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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 al.*
97 *et 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

124 **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

139 **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

198 TRAITS IN DATABASES

199 Most of the traits in BIOTIC (Table 1) and FishBase (Table 2) can be applied to most marine species. The
200 trait categories and descriptors used in BIOTIC were developed by the MarLIN project, with minor
201 amendments (Hiscock *et al.*, 1999; Tyler-Walters *et al.*, 2001). They encompass distribution, biology,
202 phenotypic and genetic attributes, and importance to humans. FishBase has evolved over 20 years and is
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

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

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 km²) (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 detritivores, 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 $< 0.2 \mu\text{m}$ 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 $> 0.2 \text{ mm}$ (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 (CaCO₃) 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 CaCO₃
457 skeletal elements. However, it is secreted under different forms: aragonite, calcite, high magnesium calcite,

458 amorphous CaCO₃ 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 CaCO₃ 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

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

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

565

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584

585 References

- 586 Andréfouët S, Costello MJ, Rast M, Sathyendranath S. 2008 Earth observations for marine and coastal
 587 biodiversity. *Remote Sensing of Environment* 112 (8), 3297-3299.
- 588 Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chuno AJ. 2011. Do species traits predict
 589 recent shifts at expanding range edges? *Ecology Letters* 14, 677-689.
- 590 Anon. 2014. Delivering Alien Invasive Species Inventories for Europe (DAISIE) European Invasive
 591 Alien Species Gateway. Accessed at <http://www.europe-aliens.org> on 1st September 2014.
- 592 Appeltans W, Ahyong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I,
 593 Berta A, Błazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL,
 594 Cairns SD, Chan TY, Chan L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF,
 595 Dawson MN, De Clerck O, Decock W, De Grave S, de Voogd NJ, Domning DP, Emig CC, Erséus C,
 596 Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Franssen CHJM, Furuya H, Garcia-Alvarez O, Gerken
 597 S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hoeksema BW,
 598 Hopcroft R, Jaime D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G,
 599 Lazarus DB, Lemaitre R, Longshaw M, Lowry J, Macpherson E, Madin LP, Mah C, Mapstone G,
 600 McLaughlin P, Meland KL, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL,
 601 Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P,
 602 Read GB, Reimer JD, Rius M, Rocha RM, Rosenberg G, Saiz-Salinas JI, Scarabino V, Schierwater B,
 603 Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C,
 604 Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Thuesen EV, Timm T, Todaro A, Turon
 605 X, Tyler S, Uetz P, van der Land J, van Ofwegen LP, van Soest RWM, Vanaverbeke J, Vanhoorne B,
 606 Walker-Smith G, Walter TC, Warren A, Williams G, Wilson SP, Hernandez F, Mees J, Costello MJ.
 607 2012. The magnitude of global marine species diversity. *Current Biology* 22, 1-14.
- 608 Aquatic Sciences and Fisheries Abstracts. 2014. ASFA Thesaurus. In: FAO Fisheries and Aquaculture
 609 Department [online]. Rome. Accessed from <http://www4.fao.org/asfa/asfa.htm> on 15 January 2014.

