in
220 groups, e.g., the group 'leaf nitrogen content' consists of the three traits: leaf nitrogen content per dry mass,
221 leaf nitrogen content per area and nitrogen content per leaf. In the case of respiration, the database contained
222 105 related traits: different organs, different reference values (e.g., dry mass, area, volume, nitrogen) and
223 the temperature dependence of respiration (e.g., Q10). Specific information for each trait is available on the
224 TRY website (http://www.try-db.org). Previously, Cornelissen *et al.* (2003) proposed 30 functional "soft
225 traits" for flowering plants for tackling large-scale ecological questions. These were grouped into vegetative
226 (e.g., growth form, height, life span, phenology), regenerative (e.g., dispersal, seed size), leaf (e.g., size,
227 nitrogen content), stem (e.g., density) and root (e.g., length, diameter, depth) traits. A study on bryophyte
228 moss communities used metrics of plant size (i.e. shoot density, mass, height, surface area to volume ratio)
229 (Michel *et al.* 2012). Traits common to all these databases were measures of growth form or habit, body
230 size, longevity, nutrition, and dispersal mechanism.
231
232   PRIORITISING TRAITS
233
234 **Distribution: environment, geography, depth, habitat, ecosystem, seascape**
235 The term distribution may be applied to the environment and habitat in which a species lives, and its spatial
236 distribution by geography, depth, and time. Temporal distribution is a numerical measure applied to
237 particular traits, such as life span, duration of a life stage or time periods when a species changes its spatial
238 distribution (e.g., population movement or migration). Thus we do not propose it as a separate trait here
239 because it can be included as a metric of traits.
240
241 *Environment*
242 In WoRMS, most species have already been attributed to one of the following environments: marine,
243 brackish, freshwater, terrestrial, and combinations thereof (Table 4). When species are recognised as a host
244 or parasite of one or more species they are then classified according to the environment of their host. A host
245 may be considered the 'habitat' of a commensal species, including parasites and mutually beneficial
246 symbiotic relationships (e.g., anemone fish). Many species change their habitat during different life stages,
247 such as from planktonic larvae to benthic adults or parasites. Thus, a core attribute of a life stage is whether
248 it is living in the pelagic or benthic environment. Pelagic may be sub-divided into pleuston, neuston,
249 plankton (drifting), nekton, phyto-, zooplankton, demersal (= hyperbenthos, benthopelagic).
250
251 The occurrence of species in the fossil record has also been implemented in WoRMS. The indication of the
252 fossil status of a taxon – Recent or Fossil or both Recent & Fossil – was found to be a necessity, as the type
253 species of genera can contain extant taxa, extant species can be attributed to fossil species in taxonomic

254 history and documenting fossil taxa can help prevent the accidental creation of junior homonyms. As the
255 indication Recent and/or Fossil is too coarse for research questions involving evolution, phylogeny,
256 biodiversity or biogeography, WoRMS is now also including detailed stratigraphic data. As WoRMS
257 follows international standards on the level of taxonomy, it was decided to also follow the international
258 standards for stratigraphy, by making use of the latest version of the hierarchically structured International
259 Stratigraphic Chart (Cohen *et al.*, 2013). Each stratigraphic range added to WoRMS is tied to a source,
260 allowing traceability of information. As the hierarchy of the International Stratigraphic Chart is included,
261 information can be added on the level available in the literature, and extrapolations can be made through
262 the WoRMS search interface: e.g.**,** all taxa appearing in a certain Age will automatically be included when
263 searching for the corresponding Era or Epoch.
264
265 *Geography*
266 WoRMS utilises a gazetteer that enables species to be attributed to any predefined geographic area,
267 including seas, oceans, and countries available at www.marineregions.org (Claus *et al.* 2014). Additional
268 regions have also been identified for fisheries management and conservation reporting but are not presently
269 included in WoRMS. Cross-mapping of geographic areas is possible to some extent. OBIS and the Global
270 Biodiversity Information Facility (GBIF) provide actual latitude and longitude coordinates for over half of
271 all marine species, often with place names and an indicator of geographic accuracy (e.g.**,** 1 km^2) (Costello
272 and Wieczorek 2014). They enable mapping of these locations as points, and from these geographic
273 distribution can be inferred. Thus, through both the georeferenced place names in WoRMS and point
274 locations in OBIS and GBIF, there are established methods to map marine species geographic distribution.
275 Where distribution is not available as latitude-longitude coordinates, we recommend using the most
276 geographically precise locality name possible; for example, 'Dublin Bay' should not be reported as the Irish
277 Sea or north-east Atlantic.
278
279 *Depth*
280 There are several terms used to describe depth zones in the literature, although not with a consistently
281 defined depth range (reviewed by Costello 2009). Terms like neritic and oceanic, epipelagic, abyssal, and
282 bathyal are concepts rather than strict depth zones. For example, the epipelagic is the zone with enough
283 light for photosynthesis, and light penetration will vary with water clarity. Thus photosynthesis occurs at
284 greater depths in offshore waters than in more turbid coastal waters. If a species would have its deepest and
285 shallowest known records reported it could then be placed within any depth zone classification. The
286 WoRMS deep sea database (Glover *et al.* 2013) has chosen 500 m as the boundary for the 'deep sea' because
287 below that temperature and light generally show little variation (Rex 1981). A minimal depth zone
288 classification could thus distinguish intertidal (or littoral, i.e., seabed exposed at low tide), subtidal (or
289 sublittoral) and deep sea (> 500 m depth) zones (Table 4). Beyond that it would be preferable to assign
290 actual depth ranges from known data (e.g.**,** from OBIS and literature).
291
292 *Habitat*
293 Habitat is highly context dependent and sometimes loosely applied. The term can sometimes be incorrectly
294 used for a locality where a species occurs, or a seascape (e.g.**,** bay, lough, estuary, island) which can contain
295 a combination of habitats (Costello 2009). However, in ecology a habitat is the physical environment in
296 which a species lives at least part of its life. Many species change habitat during different life stages, such
297 as from planktonic larvae to benthic adults or vice-versa. Habitats need to be distinguished from ecosystems
298 and seascapes. The latter are defined by environment and geography, and may contain any combination of
299 benthic and pelagic habitats. They are now best mapped by remote sensing methods (e.g.**,** acoustic, airborne,
300 satellite) (Andrefouet *et al.* 2008, Costello 2009).
301   A standard habitat and biotope classification was developed for European seas by the BioMar-LIFE
302 project (Connor *et al.* 2004, Costello and Emblow 2005) and subsequently expanded as part of the European
303 Union Nature Information System (EUNIS) classification (Galparsoro *et al.* 2012). This is now well-
304 established as part of the regulatory framework for nature conservation in Europe and its basic units of

