AlgaeTraits: a trait database for (European) seaweeds

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Abstract. The analysis of biological and ecological traits has a long history in evolutionary and ecological research. However, trait data are often scattered and standardised terminology that transcends taxonomic and biogeographical context are generally missing. As part of the development of a global trait database of marine species, we collated trait information for European seaweeds and structured the data within the standardised framework of the World Register of Marine Species (WoRMS). We collected 45,175 trait records for 21 biologically and ecologically relevant traits of seaweeds. This resulted in a trait database for 1,745 European seaweed species of which more than half (56%) of the records were documented at the species level, while the remaining 44% was documented at a higher taxonomic level and subsequently inherited at lower levels. The trait database for European seaweeds will serve as a foundation for future research on diversity and evolution of seaweeds, and their responses to global changes. The data will contribute to developing detailed trait-based ecosystem models, and will be an important tool to inform marine conservation policies. The data is publicly accessible through the AlgaeTraits portal, algaetraits.org, doi: https://doi.org/10.14284/574, (AlgaeTraits, 2022).

Keywords. Trait-based ecology, Functional groups, Macroalgae, Morphology, Life history traits

1 Introduction

Trait-based approaches, focusing on diversity of organismal characteristics rather than species diversity, are an effective data source to answer important biological questions (Costello et al., 2015; Beauchard et al., 2017; Degen et al., 2018). Traditionally, traits have been and still are of significant value for taxonomic research (Voultsiadou et al., 2017). Moreover, as they enable the description and investigation of complex ecosystems in relatively simple ways without having to laboriously study each individual component species, they are also integral to the study of the ecological and evolutionary dynamics of populations, species, communities, and ecosystems (Violle et al., 2007; Kattge et al., 2011; Degen et al., 2018; Schleuning et al., 2020). For example, the analysis of trait data can assist in estimating responses to multiple stressors, including anthropogenic and climate change impacts (Degen et al., 2018; Schleuning et al., 2020), and may provide crucial information needed to develop effective management strategies to counter negative consequences of climate change (Bremner, 2008).

Although the importance of trait-based approaches is widely recognised, there remains a general lack of accessible, standardised, and harmonised trait data for aquatic organisms (Costello et al., 2015; Beauchard et al., 2017; Degen et al., 2018; Martini et al., 2021). Recent initiatives have intended to resolve this gap and made significant progress for some marine animals, including fishes, polychaetes, copepods, and macroinvertebrates (reviewed in Martini et al., 2021), but aquatic photoautotrophs, including marine macroalgae (or seaweeds), remain underrepresented.

Seaweed traits and functional forms have been used for at least one century as a tool to answer various ecological and evolutionary questions. Since the early 1900s, traits have been explored to formulate life-form classification schemes for algae which intended to reflect habitat requirements and responses to environmental fluctuations (Chapman and Chapman, 1976; Feldmann, 1966), or describe different reproductive strategies (Clayton, 1988; De wreede and Kinger, 1988; Bell 1994) used to explain various evolutionary questions (Heesch et al., 2021). In the 1980s, Littler & Littler (1980; 1983) used the adaptive value of morphological traits to categorise algal species into morpho-functional groups, which cluster species with similar ecological functioning. As the concept of morpho-functional groups is relatively easy to apply and can limit processing time and associated costs, it has been frequently applied in seaweed ecology (Veiga et al., 2013; Vélez-Rubio et al., 2021). As a result, multiple variations of the original six morpho-functional groups have been developed and applied in a wide range of contexts. For example, they have been applied to understand the distribution of communities along spatial (Steneck and Dethier, 1994; Wieters et al., 2012; Gaspar et al., 2017) or environmental scales (Balata et al., 2007; Gaspar et al., 2017; Gómez et al., 2019; Gómez and Huovinen, 2020), the potential of communities to resist invasion (Arenas et al., 2006), and to evaluate the ecological status of coastal waters (Orfanidis et al., 2011). Yet, other recent research indicates that current morpho-functional groups may not capture enough variation to describe ecological functioning (Mauffrey et al., 2020; Ryznar et al., 2020) and call for further development towards a broader trait-based approach that includes non-morphological and other traits (Mauffrey et al., 2020).