- 610 Atalah J., Costello M.J., Anderson M. 2007 Temporal variability and intensity of grazing: a mesocosm
 611 experiment. *Marine Ecology Progress Series* 341, 15-24.
- 612 Atalah J., Otto S., Anderson M., Costello M.J., Lenz M, Wahl M. 2007 Temporal variance of disturbance
 613 did not affect diversity and structure of a marine fouling community in north-eastern New Zealand.
 614 *Marine Biology* 153 (2), 199-211.
- 615 Baird DJ, Van den Brink PJ. 2007. Using biological traits to predict species sensitivity to toxic
 616 substances. *Ecotoxicology and environmental safety* 67, 296-301.
- 617 Basher Z, Bowden DA, Costello MJ. 2014. Diversity and distribution of deep-sea shrimps in the Ross Sea
 618 region of Antarctica. *PLoS ONE* 9(7), e103195. doi:10.1371/journal.pone.0103195
- 619 Bischoff, W.W.; Mackenzie, F.T.; Bishop, F.C. 1987. Stabilities of synthetic magnesian calcites in
 620 aqueous solution: comparison with biogenic materials. *Geochimica et Cosmochimica Acta* 51, 1413–
 621 1424.
- 622 Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kuhn I, Kumschick S., Markova Z., Mrugala
 623 A., Pergl J., Pysek P., Rabitsch W., Ricciardi A., Richardson D.M., Sendek A., Vila M., Wilson J.R.U.,
 624 Winter M., Genovesi P., Bacher S. 2014. A unified classification of alien species based on the
 625 magnitude of their environmental impacts. *PLoS Biology* 12(5), e1001850.
- 626 Boström C, Törnroos A, Bonsdorff E. 2010. Invertebrate dispersal and habitat heterogeneity: expression
 627 of biological traits in a seagrass landscape. *Journal of Experimental Marine Biology and Ecology* 390
 628 (2), 106-117.
- 629 Boxshall G., Mees J., Costello M.J., Hernandez F., Gofas S., Hoeksema B.W., Klautau M., Kroh A.,
 630 Poore G.C.B., Read G., Stöhr S., de Voogd N.J., Walter C.T., De Broyer C., Horton T., Kennedy M.,
 631 Decock W., Dekeyzer S., Trias Verbeeck A., Vandepitte L., Vanhoorne B., Adlard R., Adriaens P.,
 632 Agatha S., Ahn K.J., Ah Yong S., Alvarez B., Alvarez F., Anderson G., Angel M., Artois T., Bail P.,
 633 Bailly N., Bamber R., Barber A., Bartsch I., Bellan-Santini D., Berta A., Bieler R., Bitner M.A.,
 634 Błażewicz-Paszkowycz M., Bock P., Böttger-Schnack R., Bouchet P., Boury-Esnault N., Boyko C.,
 635 Brandao S.N., Bray R., Bruce N.L., Caballer M., Cairns S., Cárdenas P., Carrera-Parra L.F., Catalano
 636 S., Cedhagen T., Chan B.K., Chan T.Y., Cheng L., Churchill M., Coleman C.O., Collins A.G., Crandall