305   depth zonation, benthic substrata and wave and current exposure are common to other classifications. Its
306   most detailed level describes a biotope, namely the physical habitat and associated community of species.
307   A species may occur in more than one biotope. Some species define a biotope or habitat by virtue of
308   providing a biogenic habitat within which other species live, such as reefs formed by corals, bivalves and
309   worms, and beds of seaweed or seagrass. Thus some species live in biological (biogenic) habitats, including
310   symbionts and parasites. Matching each species to a biotope is possible where such ecological data are
311   available. However, a simpler approach to characterise a habitat would be to record a species depth
312   distribution, and if benthic, the substratum, or if biological, the host.
313   The simplest classification of benthic substrata would be mud (including silt), sand, gravel
314   (including pebbles and cobbles), boulders, and bedrock (Table 4). As with environment, a species may
315   occur in several of these (e.g., mud and sand, boulders and bedrock). A biological habitat could be
316   subdivided into commensal, parasitic, and symbiotic. Thus the combination of depth, substratum and/or
317   biological habitat (e.g., host if a parasite or symbiont, if associated with biological habitat), could be used
318   to assign species to the habitat classification. A species' abundance is likely to vary between habitats, and
319   be facultative or obligate, such that it may occur in several which may make defining its habitat difficult.
320   We recommend only assigning species to any habitat it is frequently found in. The small number of species
321   limited to reduced or variable salinity (brackish and estuarine) habitats can be distinguished using the
322   'environment' classification. Thus we do not propose a separate trait called 'habitat' but rather users can
323   derive it as appropriate to their needs using combinations of environment, depth and substratum (Table 4).
324

325   *Ecosystem*
326   The literature can often refer to species as being associated with habitats or geographic areas
327   dominated or characterised by particular species, such as coral reef, seagrass or kelp ecosystems.
328   Ecosystems are geographic areas defined by biologically significant environmental boundaries. Thus they
329   contain a diversity of habitats, and not the same proportion or combination of habitats in different areas.
330   Because species are associated with habitats they are indirectly associated with ecosystems. Thus it is
331   difficult to assign an 'ecosystem' to a species. However, a species' environmental limits can be defined and
332   its geographic distribution can be mapped. Similarly, environmentally defined ecosystems may occur in
333   different parts of the world but with different species. Thus, associating species with ecosystems is outside
334   the scope of a species based classification. Rather, habitats could be mapped to ecosystems.
335

336   *Seascape*
337   Seascapes, sometimes called landscapes, geomorphological, topographic and physiographic features, are
338   sometimes confused with habitats (Costello 2009). However, while species are clearly associated with
339   habitats, seascapes contain an idiosyncratic combination of habitats. Thus, like the situation with
340   ecosystems, it is not necessary to assign species to seascapes because a coastal species, for example, may
341   be associated with all potential seascapes depending on the habitats they contain. Thus we consider
342   seascapes outside the scope of a species classification. They may be applied when mapping habitats in
343   particular geographic regions.
344

345   **Biological**
346   *Life stage*
347   The traits of most marine species vary significantly between life stages. Most fish, crustaceans and molluscs
348   have planktonic larvae but some cnidarians have pelagic adult stages. Thus it is essential to qualify a trait
349   by the life stage to which it applies. For some taxa, such as peracaridean crustaceans which brood their eggs
350   and lack free living larvae, the traits may be the same for adults and juveniles. Thus we propose four basic
351   life stages: adult (mature), juvenile (immature but morphologically adult), larva (morphologically different
352   from adult form), and egg (or propagule, spore). Some taxa have specific nomenclature for different life
353   stages and multiple larval forms (e.g., nauplius, zoea, megalopa, phyllosoma, veliger) but these cannot be
354   applied across all species. At present, we propose to prioritise traits for the adult life stage only because this
355   is generally more available, can be applied to more species, and would be users' first expectation.