Seaweed trait information remains largely scattered, not widely available, and not semantically standardised, which has hampered the development and application of phycological trait-based approaches over broad taxonomic, spatial, or temporal scales. To overcome such drawbacks and enhance the development of a common ontology favouring the use and comparability of trait-based approaches on seaweeds, we present AlgaeTraits, a seaweed trait database for 1,745 species occurring along the Atlantic and Mediterranean coasts of Europe. We expand the spectrum of commonly used functional traits (i.e., measurable or quantifiable properties of individuals;

105 McGill et al., 2006) to include data on habitat, seasonality, morphology, life cycle, life history, and
106 biogeographical range (Fig. 1, Table A1). In total, we describe 21 traits linked to taxonomic information, covering
107 nine of the 10 previously prioritised traits in Costello et al. (2015). These data are available on the AlgaeTraits
108 data portal algaetraits.org, doi: https://doi.org/10.14284/574 (AlgaeTraits, 2022), which is a subregister of the
109 World Register of Marine species (WoRMS, 2022; Marine Species Traits, 2022). Here we introduce AlgaeTraits
110 by (i) presenting the methodologies used to collect data, (ii) highlighting trait coverage for the current and first
111 version of the database and (iii) exploring trait variability for a selected subset of traits.

112 **2 Data**

113 **2.1 Trait collection**

114 Trait data collection started with an extensive literature review in 2013, supported by the Biology project of the
115 European Marine Observation and Data Network (EMODnet). In 2015, the data were further refined with expert
116 opinions (Supplement S1). In total, more than 200 references were used and 33 experts (all co-authors on this
117 article) contributed by filling out a survey. For specific traits where interspecific variation is known to be minimal,
118 trait information was documented in the World Register of Marine Species (WoRMS, 2022) at the genus level.
119 The database behind WoRMS (Aphia (Vandepitte et al., 2015; 2018), see further) is built in such a way that the
120 information at the genus level is then automatically inherited to all species within this genus, if no information at
121 the species level was provided or available. Traits that may have substantial interspecific variation, such as
122 Blooming, Seasonality, Wave exposure, Zonation, and Body Size (Table A1), were not inherited from the genus
123 to species level, and were only documented at the species level. Contributions were quality-checked to verify if
124 they conformed to the survey and the database format.

125 **2.2 Trait data**

126 We included 21 traits for marine seaweeds, of which eight ecological traits, four morphological traits, six life
127 cycle traits, and three life history related traits (Fig. 1, Table A1). Ecological traits relate to the habitat of the
128 seaweed with respect to 'Environment' (Marine, Freshwater, Brackish), tidal 'Zonation', various degrees of
129 'Wave exposure', 'Environmental position' (substrate), 'Tolerance to organic pollutants', 'Vertical space use',
130 and 'Seasonality'. In the few instances where seaweed species are known for their potential to form blooms this
131 has been indicated as well (Fig. 1, Table A1). Morphological traits describe the thallus based on 'Body Shape',
132 'Body Size', 'Calcification', and 'Cytomorphology' (Fig. 1, Table A1). 'Body size' is the only quantitative trait
133 included in AlgaeTraits and can be documented as a mean, maximum, or minimum value to describe the thallus
134 length or diameter. Life history related traits describe patterns that influence demography and population
135 dynamics, while life cycle traits relate to the various stages an organism undergoes from one stage in its
136 development (e.g. fertilisation) to the same stage in the next generation (Albecker et al. 2021) (Fig. 1, Table A1).
137 In addition to these 21 traits, species distributions were documented as ecoregions defined by Spalding et al.
138 (2007) and can be used to subset the database according to geographic region. Moreover, WoRMS also displays
139 species' occurrences of the Ocean Biodiversity Information System (OBIS; www.obis.org) (Fig. 1). Contrary to
140 the other traits, 'Environment' and 'Distribution' were not uploaded as traits (i.e., attributes) in the database

141 system (Aphia, see further) but as environment flags and distributions. This implies that 'Environment' and
142 'Distribution' are slightly different visualised on the AlgaeTraits data portal (www.AlgaeTraits.org).