 637 K.A., Cribb T., Dahdouh-Guebas F., Daneliya M., Dauvin J.C., Davie P., Dayrat B., De Grave S.,
 638 d'Hondt J.L., Díaz M.C., Dijkstra H., Dohrmann M., Dolan J., Doner S., Eibye-Jacobsen D., Eitel M.,
 639 Emig C., Epler J., Fauchald K., Fautin D., Feist S., Fišer C., Foster W., Frank J.H., Fransen C., Fraussen
 640 K., Furuya H., Garcia-Alvarez O., Gasca Serrano R., Gaviria-Melo S., Gerken S., Gheerardyn H.,
 641 Gibson D., Gil J., Gittenberger A., Glasby C., Glover A., González Solís D., Gordon D., Grabowski M.,
 642 Guerra-García J.M., Guiry M.D., Hajdu E., Hallermann J., Harasewych J., Harris L., Hayward B.,
 643 Hendrycks E., Ho J.s., Hoeg J., Holsinger J., Hooper J., Houart R., Hughes L., Hummon W., Iseto T.,
 644 Ivanenko S., Janussen D., Jarms G., Jazdzewski K., Just J., Kamal'tynov R.M., Kaminski M., Kantor Y.,
 645 Karanovic I., Kelly M., Kim Y.H., King R., Kirk P., Kolb J., Krapp-Schickel T., Krijnen C., Kristensen
 646 R., Kronenberg G., Krylova E., LaFollette P., Lambert G., Lazarus D., LeCroy S., Lemaitre R., Lester
 647 B., Londoño Mesa M.H., Longshaw M., Lowry J., Macpherson E., Madin L., Mah C., Manconi R.,
 648 Mapstone G., Marshall B., Marshall D.J., Meland K., Messing C., Mills C., Molodtsova T., Monsecour
 649 K., Mooi R., Moreira da Rocha R., Moretzsohn F., Mortimer J., Neuhaus B., Ng P., Nielsen C.,
 650 Nishikawa T., Norenburg J., O'Hara T., Oliverio M., Opresko D., Osawa M., Patterson D., Paulay G.,
 651 Paxton H., Peñas A., Perrin W., Pilger J.F., Pisera A., Polhemus D., Pugh P., Reid D.G., Reimer J.D.,
 652 Reuscher M., Rius M., Robin A., Rolán E., Rosenberg G., Rützler K., Rzhavsky A., Saiz-Salinas J.,
 653 Salazar-Vallejo S., Sames B., Sartori A., Satoh A., Scarabino V., Schatz H., Schierwater B., Schmidt-
 654 Rhaesa A., Schönberg C., Schotte M., Schuchert P., Schwabe E., Segers H., Self-Sullivan C., Senna
 655 A.R., Serejo C., Shamsi S., Shenkar N., Siegel V., Sinniger F., Sivell D., Sket B., Smit H., Sterrer W.,
 656 Stienen E., Suárez-Morales E., Summers M., Swalla B.J., Tabachnick K.R., Taiti S., Tang D., Tasker
 657 M., Taylor J., Tëmkin I., ten Hove H., ter Poorten J.J., Terryn Y., Thomas J., Thuesen E.V., Thurston
 658 M., Thuy B., Timi J.T., Timm T., Todaro A., Tucker J., Turon X., Tyler S., Uetz P., Vacelet J., Vader
 659 W., Väinölä R., van Ofwegen L., van Soest R., Van Syoc R., Vanaverbeke J., Vervaet F., von Cosel R.,
 660 Vonk R., Vos C., Walker-Smith G., Watling L., White K., Whitmore D., Williams G., Wilson G.D.,