356
357 *Body size*
358 Body size is perhaps the most fundamental trait as it correlates with other traits, for example, enabling
359 conversion of length and abundance to biomass (e.g., Gifford and Caron 2000, Postel *et al.* 2000). In a
360 review of 22 research areas using traits, body size was the most commonly used (Naeem and Bunker 2009).
361 It is also the most widely available trait (Table 3; Webb *et al.* 2009, Tyler *et al.* 2012). Field sampling
362 typically selects species based on body size, whether large enough to be identifiable on sight in the field,
363 or if captured through nets (plankton) or sieves (benthos) of particular mesh size. Larger animal species
364 tend to be top predators and smaller tend to be herbivores and/or detrivores, so body size correlates with
365 food web structure, trophic levels, and energy flow in ecosystem (Gerlach *et al.* 1985). Some studies found
366 peaks and troughs in body size distributions of benthic fauna (e.g., Gerlach *et al.* 1985). However, other
367 studies did not, instead finding that size-distribution patterns reflected the species present rather than any
368 habitat influenced structure (Dolbeth *et al.* 2014). Pelagic species have long been classified by body size
369 because it is conveniently related to sampling method and can simplify data presentation and analysis (Platt
370 and Denman 1977). Nine classes of body length, each increasing by a factor of ten from 0.02 μm virio-
371 plankton to 20 m nekton, are commonly used but this does not imply any ecological meaning to the size
372 classes (Sieburth *et al.* 1978). That said, viruses are all in the < 0.2 μm size class; most bacteria in the 0.02-
373 2.0 μm; most fungi, phytoplankton and protozoa spread across the next two (2-200 μm); and most
374 metazoans are > 0.2 mm (Sieburth *et al.* 1978). There can be considerable size differences between larvae,
375 juveniles and adults in metazoans; so a species may span several size classes.
376   Classifications based on body size such as macrobenthos, meiobenthos, and nekton, are for
377 convenience rather than reflecting any true biological classification; so there is no a priori reason to place
378 a whole species or life stage into a size class. We propose that this trait is defined as the typical maximum
379 size reached by an individual of the species, be it body length, or diameter if circular (Table 4). The length
380 of appendages, such as antennae, legs, wings, or tentacles, is excluded from 'body length' although, of
381 course, may be included in taxon-specific traits. Some taxa may have additional length measurements to
382 body length, such as wing span of birds, arms of octopuses, tentacles of jellyfish, and antennae of
383 crustaceans. Thus, 'body length' of a coral's body size will be that of its largest polyp (not the colony, if
384 colonial), and an octopus's length would exclude its arms. Where sexes differ in maximum body-size then
385 the default would be the largest adult body length, but an additional field could be created where users wish
386 to recognise differences between sexes. Similarly, traits could be associated with a geographic distribution
387 where they vary sufficiently between populations. The maximum body weight for a species' life stage can
388 be more useful for studies on ecosystem energetics and should also be included where possible (Table 4).
389 This would include its skeleton and thus its shell unless it was specified otherwise. The units may be wet
390 weight or dry weight and need to be defined.
391
392 *Life history*
393 Traits describing the persistence of individuals and/or populations include growth rate and longevity (life
394 span). Growth rate and age of maturation determine population generation time. The life span of individuals
395 can indicate population stability over time and dispersal potential of various life stages (e.g., longer
396 planktonic larva life span) and be measured in days, months and years. Fecundity indicates potential
397 abundance, population productivity, and recovery from population decline, and can be measured as the
398 number of eggs per female per spawning. Recruitment is the actual number of eggs surviving to become
399 juveniles. However, most of these traits are only available for a few species and some are difficult to apply
400 at a species level. Other biological traits can characterize the mode of reproduction of a species, such as
401 whether ovoviviparous, viviparous, hermaphroditic, parthenogenic, asexual, protogynous, iteroparous or
402 semelparous, involving brooding, nesting, or parental care. As a first step, we propose to distinguish species
403 with sexual and asexual reproduction because such information is easily available for most taxa and may
404 be significant with regard to the ability of a species to disperse, become invasive, and/or recover from a
405 population decline. As with other traits, a species can be either or both.
406