2.3 Taxonomy

144 The total number of described seaweeds is estimated at 9,250 species on a global scale (Appeltans et al., 2012;
145 Guiry 2012), of which at least 1,800 species occur in Europe (Costello et al., 2022). The taxonomic classification
146 of these species is not always straightforward and is continuously updated. To provide the best possible taxonomic
147 accuracy, the trait data were implemented in WoRMS. WoRMS aims to provide a complete taxonomic
148 authoritative list of all currently published names of marine species and is synchronised with AlgaeBase, the most
149 complete database on global algal taxonomic information (Guiry and Guiry, 2022).

2.4 Meta-data

151 Every trait value is linked to a source (expert or literature) and a note field that can be used to include relevant
152 meta-data related to specific trait-values. As values for the traits 'Asexual reproduction', 'Macroalgal Blooming',
153 'Body Size', and 'Seasonality' may display considerable geographic variation we assigned a specific locality to
154 these trait values. Localities are defined as georegions obtained from the Marine Regions platform, which provides
155 a hierarchical, standardised list of georeferenced marine regions and areas (www.MarineRegions.org) As
156 mentioned above, life cycles of seaweeds can be complex and often consist of different life stages with radically
157 different morphological, physiological, and ecological characteristics (Fig. 2). When relevant, trait values are
158 documented for the specific life cycle stage they apply to (i.e., sporophyte, gametophyte, microthallus,
159 macrothallus).

2.5 Database structure and management

161 The AlgaeTraits database is a thematic subregister of WoRMS, part of the Aphia platform. The Aphia platform is
162 an MS SQL (Microsoft Structured Query Language) database specifically built to include taxonomic data and
163 related information such as biological traits. In total, Aphia contains more than 400 data fields, which are
164 maintained by more than 500 experts under guidance of the WoRMS steering committee, which takes the lead on
165 setting priorities and future directions, and coordination of the experts (Vandepitte et al., 2015; 2018). Both editors
166 and database users are supported by a data management team that includes technical and scientific staff hosted at
167 the Flanders Marine Institute (VLIZ) and can be contacted through info@marinespecies.org. This data
168 management team is committed to safeguarding the integrity and online access of the database.

3 Results

170 Twenty-one traits were documented resulting in 45,195 entries for 2,830 accepted taxa according to AlgaeBase,
171 among which 681 were at the genus level and 1,742 at the species level. Fifty-six percent of the trait entries for
172 species were inherited from the genus level. 'Environment' and 'Cytomorphology' were the traits most
173 documented for species, while the least information was provided for the traits that show substantial variation
174 within genera and that were not inherited from genus to species level (Fig. 3).

3.1 Morphology-related traits

3.1.1 Body shape

Seaweeds are known for their wide variation in body shapes, as illustrated in Fig. 4. For example, seaweeds can exist as filaments (filamentous) or be leaf- (foliose) or cushion-like (saccate). They can trail closely along the surface (prostrate) or be upright (erect), or take many other shapes (Table A1, Fig. 4). 'Body shape' had a high data coverage of 96% (1,678 species) at the species level (Fig. 3, Fig. 5-7).

3.1.2. Body size

Seaweed 'Body size' was described in several dimensions (thallus length, diameter, width, thickness, height) and varied from a few micrometres in thickness or width (e.g., filamentous, turf forming species such as *Hapalospongidion macrocarpum*) to several metres long (e.g., kelp such as *Saccharina latissima*). Compared to other traits, 'Body size' had a relatively low data coverage of 28% (490 species) for European accepted seaweed species (Fig. 3, Fig. 5-7).