- 661 Wyatt N., Zanol J., Zeidler W. (2014). World Register of Marine Species. Available from
 662 <http://www.marinespecies.org> at VLIZ. Accessed 2014-01-16
- 663 Brine O, Hunt L, Costello MJ. 2013. Marine biofouling on recreational boats on swing moorings and berths.
 664 *Management of Biological Invasions* 4 (4), 327–341.
- 665 Byrne M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history
 666 stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanogr Marine Biology*
 667 *Annual Reviews* 49, 1–42.
- 668 Byrne, M., & Przeslawski, R. (2013). Multistressor impacts of warming and acidification of the ocean on
 669 marine invertebrates' life histories. *Integrative and comparative biology*, 53(4), 582-596.
- 670 CITES 2014. Convention on International Trade in Endangered Species of Wild Fauna and Flora,
 671 Appendices I, II and III. [http://www.cites.org/sites/default/files/eng/app/2014/E-Appendices-2014-09-](http://www.cites.org/sites/default/files/eng/app/2014/E-Appendices-2014-09-14.pdf)
 672 [14.pdf](http://www.cites.org/sites/default/files/eng/app/2014/E-Appendices-2014-09-14.pdf). Accessed 15 January 2015.
- 673 Claus, S.; Papatsiotsos, A.; De los Rios, M.; Kreiken, W.; Villars, N.; Mees, J.; Dronkers, J. (2008). The
 674 Coastal and Marine Wiki: an Internet encyclopaedia providing up-to date high quality information for
 675 and by coastal and marine professionals, in: Iona, Sissy; Maillard, C.; Tosello, V. (Ed.) (2008).
 676 International Marine Data and Information Systems Conference IMDIS-2008, 31 March - 2 April 2008,
 677 Athens, Greece: Book of abstracts. pp. 224-225.
- 678 Claus, S.; De Hauwere, N.; Vanhoorne, B.; Deckers, P.; Souza Dias, F.; Hernandez, F.; Mees, J. (2014).
 679 Marine Regions: Towards a global standard for georeferenced marine names and boundaries. *Mar.*
 680 *Geod.* 37(2): 99-125. hdl.handle.net/10.1080/01490419.2014.902881,
- 681 Cohen, K.M.; Finney, S.C.; Gibbard, P.L.; Fan, J.-X.; (2013; updated). The ICS International
 682 Chronostratigraphic Chart. *Episodes* 36, 199-204.
- 683 Connor DW, Allen JH, Golding N, Howell KH, Lieberknecht LM, Northen KO, Reker JB 2004. The
 684 Marine Habitat Classification for Britain and Ireland Version 04.05 JNCC, Peterborough ISBN 1 861
 685 07561 8 (internet version). jncc.defra.gov.uk/MarineHabitatClassification
- 686 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter
 687 Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H. 2003. A handbook of
 688 protocols for standardised and easy measurement of plant functional traits worldwide. *Australian*
 689 *Journal of Botany* 51, 335-380.
- 690 Costello M.J. 2009. Distinguishing marine habitat classification concepts for ecological data
 691 management. *Marine Ecology Progress Series* 397, 253-268.
- 692 Costello, M.J., Emblow C. 2005. A classification of inshore marine biotopes. In: Wilson J. G. (ed.), *The*
 693 *intertidal ecosystem: the value of Ireland's shores*. Royal Irish Academy, Dublin, 25-35.
- 694 Costello, M.J., Vanden Berghe E. 2006. "Ocean Biodiversity Informatics" enabling a new era in marine
 695 biology research and management. *Marine Ecology Progress Series* 316, 203-214.
- 696 Costello M.J., Stocks K., Zhang Y., Grassle J.F., Fautin D.G. 2007. About the Ocean Biogeographic
 697 Information System. Retrieved from <http://hdl.handle.net/2292/236> 1st September 2014.
- 698 Costello MJ, Appeltans W, Bailly N, Berendsohn WG, de Jong Y, Edwards M, Froese R, Huettmann F,
 699 Los W, Mees J, Segers H, Bisby FA. 2014c. Strategies for the sustainability of online open-access
 700 biodiversity databases. *Biological Conservation* 173, 155-165.
- 701 Costello MJ, Bouchet P, Boxshall G, Fauchald K, Gordon DP, Hoeksema BW, Poore GCB, van Soest
 702 RWM, Stöhr S, Walter TC, Vanhoorne B, Decock W, Appeltans W. (2013a) Global coordination and
 703 standardisation in marine biodiversity through the World Register of Marine Species (WoRMS) and
 704 related databases. *PLoS ONE* 8(1), e51629.
- 705 Costello MJ, Harris P, Pearce B, Fauchald K, Fiorentino A, Bourillet J-F, Hamylton S (editors) 2010. A
 706 glossary of terminology used in marine biology, ecology, and geology. Version 1.0. Accessed from
 707 <http://www.marinespecies.org/glossary> 1st September 2014.
- 708 Costello MJ, Wilson SP. 2011. Predicting the number of known and unknown species in European seas
 709 using rates of description. *Global Ecology and Biogeography* 20, 319-330.
- 710 Costello MJ, Wilson SP, Houlding B. 2012. Predicting total global species richness using rates of species
 711 description and estimates of taxonomic effort. *Systematic Biology* 61(5): 871-883.