407 *Physiology*
408 Species responses to climate change, particularly temperature rise and ocean acidification, will depend on
409 their physiological tolerances. Thermal tolerance may be inferred from comparing species distributions to
410 environmental data, such as conducted in species distribution modelling (e.g., Basher *et al.* 2014). We do
411 not prioritise the inclusion of experimental data because they will only be available for a small number of
412 species. However, we see physiological traits as being of increasing interest and the availability of data
413 should be reviewed in the future.
414
415 **Ecological**
416 The three major classes of traits used in ecology relate to habitat, as covered previously, and habit and
417 feeding. In ecology, habit is the external appearance or form of a species (Lincoln *et al.* 1998). Perhaps
418 because more common usage refers to behaviour, this means a wide variety of traits have been related to
419 habit. Habit is considered important because it can determine the mode of dispersal and ecological role
420 (e.g., habitat forming) of species in an ecosystem. Rather than use the term, we propose to focus on the
421 related trait categories of Mobility and Skeleton (Table 4). Species whose habit forms a physical habitat for
422 other species are very important in ecology and often define 'biogenic' habitats. However, whether species
423 form such habitats can depend on local conditions and abundance. Species may be colonial, tubicolous,
424 encrusting, produce shells, or erect (e.g., seaweed) but they do not necessarily form reefs or forests. Future
425 research needs to consider how to classify such variable attributes of species.
426
427 *Mobility*
428   The traits influencing a species dispersal potential tend to be encompassed by the growth form of
429 individual animals (e.g., whether the life stage is mobile or sessile), abundance, and longevity. Dispersal of
430 individual life stages is a variable of great interest regarding invasive species. However, it is rarely known
431 from direct measurements and is estimated from observed colonization events. Thus, we do not propose a
432 classification of dispersal per se but leave users to select traits that may influence dispersal of their taxa of
433 interest. Instead, we propose a simple trait of mobility that can be scored as yes or no (if immobile) (Table
434 4), or ideally, assigned a distance of 'ambit' or dispersal potential (e.g., 0 m, < 1 m if sedentary, > 1 m, >
435 10 m, etc.). All pelagic species will be classified as mobile by virtue of their medium, but only sessile
436 benthic species as immobile (depending on their life stage). Where a species may be a host for a parasite or
437 symbionts, then the latter is included in the trait 'biological' under substrata, and parasite under diet (Table
438 4).
439   Future development of this trait category may sub-divide it into sessile, sedentary, mobile (vagile,
440 errant), solitary, aggregated, gregarious, fossorial, and interstitial. Aggregated could be sub-divided into
441 schooling, swarming, and colonial (fixed together in colony). Mobile could be sub-divided into swimming,
442 drifting (including rafting), crawling, burrowing, flying, gliding, and jet propulsion. Variants on these terms
443 can be significantly different. For example, a species may live in burrows but not create them itself, so it is
444 'burrow living' but not fossorial.
445
446 *Skeleton*
447 The presence of hard skeletons, including shells, is an important factor in determining the fossil record of
448 species. In addition, organisms with calcareous skeletons may be affected by ocean acidification. Ocean
449 acidification is predicted to increase the physiological costs for species with calcareous skeletons and shells
450 (Byrne 2011, Byrne and Przeslawski 2013), as it can impact marine organisms through a decreased calcium
451 carbonate ($CaCO_3$) saturation, thus affecting the calcification rates. The effect of this even increases at high
452 latitudes and regions that intersect with pronounced hypoxic zones (Fabry *et al.*, 2008), thus stressing the
453 need to not only know whether a species has calcareous structures, but also to have information on its
454 whereabouts (distribution).
455   Many planktonic and benthic groups, such as Coccolithophora, Foraminifera, Pteropoda, Mollusca,
456 Echinodermata, Crustacea, Cnidaria, Porifera, Bryozoa, Annelida, Brachiopoda and Tunicata – have $CaCO_3$
457 skeletal elements. However, it is secreted under different forms: aragonite, calcite, high magnesium calcite,

458   amorphous CaCO$_3$ or a mixture of these phases (Mucci, 1983; Lowenstam & Weiner, 1989). Aragonite is
459   about 50% more soluble in seawater than calcite (Mucci, 1983). Documenting the presence of a hard
460   skeleton in combination with the present CaCO$_3$ phase has been identified as a priority trait, as this can both
461   be used in determining the fossil record of a species and its susceptibility to ocean acidification.
462   Many taxa lack calcareous skeletons. Diatoms have silica based skeletons, so availability of silica
463   can affect primary productivity. Arthropods and some fungi have chitinous skeletons, while plants' cell
464   walls have a range of materials including cellulose and lignin. It may be important to users whether
465   skeletons occur internally (e.g., fish) and/or externally to the body wall. Thus, we have prioritised four
466   skeletal materials, calcareous, chitinous, silicious, and plant cell walls, and whether these form endo- or
467   exo-skeletons (Table 4). Species without a hard skeleton can be so noted, as well. A considerable number
468   of species lack such a skeleton, including worm-like taxa, gelatinous zooplankton, sea anemones, some
469   molluscs (e.g., octopus, slugs). Gelatinous zooplankton, including jellyfish, salps and ctenophores, tend to
470   be damaged and under-sampled by plankton nets. However, they are important predators, and some are
471   hazardous to humans and can be considered pests. Based on the priority traits, a search of WoRMS on
472   'pelagic' and 'skeleton absent' will find soft-bodied plankton of which many could be considered
473   gelatinous.
474
475   *Diet and trophic level*
476   Feeding can relate to either what a species feeds on, i.e. its diet if an animal, and/or how it feeds. Associated
477   traits can become complex and species specific. We thus propose a simple classification of diet. We exclude
478   scavenger because this is a behaviour rather than food type. Unless a food source is known it should not be
479   assumed. Often, it is assumed that small invertebrates are omnivores or detritivores, when the actual
480   importance of animal, plant and detritus in their diet is unknown, even if feeding has been observed. Some
481   classifications include decomposers, but decomposition can be by a combination of carnivores or herbivores
482   and microbial decay. Thus it is covered by the other feeding categories and chemoautotrophs (heterotrophs).
483   We considered traits that described a species feeding method, such as particulate, suspension,
484   deposit, filter and grazing feeding. These can be important in terms of classifying the functional role of
485   species in an ecosystem. However, of greater importance is the trophic level a species occupies. That is,
486   whether it is a detritivore, herbivore, primary, secondary or tertiary level carnivore. This can be inferred
487   from the species diet and where available supported by isotope data (e.g., Heymans *et al.* 2014).
488
489   **Species' importance to society**
490   What users often wish to know is what the "status" of a species is with regard to its importance to
491   society. This is not a fundamental trait of the species but reflects its current 'status' in some regard. This
492   status may change over time, such as when a new fishery is established, a species becomes invasive, or it
493   becomes more or less threatened with extinction. Thus, although the 'status' of a species is not a 'trait' as
494   such, it is included in WoRMS. A species conservation status can be indicated by its inclusion in the IUCN
495   Red List (IUCN, 2014), EU Habitats and Bird Directives (European Union 1992, European Union 2009),
496   OSPAR List of Threatened and Declining Species and Habitats (OSPAR 2008) and CITES (CITES 2014).
497   The status of species known to cause Harmful Alga Blooms (HAB) is recorded within the WoRMS HAB
498   Thematic Database (Moestrup *et al.* 2013). Species of importance for fisheries and aquaculture can be
499   recognised by their listing in official catch statistics (Garibaldi and Busilacchi 2002).
500   The IUCN Red List assessments require data on population trends in terms of abundance, natural
501   mortality rates, and number of breeding individuals. Population–level are outside the scope of the present
502   paper which concerns species level traits only. However, future classification could include traits related to
503   fecundity, generation time, age at maturity, and geographic range, because these are used in the Red List
504   assessments, and correlated traits such as maximum body size and age. These traits, plus growth rate and
505   aggregation behaviour, also determine fish species susceptibility to overfishing (Morato *et al.* 2006).
506   A further category that denotes societal importance of a species is its value as an indicator of
507   ecosystem condition. The Marine Strategy Framework Directive is the key European marine environmental
508   policy instrument. Its aim is 'Good Environmental Status' in European waters (MSFD 2008/56/EC). Good