3.1.3 Calcification

Several species in different taxonomic groups have calcified thalli (Fig. 8-10). In the green seaweed orders Dasycladales and Bryopsidales, calcification can occur as intra- or extracellular aragonite deposition, and both orders contain calcified articulated and calcified non-articulated species (Fig. 8). In European brown seaweeds, calcification is restricted to *Padina* (Dictyotales), where the surface of several species is covered with aragonite crystals (Benita et al. 2018) (Fig. 4A, Fig. 9). Calcification in various forms is present in four European orders of red seaweeds; in the Corallinales and Sporoplithales as calcite in the cell walls (Fig. 4D, Fig. 10), whereas the Peyssonneliales and Nemaliales deposit aragonite (Pentecost 1980). 'Calcification' had a high data coverage of 96% (1,670 species) on a European level (Fig. 3, Fig. 5-7).

3.1.4 Cytomorphology

'Cytomorphology' was the trait best documented on a European level and reached a data coverage of 99% (1,726 species) (Fig. 4, Fig. 5-7). Although the trait which distinguishes uni- from multicellular organisms and therefore might be perceived as trivial, in a seaweed context, it does set apart macroscopic multicellular thalli from a series of exotic cytomorphologies, including coenocytic and siphonal growth forms. Especially in green seaweeds (e.g., Bryopsidales and Dasycladales), the morphology of the thallus is decoupled from the formation of cells, which may result in thalli tens of centimetres tall and differentiated in blade-like structures, stolons and rhizoids, while still being essentially unicellular.

3.2 Ecology-related traits

3.2.1 Environmental position

'Environmental position' was well documented on the European level with 94% (1,636 species) (Fig. 3, Fig. 5-7). Most seaweeds grow attached to rock (epilithic) or other macrophytes (epiphytic), while some other species grow on animals (epizoic) or within rocks (endolithic), macrophytes (endophytic) or animals (endozoic) (Table A1). Many seaweeds are not very specific with respect to the substrate onto which they are attached. The same

species may grow epilithically or epiphytically, but some species show high substrate specificity. Several diminutive algal species (e.g., *Acrochaete, Acrochaetium, Laminariocolax* and *Myrionema*) grow exclusively epiphytically, endophytically or even endozoically on a variety of hosts. At least for some species (e.g., *Vertebrata lanosa* being associated with *Ascophyllum nodosum*), high substrate specificity has been demonstrated (Garbary 2017).

3.2.2 Macroalgal blooming

'Macroalgal blooming' indicates the demonstrated capacity of a species to produce blooms. This trait had relatively low data coverage of 13% (233 species) on a European level (Fig. 3, Fig. 5-7). Notorious examples of blooming species include *Ulva prolifera*, *Cladophora glomerata*, *Caulerpa cylindracea*, holopelagic *Sargassum* and *Rugulopteryx okamurae,* and events have been often linked to eutrophication (Charlier et al. 2008; Smetacek and Zingone 2013). The trait, however, shows considerable variation with geographic location. This is exemplified by several non-native species, which bloom in the invaded region while showing non such behaviour in their regions of origin. This variation was incorporated in the database by linking entries for 'Macroalgal blooming' to geographic localities.

3.2.3 Seasonality

'Seasonality' had a relatively low data coverage of 14% on a European level (249 species) (Fig. 3, Fig. 5-7). Seaweeds with large geographical ranges adapt to local seasonal conditions by adjusting their phenology (Lüning 1991). It is therefore possible for a species to be present in one season in one part of its range while being absent elsewhere.

3.2.4 Vertical space

All types of 'Vertical space' (encrusting, turf, sub-canopy, canopy; Table A1) occur and vary among and within orders of the green (Fig. 8), brown (Fig. 9) and red seaweeds (Fig. 10). 'Vertical space' had a moderate coverage of 46% on European level (808 species) (Fig. 3, Fig. 5-7).

3.2.5 Tolerance to organic pollutants

Some seaweeds have a lower tolerance to turbidity or nutrient concentrations than others (Table A1). For example, *Choristocarpus tenellus* is mainly observed in waters with low nutrient levels and high visibility (oligotrophic, clear water; Table A1), while *Ulva* spp. are mainly observed from waters with mid to high nutrient concentration (meso-, eutrophic; Table A1). 'Tolerance to organic pollutants' was covered for 39% of European accepted seaweeds (678 species) (Fig. 3, Fig. 5-7).