- 712 Costello MJ, Wilson S, Houlding B. 2013a. More taxonomists but a declining catch of species discovered
713 per unit effort. *Systematic Biology* 62(4), 616–624.
- 714 Costello MJ, May RM, Stork NE 2013c. Can we name Earth’s species before they go extinct? *Science*
715 339, 413-416.
- 716 Costello MJ, May RM, Stork NE 2013d. Response to Comments on “Can we name Earth’s species before
717 they go extinct?” *Science* 341, 237.
- 718 Costello MJ, Wicczorek J. 2014. Best practice for biodiversity data management and publication.
719 *Biological Conservation*, 173, 68-73.
- 720 Costello MJ, Houlding B., Wilson S. 2014a. As in other taxa, relatively fewer beetles are being described
721 by an increasing number of authors: Response to Löbl and Leschen. *Systematic Entomology* 39, 395–
722 399.
- 723 Costello MJ. Houlding B, Joppa, L. 2014b. Further evidence of more taxonomists discovering new
724 species, and that most species have been named: response to Bebbler *et al.* (2014). *New Phytologist* 202,
725 739–740.
- 726 Costello M.J., Vanhoorne B., Appeltans W. 2015. Progressing conservation of biodiversity through
727 taxonomy, data publication and collaborative infrastructures. *Conservation Biology*, in press.
- 728 Cumming, G. S., Child, M. F. (2009). Contrasting spatial patterns of taxonomic and functional richness
729 offer insights into potential loss of ecosystem services. *Philosophical Transactions of the Royal Society*
730 *B: Biological Sciences* 364(1524), 1683-1692.
- 731 Dolbeth M, Raffaelli D, Pardal MÃ. 2014. Patterns in estuarine macrofauna body-size distributions: the
732 role of habitat and disturbance impact. *Journal of Sea Research* 85, 404-412.
- 733 European Union 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural
734 habitats and of wild fauna and flora.
735 http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm. Accessed 12 January
736 2015.
- 737 European Union 2009. Directive 2009/147/EC of the European Parliament and of the Council of 30
738 November 2009 on the conservation of wild birds. [http://eur-lex.europa.eu/legal-](http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32009L0147&from=EN)
739 [content/EN/TXT/PDF/?uri=CELEX:32009L0147&from=EN](http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32009L0147&from=EN). Accessed 12 January 2015
- 740 Fabry, V.J.; Seibel, B.A.; Feely, R.A.; Orr, J.C. 2008. Impacts of ocean acidification on marine fauna and
741 ecosystem processes. *ICES Journal of Marine Science* 65, 414-432.
- 742 Froese, R., Pauly, D. (editors) 2014. FishBase. World Wide Web electronic publication. Version
743 (04/2014). Accessed from www.fishbase.org 1st September 2014.
- 744 Gallien, L., Carboni, M., Münkemüller, T. 2014. Identifying the signal of environmental filtering and
745 competition in invasion patterns—a contest of approaches from community ecology. *Methods in Ecology*
746 *and Evolution* 5(10), 1002-1011.
- 747 Galparsoro, I., Connor, D.W., Borja, A., Aish, A., Amorim, P., Bajjouk, T., Chambers, C., Coggan, R.,
748 Dirberg, G., Ellwood, H., Evans, D., Goodin, K.L., Grehan, A., Haldin, J., Howell, K., Jenkins, C.,
749 Michez, N., Mo, G.L., Buhl-Mortensen, P., Pearce, B., Populus, J., Salomidi, M., Sanchez, F., Serrano,
750 A., Shumchenia, E., Tempera, F., Vasquez, M., 2012. Using EUNIS habitat classification for benthic
751 mapping in European seas: present concerns and future needs. *Marine Pollution Bulletin* 64, 2630–
752 2638.
- 753 Garibaldi, L.; Busilacchi, S. 2002. ASFIS list of species for fishery statistics purposes. ASFIS Reference
754 Series No. 15, Rome, FAO. 258p.
- 755 Gerlach, S. A., Hahn, A. E., Schrage, M. (1985). Size spectra of benthic biomass and metabolism. *Marine*
756 *Ecology Progress Series*, 26(1-2), 161-173.
- 757 Gifford DJ, Caron DA. 2000. Sampling preservation, enumeration and biomass of marine
758 protozooplankton. In: *ICES Zooplankton Methodology Manual*, Academic Press, pp 193-217.
- 759 Glover, A.G., Higgs, N., Horton, T. (2013) World Register of Deep-Sea species. Accessed at
760 <http://www.marinespecies.org/deepsea> on 2013-07-25
- 761 Grave S De, Smith KG, Adeler N a., Allen DJ, Alvarez F, Anker A, Cai Y, Carrizo SF, Klotz W,
762 Mantelatto FL, Page TJ, Shy J-Y, Villalobos JL, Wowor D (2015) Dead shrimp blues: a global