509 Environmental Status is divided into 11 descriptors, of which five are based on species composition: D1
510 biological diversity, D2 non-indigenous species, D3 commercial fish and shellfish, D4 food-webs, and D6
511 seafloor integrity. Once formalized, these status indicators, and equivalents for other regions of the world,
512 will be added to the species in WoRMS.
513   Information on introduced species locations, dates recorded and population trends and impacts are
514 required for management (McGeoch *et al.* 2015). This classification of species is the most difficult of all
515 species attributes because of changing species status arising from misidentifications, and species becoming
516 invasive in one place, perhaps temporarily, and not in others. Thus there is a more complex terminology
517 and structure required in the database which will be required to be described elsewhere. To date, the status
518 of almost 1,400 introduced species has been recorded in WoRMS (Pagad *et al.* 2015).
519   At present, the conservation of marine species has been focused on chordates, including mammals,
520 birds, reptiles and fish because these are most threatened with extinction (Table 5). Of European marine
521 species, the EU Bird and Habitats Directives list 100% of reptiles, 67% of lampreys, 65% of mammals,
522 61% of birds, 2% of fish, and < 0.4% of all other taxa to be in need of protection. Globally, the taxa with
523 most endangered species are birds (26%), mammals (23%), reptiles (12%), and fish (3%). However, over
524 2% of cnidarians (hard corals) are considered endangered by IUCN and trade in 20% is restricted under
525 CITES. Although 74% of marine mammal species are listed under CITES, only 9% of reptiles, 3 % of birds
526 and < 1 % of fish and other taxa. The same higher taxa dominate species of economic importance as listed
527 by FAO, namely as percentage of WoRMS: 76% mammals, 33% fish, 21% birds, 18% lampreys, and 14%
528 reptiles. In contrast, introduced species are of very different taxa, namely of WoRMS 5% sipuncula, 3%
529 entoprocta and tunicata, and 2% ctenophora, plants, and annelids (Table 5).
530
531   DISCUSSION
532 Based on the criteria of applicability across most taxa, availability for most species, and potential usage,
533 we prioritized 10 traits for inclusion in WoRMS (Table 4). Poelen *et al.* (2014) similarly prioritised
534 taxonomy, environment, geographic location, altitude and depth, and functional group (e.g., planktonic) as
535 proposed here. Taxonomy is already fully implemented, and the others partially. Indeed, as all traits are not
536 available for all species their completion will be a continuing process. In addition, the conservation and
537 introduced (potential pest) status of species will need to be regularly reviewed.
538   We see immediate applications for the traits. Research into species biogeography will be able to
539 compare the distribution of taxa across 'environments' and depth gradients, and classify them by body size
540 and trophic levels. OBIS uses WoRMS as their taxonomic standard and could also use the traits. Then OBIS
541 users could select species not just by taxonomy but by their traits and, for example, conservation status or
542 fishery importance. Ocean acidification studies will be able to compare the distribution of taxa with
543 different skeletal composition. Paleontologists will be able to compare the species richness of taxa likely to
544 be better preserved as fossils with taxa without durable skeletons. Gelatinous zooplankton occur in different
545 phyla but could now be grouped by this trait. Analyses could test whether threatened, introduced and/or
546 invasive species are a random subset of all marine species, or have particular traits that may predispose
547 them to being threatened, introduced or becoming invasive respectively. For example, are mobile and/or
548 asexual species more likely to be introduced, and less likely to be of conservation concern, because only
549 one individual is required for dispersal?
550   Some users may be most interested in secondary traits, that is, traits dependent on combinations of
551 the primary traits reviewed here. For example, bioturbation potential is predicted from a combination of
552 known information for related species with regard to mobility, burrowing behaviour, biomass and
553 abundance (Queirós *et al.* 2013). Dispersal potential may be predicted by combinations of mobility and
554 environment (Angert *et al.* 2011). We understand some users will want additional sub-divisions of traits,
555 for example, of salinity by estuarine ecologists (Reusser and Lee 2011). The latter authors also sub-divided
556 benthic, pelagic, and reproductive traits, but then combine environment, habitat, and seascapes, within a
557 very broad definition of biogeography. Users that wish to implement specialist traits for a particular taxon
558 are welcome to do so, and WoRMS is available to provide the infrastructure. If these are unique to the taxon

then the development of such trait classifications is simplified. However, where they may overlap will require consideration of specialists on other taxa.