3.2.6 Wave exposure

Some seaweed species are solely known from habitats with low energy wave forces (sheltered; Table A1) such as *Chaetomorpha adrianii* or from habitats with solely high energy wave forces (exposed; Table A1) such as *Valonia utricularis*. Other seaweeds can occur in a variety of wave exposures including sheltered semi-exposed and exposed such as the non-native *Sargassum muticum*. 'Wave exposure' had a relatively low coverage of 18% on the European level (315 species) (Fig. 3, Fig. 5-7).

3.2.7 Zonation

Many species are physiologically adapted to endure the stress of tidal differences and daily changes between desiccation and submersion (e.g. *Pelvetia canaliculata*). Other species will only occur below the low water mark and do not endure such high variation in desiccation, salinity, temperature or other stressors under normal conditions (e.g. *Alaria esculenta*). 'Zonation' had a relatively low data coverage of 18% on a European level (316 species) (Fig. 3, Fig. 5-7).

3.3 Life cycle related traits

3.3.1 Life cycle

Information on 'Life cycle' was available for 95% of European seaweed species (1,660 species) (Fig. 3, Fig. 5-7). Many seaweeds have a biphasic or haplodiplontic life cycle in which a diploid sporophytic and a haploid gametophytic life phases alternate. These can have a similar (isomorphic; e.g., *Chondrus crispus*) or distinct (heteromorphic) body shape (e.g., Laminariales) (Fig. 2). Haplodiplontic life cycles are the dominant type of life cycle in the brown (Fig. 9) and red (Fig. 10) seaweeds. Other seaweeds have a monophasic life cycle that is either diploid (diplontic) or haploid (haplontic) (Fig. 2). Variation in the life cycle has been documented in several species either in the lab (e.g., in reds, Maggs 1988; in *Ectocarpus*, Coelho et al., 2012) or in the field (e.g., in *Gracilaria*, Destombe et al., 1989). However, the knowledge about the processes driving this variation (e.g. epigenetic (plastic) or genetic bases) is not known.

3.3.2 Asexual reproduction

In many seaweeds, sexual reproduction occurs alongside asexual reproduction (i.e., partial clonality) that does not involve fusion of gametes or meiosis and usually results in progeny with an identical genetic constitution to the parent and to each other (Table A1). Asexual reproduction is widely spread in green, brown, and red seaweeds (Fig. 8-10) and can happen through fragmentation, direct development of spores, parthenogenesis, or other mechanisms. 'Asexual reproduction' had a high data coverage of 95% on a European level (1,649 species) (Fig. 3, Fig. 5-7).

3.3.3 Dispersion mode

Seaweed dispersal is heavily influenced by ocean currents and water motion (but in red seaweeds, animal mediated transport of male gametes could be important, Lavaut et al., 2022) and is in most cases limited in spatial scale. But dispersal over longer distances is also possible when the species can for example drift, or the dispersal is mediated by vectors such as boat hulls (Table 1A). 'Dispersion mode' has a moderate data coverage of 80% on the European level (1,401 species) (Fig. 3, Fig. 5-7).

3.3.4 Gamete type

'Gamete type' varies among and within orders of green and brown seaweeds (Fig. 8, Fig. 9). In red seaweeds, 'Gamete type' is more conserved: male gamete is unflagellated (spermatia) and fertilisation takes place in the female organ called the carpogonium. This type of reproduction is considered oogamous when information is available. This trait was documented for 95% of the European seaweeds (1,661 species) (Fig. 3, Fig. 5-7).

3.3.5 Gametophyte arrangements

In seaweeds, the male and female gametes can be formed on the same or separate thalli (mono- vs. di-), sex determination can happen in both the haploid and diploid life phase depending on the taxon (-oicous vs. -oecious) (Fig. 3, Table A1). For example, in fucoids, sex determination occurs in the diploid-dominant stage, whereas, in all red seaweeds, sex determination occurs in the haploid stage. 'Gametophyte arrangement' was documented for 93% of the European seaweed species (1626 species) (Fig. 3, Fig. 5-7).