- 763 assessment of extinction risk in freshwater shrimps (Crustacea: Decapoda: Caridea). PLoS ONE 10,
764 e0120198.
- 765 IUCN. 2012. *IUCN Red List Categories and Criteria: Version 3.1*. Second edition. Gland, Switzerland
766 and Cambridge, UK: IUCN. iv + 32pp.
- 767 IUCN 2014. The IUCN Red List of Threatened Species. Version 2014.3. <http://www.iucnredlist.org>.
768 Accessed 16 December 2014.
- 769 Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T., Essl, F., Evans, T., Gaertner M., Hulme P.E.,
770 Kuhn I., Mrugala A., Pergl J., Pysek P., Rabitsch W., Ricciardi A., Richardson D.M., Sendek A., Vila
771 M., Winter M., Kumschick, S. 2014. Defining the Impact of Non-Native Species. *Conservation Biology*
772 28(5), 1188-1194.
- 773 Hayes, K., C. Sliwa, S. Migus, F. McEnnulty, and P. Dunstan 2005, National priority pests, Part two
774 ranking of Australian marine pests. Australian Government Department of the Environment and
775 Heritage, Parks <http://www.marine.csiro.au/crimp/reports/PriorityPestsFinalreport.pdf>
- 776 Heymans JJ, Coll M, Libralato S, Morissette L, Christensen V (2014) Global Patterns in Ecological
777 Indicators of Marine Food Webs: A Modelling Approach. PLoS ONE 9(4), e95845.
- 778 Hiscock K., Jackson A. and Lear D. (1999). Assessing seabed species and ecosystems sensitivities.
779 Existing approaches and development. Report to the Department of the Environment Transport and the
780 Regions from the Marine Life Information Network. *Marine Biological Association of the United*
781 *Kingdom, Plymouth*, pp. www.marlin.ac.uk
- 782 Katsanevakis S, Bogucarskis K, Gatto F, Vandekerkhove J, Deriu I, Cardoso AS, 2012. Building the
783 European Alien Species Information Network (EASIN): a novel approach for the exploration of
784 distributed alien species data. *BioInvasions Records* 1, 235-245.
- 785 Kattge J, Díaz S, Lavorel S, Prentice I C, Leadley P, Bönlisch G, Garnier E, Westoby M, Reich P B,
786 Wright I J, Cornelissen J H C, Violle C, Harrison S P, Van Bodegom P M, Reichstein M, Enquist B J,
787 Soudzilovskaia N A, Ackerly D D, Anand M, Atkin O, Bahn M, Baker T R, Baldocchi D, Bekker R,
788 Blanco C C, Blonder B, Bond W J, Bradstock R, Bunker D E, Casanoves F, Cavender-Bares J,
789 Chambers J Q, Chapin Iii F S, Chave J, Coomes D, Cornwell W K, Craine J M, Dobrin B H, Duarte L,
790 Durka W, Elser J, Esser G, Estiarte M, Fagan W F, Fang J, Fernández-Méndez F, Fidelis A, Finegan B,
791 Flores O, Ford H, Frank D, Freschet G T, Fyllas N M, Gallagher R V, Green W A, Gutierrez A G,
792 Hickler T, Higgins S I, Hodgson J G, Jalili A, Jansen S, Joly C A, Kerkhoff A J, Kirkup D, Kitajima K,
793 Kleyer M, Klotz S, Knops J M H, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee T D, Leishman M,
794 Lens F, Lenz T, Lewis S L, Lloyd J, Llusià J, Louault F, Ma S, Mahecha M D, Manning P, Massad T,
795 Medlyn B E, Messier J, Moles A T, Müller S C, Nadrowski K, Naeem S, Niinemets Ü, Nöllert S, Nüske
796 A, Ogaya R, Oleksyn J, Onipchenko V G, Onoda Y, Ordoñez J, Overbeck G, Ozinga W A, Patiño S,
797 Paula S, Pausas J G, Peñuelas J, Phillips O L, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A,
798 Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negret B, Sardans J, Shiodera S, Shipley B,
799 Siefert A, Sosinski E, Soussana J.-F, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M,
800 Weiher E, White M, White S, Wright S J, Yguel B, Zaehle S, Zanne A E, Wirth C. 2011. TRY – a
801 global database of plant traits. *Global Change Biology* 17, 2905–2935. doi: 10.1111/j.1365-
802 2486.2011.02451.x
- 803 Lasram, F.B.R., Mouillot, D. 2009. Increasing southern invasion enhances congruence between endemic
804 and exotic Mediterranean fish fauna. *Biological Invasions* 11,697- 711
- 805 Lepczyk CA, Lortie CJ, Anderson LJ. 2008. An ontology of landscapes. *Ecological Complexity* 5, 272-
806 279.
- 807 Lincoln RJ, Boxshall GA, Clark PF. 1998. A dictionary of ecology, evolution and systematics. 2nd
808 Edition. Cambridge University Press, Cambridge.
- 809 Lowenstam, H.A.; Weiner, S. 1989. *On biomineralization*. Oxford University Press. Oxford.
- 810 Marshall, C., Tyler-Walters, H., Langmead, O., Jackson, E., Lear, D., Somerfield, P, 2006. *BIOTIC -*
811 *Biological Traits Information Catalogue*. Marine Life Information Network. Plymouth: Marine
812 Biological Association of the United Kingdom. Accessed 1st August 2013 from
813 www.marlin.ac.uk/biotic.