It is relatively easy to add more trait fields to a database. However, this can increase complexity, redundancy, duplication, and overlap between traits. We thus recommend that expansion of the trait classification in databases proceed cautiously and concisely, only adding traits with a proposed use and that are available for the taxa of interest.

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Table 1(on next page)

Benthic invertebrate traits in BIOTIC.

Table 1. List of benthic invertebrate traits compiled in the biological traits information catalogue BIOTIC (Marshall et al. 2006). Where more than one category of traits applies, all relevant categories are recorded.

1
2   Table 1. List of benthic invertebrate traits compiled in the biological traits information catalogue BIOTIC
3   (Marshall *et al.* 2006). Where more than one category of traits applies, all relevant categories are
4   recorded.

Subject area	*Traits* (categories)
Biology	*Growth form* - 44 categories e.g.**,** Algal gravel, Bivalved, Foliose, Turbinate, Encrusting, *Growth rate* (expressed as μm, mm, cm per day/month/year)
	Size (max.) - 6 categories from Very small(<1cm) to Large(>50cm)
	Environmental position - 14 categories e.g.**,** Epibenthic, Infaunal, Interstitial, Pelagic, Demersal
	Habit - 10 categories e.g.**,** Attached, Bed forming, Burrow dwelling, Erect Encrusting
	Height (above substratum) – (mm/cm/m)
	Flexibility - High (>45°) / Low (10 – 45°) / None (<10°)
	Fragility - Fragile, Intermediary, Robust
	Mobility/movement - Swimmer, Crawler, Burrower, Drifter, Attached (permanent, temporary)
	Dispersal potential (adult) - 7 categories from None, Very limited (<1m)to >10km
	Feeding method - 19 categories e.g.**,** Autotroph, Detritivore, Grazer, Predator
	Typical food type (descriptive text)
	Bioturbator - 4 categories e.g.**,** Diffusive mixing, Conveyor belt transport,
	Sociability -Free living, Gregarious, Colonial
	Dependency –Independent, Parasitic, Mutualist, Inquilinist, Commensal, Host
	Toxicity - (Yes/No)
	Host (for another species) - (Yes/No)
Habitat	*Distribution (UK & Global)* - (descriptive text)
	Biogeographic range - (descriptive text)
	Migratory - Resident, Passive, Active (Diel, Seasonal)
	Depth range (expressed as metres below chart datum)
	Substratum preferences – 38 categories, e.g.**,** Bedrock, Boulders, Mud, Gravel, Mixed, Other
	Physiography - 9 categories e.g.**,** Open coast, Strait / sound, Sea loch, Ria / Voe, Estuary
	Biological zone – Benthic (15 categories), Pelagic (8 categories)
	Wave exposure - 8 categories form Extremely Exposed, to Ultra Sheltered
	Tidal strength - Very Strong, Strong, Moderately Strong, Weak, Very Weak (negligible)
	Salinity (range) - Full (30-40 psu), Variable (18-40 psu), Reduced (18-30 psu), Low (<18 psu)
Life-history	*Reproductive type*- 17 categories e.g.**,** Budding, Fission, Gonochoristic, Hermaphrodite
	Regeneration potential – yes/no
	Reproductive frequency - 7 categories e.g.**,** Semelparous, Annual episodic, Biannual protracted
	Reproductive season- (range of months or seasons)
	Reproductive location - As adult, Adult burrow, Brooding, Sediment surface, Water column
	Life -span (max.) - 8 categories from <1 year, to 100+ years
	Generation time 8 categories from <1 year, to 100+ years
	Age at maturity - 8 categories from <1 year, to 100+ years
	Fecundity – number of eggs
	Egg or propagule size – value (μm, mm, cm)
	Fertilization type - External, Internal, Self-fertile, None (asexual)
	Developmental mechanism – 10 categories e.g.**,** Planktotrophic, Oviparous, Viviparous
Larval	*Larva dispersal potential* - 7 categories from None, Very limited (<1m) >10km
	Larval settlement period - (range of months or seasons)
	Duration of larval stage -<1 day, 1 day, 2-10 days, 11-30 days, 1-2 months, 1-6 months, >6 months

5

Table 2(on next page)

Traits in FishBase.

Table 2. A summary of traits included in FishBase (Froese and Pauly 2014).

1

2 Table 2. A summary of traits included in FishBase (Froese and Pauly 2014).

3

Taxonomy	Biology		Status
Common names	Age	Mass conversion	Introductions
Synonyms	Size	Metabolism	Aquaculture
	Growth	Diseases	Aquaculture profile
Distribution	Length-weight relationship	Fish sounds	Processing
Countries	Length-length	Gill area	
FAO areas	Length-frequencies	Otoliths	Genetics
Ecosystems	Morphometrics	Brains	Strains
Occurrences	Morphology	Vision	Allele frequencies
	Maturity	Swimming speed	Heritability
Ecology	Spawning	Swimming type	
Diet	Fecundity	Ecotoxicology	Stocks
Food items	Eggs	Ciguatera	Recruitment
Food consumption	Egg development		Abundance
Ration	Larvae		
Predators	Larval dynamics		
	Reproduction		

4

5

Table 3(on next page)

Completeness of traits in BIOTIC.