- 814 McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C, Sheppard A. 2015.
 815 Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion.
 816 Submitted.
- 817 Michel P, Lee WG, During HJ, Cornelissen JHC. 2012. Species traits and their non-additive interactions
 818 control the water economy of bryophyte cushions. *Journal of Ecology* 100 (1), 222–231.
- 819 Moestrup, Ø, Akselman, R., Cronberg, G., Elbraechter, M., Fraga, S., Halim, Y., Hansen, G., Hoppenrath,
 820 M., Larsen, J., Lundholm, N., Nguyen, L. N., Zingone, A. (Eds) (2013). IOC-UNESCO Taxonomic
 821 Reference List of Harmful Micro Algae. Available online at <http://www.marinespecies.org/HAB>.
 822 Accessed on 2013-07-25
- 823 Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D. 2008. Assessing the global threat of invasive
 824 species to marine biodiversity- *Frontiers in Ecology and the Environment* 6 (9), 485-492.
- 825 Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G., Worm, B. (2011). How many species are there on
 826 Earth and in the ocean? *PLoS Biology* 9(8), e1001127.
- 827 Morato, T., Cheung, W. W. L., & Pitcher, T. J. (2006). Vulnerability of seamount fish to fishing: fuzzy
 828 analysis of life-history attributes. *Journal of Fish Biology*, 68(1), 209-221.
- 829 Mucci, A. 1983. The solubility of calcite and aragonite in seawater at various salinities, temperatures and
 830 1 atmosphere total pressure. *American Journal of Science* 238: 780-199.
- 831 Naeem S, Bunker DE. 2009. TraitNet: furthering biodiversity research through the curation, discovery
 832 and sharing of species trait data. In: *Biodiversity, ecosystem functioning, and human wellbeing. An*
 833 *ecological and economic perspective*, Naeem S, Bunker DE, Hector A, Loreau M, Perrings C. (eds),
 834 Oxford University Press, Oxford. 281-356..
- 835 OSPAR 2008. OSPAR List of threatened and/or declining species and habitats. Reference Number 2008-
 836 6. [http://www.ospar.org/documents/DBASE/DECRECS/Agreements/08-](http://www.ospar.org/documents/DBASE/DECRECS/Agreements/08-06e_OSPAR%20List%20species%20and%20habitats.doc)
 837 [06e_OSPAR%20List%20species%20and%20habitats.doc](http://www.ospar.org/documents/DBASE/DECRECS/Agreements/08-06e_OSPAR%20List%20species%20and%20habitats.doc). Accessed 6 January 2015.
- 838 Pagad S., Hayes K, Katsanevakis S., Costello MJ. 2015. World Register of Introduced Marine Species
 839 (WRIMS). Accessed at <http://www.marinespecies.org/introduced> on 2015-01-16.
- 840 Platt T, Denman K. 1977. Organisation in the pelagic ecosystem. *Helgolander wiss. Meeresunters* 30,
 841 575-581.
- 842 Poelen J H., Simons J D., Mungall C J., 2014. Global Biotic Interactions: an open infrastructure to share
 843 and analyze species-interaction datasets, *Ecological Informatics* 24, 148-159.
- 844 Postel L, Fock H, Hagen W. 2000. Biomass and abundance. In: *ICES Zooplankton Methodology Manual*,
 845 Academic Press, pp 83-192.
- 846 Queirós AM, Birchenough SN, Bremner J, Godbold JA, Parker RE, Romero-Ramirez A, Reiss H, Solan
 847 M, Somerfield PJ, Van Colen C, Van Hoey G, Widdicombe S.. 2013. A bioturbation classification of
 848 European marine infaunal invertebrates. *Ecology and Evolution* 3(11), 3958-3985.
- 849 Reusser DA, Lee H. 2011. Evolution of natural history information in the 21st century – developing an
 850 integrated framework for biological and geographical data. *Journal of Biogeography* 38, 1225-1239.
- 851 Rex, M.A., 1981. Community structure in the deep-sea benthos. *Annual Review of Ecology and*
 852 *Systematics*, 12: 331-353.
- 853 Schmidt-Kloiber A., Hering D. 2015. www.freshwaterecology.info – An online tool that unifies,
 854 standardises and codifies more than 20,000 European freshwater organisms and their ecological
 855 preferences. *Ecological Indicators* 53, 271–282.
- 856 Sieburth JMcN, Smetacek V, Lenz J. 1978. Pelagic size structure: heterotrophic compartments of the
 857 plankton and their relationship to plankton size fractions. *Limnology and Oceanography* 23, 1256-1263.
- 858 Törnroos, A., Bonsdorff, E. (2012). Developing the multitrait concept for functional diversity: lessons
 859 from a system rich in functions but poor in species. *Ecological Applications*, 22(8), 2221-2236.
- 860 Tyler-Walters H., Hiscock K., Lear D. and Jackson A. (2001). Identifying species and ecosystem
 861 sensitivities. *Final report to the Department for the Environment, Food and Rural Affairs from the*
 862 *Marine Life Information Network (MarLIN)*. DEFRA Contract No. CW0826. *Marine Biological*
 863 *Association of the United Kingdom, Plymouth*, 257 pp.