Table 3. The completeness of trait information for species in BIOTIC (Marshall et al. 2006).

1   Table 3. The completeness of trait information for species in BIOTIC (Marshall *et al.* 2006).

2

Trait	No. species	Percentage of species (n=685)
Body-size	664	96.93
Mobility	407	59.42
Sociability	395	57.66
Feeding method	392	57.23
Habit	369	53.87
Fragility	366	53.43
Flexibility	363	52.99
Developmental mechanism	340	49.64
Regeneration	330	48.18
Reproductive type	322	47.01
Dependency	315	45.99
Growth form	302	44.09
Substratum	296	43.21
Food Type	288	42.04
Distribution in UK	283	41.31
Depth Range	283	41.31
Global Distribution	282	41.17
Environmental position	282	41.17
Life-span	276	40.29
Reproductive Season	272	39.71
Fertilization Type	258	37.66
Reproductive Frequency	254	37.08
Reproductive Location	247	36.06
Maturity	236	34.45
Migratory	232	33.87
Larval Settling Time	230	33.58
Biological zone	221	32.26
Dispersal Potential (Adult)	215	31.39
Salinity	212	30.95
Physiography	206	30.07
Dispersal Potential (Larvae)	166	24.23
Wave exposure	166	24.23
Bioturbator	158	23.07
Egg Size	158	23.07
Fecundity	155	22.63
Larval Settlement Period	148	21.61
Tidal strength	138	20.15
Generation Time	136	19.85
Growth Rate	115	16.79
Height	96	14.01
Biogeography	93	13.58
Toxic	50	7.30
Host	6	0.88

3

Table 4 (on next page)

Proposed priority traits for WoRMS.

Table 4. The 10 proposed priority traits and how they would be applied to adult marine species.

1
2   Table 4. The 10 proposed priority traits and how they would be applied to adult marine species.
3

Trait	Relevance	Categories	Numerical
1. **Taxonomic**	Related species have similar traits so taxonomic relationships predict traits of related species	Phylum to Genus	Not applicable
2. **Environment**	Most studies are confined to a particular environment so this trait allows users to quickly isolate species of interest for their purpose.	Marine, brackish, freshwater, terrestrial, pelagic, benthic	Not applicable
3. **Geography**	Distribution is the most sought after information on species after its taxonomy.	Locality name	Latitude-longitude coordinates (in OBIS)
4. **Depth**	The most widely available variable to distinguish species' habitat.	Intertidal, subtidal, epipelagic, deep-sea (>500 m)	Deepest and shallowest depth recorded in (1) literature and (2) in OBIS. Above and below Chart datum (± m).
5. **Body-size**	Related to position in food web, species abundance, metabolic rates, and dispersal.	--	Maximum body length in mm excluding appendages. Maximum total body weight of individual.
6. **Substratum**	A key physical factor determining species habitat.	sediment, hard, biological	Not applicable
7. **Mobility**	Indicates the dispersal potential of the life-stage.	Mobile, immobile (sessile)	Potential metres in life-time
8. **Skeleton**	Calcareous important for ocean acidification and fossil record. Gelatinous important due to sampling difficulties, role as predators, and hazard to humans.	Calcareous (aragonite, calcite), chitinous, silicious, exoskeleton, endoskeleton, plant cell wall	Not applicable
9. **Diet**	Influence on abundance of other species, determines position in food web.	Carnivore, herbivore, parasite, detrivore, phototrophic, chemoautotrophic	Isotopic signature Trophic level
10. **Reproduction**	May relate to the ability of a population to recover from reduced abundance or invisibility.	Sexual, asexual	

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Table 5(on next page)

Numbers of species in ERMS and WoRMS, and that are alien, cause HAB, and of conservation and economic importance.

Table 5. The number of species in higher taxa that occur in the European and World Registers of Marine Species (ERMS, WoRMS); are considered alien (=introduced) (or their origin in uncertain or unknown); been listed as of conservation importance by the European Union Birds or Habitats Directives; listed of regional ecological importance under the Oslo-Paris Convention (OSPAR); are associated with Harmful Algal Blooms (HAB); or are listed as being of international commercial fishery or aquaculture importance by the Food and Agricultural Organisation (FAO).