- 864 Tyler, E.H.M., Somerfield, P.J., Vanden Berghe, E., Bremner, J., Jackson, E., Langmead, O. 2012.
865 Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating
866 biological traits into macroecology. *Global Ecology and Biogeography* 21, 922-934.
- 867 Vermeij, G. J., Leighton, L. R. (2009). Does global diversity mean anything? *Palaeobiology* 29 (1), 3-7.
- 868 Wahl M, Link H, Alexandridis N, Thomason JC, Cifuentes M, Costello MJ, da Gama BAP, Hillock K,
869 Hobday AJ, Kaufmann MJ, Keller S, Kraufvelin P, Krüger I, Lauterbach L, Antunes BL, Molis M,
870 Nakaoka M, Nyström J, Radzi ZB, Stockhausen B, Thiel M, Vance T, Weseloh A, Whittle M,
871 Wiesmann L, Wunderer L, Yamakita T, Lenz M. (2011) Re-structuring of marine communities exposed
872 to environmental change: a global study on the interactive effects of species and functional richness.
873 PLoS ONE 6(5), e19514. doi:10.1371/journal.pone.0019514.
- 874 Walter, L.M.; Morse, J.W. 1985. Magnesian calcite stabilities: a re-evaluation. *Geochimica et*
875 *Cosmochimica Acta*, 49, 1503–1513.
- 876 Webb TJ, Tyler EHM, Somerfield PJ. 2009. Life history mediates large-scale population ecology in
877 marine benthic taxa. *Marine Ecology Progress Series* 396, 293-306.
- 878

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

Table 2 (on next page)

Traits in FishBase.

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

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

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

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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

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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.

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

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 (\pm 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, detritivore, 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	

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 is 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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