1   Table 5. The number of species in higher taxa that occur in the European and World Registers of
2   Marine Species (ERMS, WoRMS); are considered alien (=introduced) (or their origin in
3   uncertain or unknown); been listed as of conservation importance by the European Union Birds
4   or Habitats Directives; listed of regional ecological importance under the Oslo-Paris Convention
5   (OSPAR); are associated with Harmful Algal Blooms (HAB); or are listed as being of
6   international commercial fishery or aquaculture importance by the Food and Agricultural
7   Organisation (FAO).
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Taxon Kingdom, Phylum, or Class.	ERMS	WoRMS	Alien	origin unknown	origin uncertain	EU Directive	OSPAR	HAB	FAO
Agnatha	6	93	0	0	0	3	0	0	17
Annelida	2,170	12,658	158	21	19	0	0	0	19
Aves	234	645	2	0	0	91	9	0	133
Bacteria	181	1,716	4	0	0	0	0	1	1
Bryozoa	800	6,112	58	4	3	0	0	0	0
Chaetognatha	41	131	1	0	0	0	0	0	0
Chelicerata	517	2,939	4	0	1	0	0	0	12
Chromista	3,929	20,285	172	26	1	0	0	115	42
Cnidaria	1,294	10,760	76	6	6	1	0	0	86
Crustacea	7,062	53,321	287	15	6	1	1	0	643
Ctenophora	39	187	4	0	0	0	0	0	1
Echinodermata	652	7,277	15	1	1	1	0	0	151
Echiura	37	197	1	0	1	0	0	0	0
Entoprocta	60	174	4	1	0	0	0	0	0
Fungi	399	1,363	8	0	0	0	0	0	0
Hexapoda	88	1,461	2	0	0	0	0	0	0
Mammalia	54	140	1	0	1	35	4	0	107
Mollusca	4,294	45,128	291	9	8	4	4	0	1,323
Nematoda	2,103	7,012	1	0	0	0	0	0	0
Pisces	1,451	17,858	206	3	6	28	22	0	5,892
Plantae	1,666	8,800	157	16	3	3	0	0	154
Platyhelminthes	2,133	12,134	16	2	3	0	0	0	0
Porifera	1,542	8,383	11	1	4	0	0	0	20
Reptilia	5	107	1	0	0	5	2	0	15
Rotifera	109	186	2	0	0	0	0	0	2
Sipuncula	42	147	7	0	0	0	0	0	2
Tunicata	495	3,031	59	20	1	0	0	0	24
TOTAL	33,149	227,585	1,548	125	64	172	42	116	8,644

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Table 6(on next page)

Number of species assessed for conservation concern.

Table 6. The number of species in higher taxa that had their conservation risk assessed on the global IUCN Red List as Extinct, Extinct in the wild, Critically Endangered, Vulnerable, Near threatened; or Least concern; and international trade restricted (listed by CITES). Taxa not represented in these categories were: Acanthocephala, Agnatha, Amphibia, Annelida, Brachiopoda, Bryozoa, Cephalochordata, Cephalorhyncha, Chaetognatha, Chelicerata, Ctenophora, Cycliophora, Dicyemida, Echiura, Entoprocta, Fungi, Gastrotricha, Gnathostomulida, Hemichordata, Hexapoda, Myriapoda, Myxozoa, Nematoda, Nemertea, Orthonectida, Phoronida, Placozoa, Platyhelminthes, Protozoa, Rotifera, Sipuncula, Tardigrada, Tunicata, Viruses, Xenacoelomorpha.

1 Table 6. The number of species in higher taxa that had their conservation risk assessed on the
2 global IUCN Red List as Extinct, Extinct in the wild, Critically Endangered, Vulnerable, Near
3 threatened; or Least concern; and international trade restricted (listed by CITES). Taxa not
4 represented in these categories were: Acanthocephala, Agnatha, Amphibia, Annelida,
5 Brachiopoda, Bryozoa, Cephalochordata, Cephalorhyncha, Chaetognatha, Chelicerata,
6 Ctenophora, Cycliophora, Dicyemida, Echiura, Entoprocta, Fungi, Gastrotricha,
7 Gnathostomulida, Hemichordata, Hexapoda, Myriapoda, Myxozoa, Nematoda, Nemertea,
8 Orthonectida, Phoronida, Placozoa, Platyhelminthes, Protozoa, Rotifera, Sipuncula, Tardigrada,
9 Tunicata, Viruses, Xenacoelomorpha.
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Taxon Kingdom or Phylum	Extinct	Extinct in wild	Critically endangered	Endangered	Vulnerable	Near threatened	Least concern	CITES
Chromista	0	0	4	1	1	0	0	0
Plantae	1	0	8	6	16	12	108	6
Porifera	0	0	0	0	0	0	0	0
Cnidaria	0	0	7	25	204	176	297	2,097
Mollusca	4	0	7	16	36	30	769	2
Crustacea	0	0	6	1	1	2	162	0
Echinodermata	0	0	0	0	9	1	111	1
Pisces	1	0	60	93	314	236	3,469	95
Reptilia	0	0	4	3	6	4	48	9
Aves	9	0	26	58	86	78	600	22
Mammalia	4	0	3	12	17	9	44	104
TOTAL	19	0	126	215	691	548	5,608	2,336

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Table 7(on next page)

Number of species in taxa not included in Tables 5 and 6.

Table 7. Number of species in taxa in the European and World Registers of Marine Species (ERMS, WoRMS) but not represented in any of the categories in Tables 5 and 6.

1   Table 7. Number of species in taxa in the European and World Registers of Marine Species
2   (ERMS, WoRMS) but not represented in any of the categories in Tables 5 and 6.
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Taxon Kingdom or Phylum.	ERMS	WoRMS
Acanthocephala	62	446
Amphibia	0	1
Archaea	--	119
Brachiopoda	39	395
Cephalochordata	2	30
Cephalorhyncha	62	236
Cycliophora	1	2
Dicyemida	17	122
Gastrotricha	256	491
Gnathostomulida	25	98
Hemichordata	17	130
Myriapoda	13	68
Myxozoa	212	473
Nemertea	378	1,359
Orthonectida	19	25
Phoronida	9	17
Placozoa	1	1
Protozoa	350	623
Tardigrada	83	170
Viruses	--	111
Xenacoelomorpha	200	423

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Table 8(on next page)

Images available to illustrate paper on web.

not applicable

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