3.3.6 Spawning

For the majority of the brown and green seaweeds, fertilisation occurs in the water column, but in red seaweeds, male gametes are not flagellated and fertilisation occurs on the female gametophyte and gives rise to the 'third phase' of the life cycle called the carposporophyte. 'Spawning' has been documented for 95% of European species (1,658 species) (Fig. 3, Fig. 5-7).

3.4 Life history-related traits

3.4.1 Generation time

Of all traits, least information was collected for the trait 'Generation time' (Fig. 4B). In seaweeds, generation time can vary from just a few weeks in *Ulva* (Wichard et al., 2015) to multiple decades such as in *Gracilaria* (Engel et. al 2001) or *Ascophyllum* (Åberg 1992). Generation time was documented for only 7% of the European seaweed (117 species) (Fig. 3, Fig. 5-7).

3.4.1 Life span

'Life span' varies within and among European green, brown, and red seaweeds (Fig. 8-10). Perennial macroalgae can live up to multiple years such as for several years, such as many kelp species (Laminariales), or *Gracilaria gracilis* that can live for more than 50 years (Engel et al., 2001), or *Ascophyllum nodosum*, which can live for more than 120 years (Åberg 1992) . In contrast, annuals live only a few months, such as several small filamentous species (e.g. *Chaetomorpha*). At the European level, data coverage was high for 'Life span', 95% (1,652 species) (Fig. 3, Fig. 5-7).

3.4.5 Reproductive frequency

Data coverage was limited for 'Reproductive frequency', with data available for only 25% for the European species (427 species) (Fig. 3, Fig. 5-7).

4. Discussion

AlgaeTraits includes 21 traits, 1,742 European seaweed species, and is structured within a general framework and ontology aiming to describe all marine species (Costello et al., 2015). With a mean coverage of ~60% per trait, this database will be a solid tool for a variety of biological research and related fields, including marine conservation, nature-based solutions, and aquaculture. For example, traits can be used to monitor community and ecosystem changes (McGill et al., 2006; Vélez-Rubio et al., 2021) or to identify conservation priorities (Albouy

et al., 2017; Cardeccia et al., 2018; Esmaeili et al., 2022). In addition, they can be incorporated into predictive modelling to assess eco-evolutionary consequences of climate change (Schleuning et al., 2020), can contribute to predicting the invasiveness of species (Nyberg and Wallentinus, 2005; Quell et al. 2021), be used in research aiming to better understand the driving forces of evolutionary trait history (Heesch et al., 2021), or the mechanisms of community assembly (Weiss and Ray, 2019), and can even help to assess ecosystem services vulnerability (Díaz et al., 2013; Stevenson, 2014).

The AlgaeTraits database complements recent efforts to collect and publicly provide well-structured and organised seaweed trait data. Just as MarLIN (2006) and SeaTraIn (2022) we focussed on biologically important traits. But contrary to these other initiatives, AlgaeTraits includes all European seaweed species, and presents a different, yet overlapping, set of traits. MarLIN (2006) covers over 40 traits, of which 12 overlap with AlgaeTraits, but is limited to only 30 seaweed species. SeaTrain (2022) covers around 10 traits, of which two traits overlap with AlgaeTraits, and includes 96 seaweed species. As to taxonomic coverage (1,742 species) and inclusion of functional important traits as prioritised by Costello et al. (2015), AlgaeTraits is the most extensive seaweed trait database published so far.

In this first version of AlgaeTraits, not all traits are available for all species yet, and the current list of traits is not yet complete. For example, other key eco-evolutionary traits that might be considered to be included in the database are 'Tolerance to light', 'Tolerance to temperature', 'Tolerance to grazing', 'Tolerance to sedimentation' or 'Tolerance to epiphytism'. There is currently no possibility to describe parasitic algal life forms in the database, ignoring a relatively diverse group of red algae. Completion and further refining and expanding the database will be an ongoing effort of the AlgaeTraits editor community. AlgaeTraits currently has five thematic editors, who actively update the trait information on a voluntary basis. During an upcoming workshop (December 2022), more experts will be trained to contribute to AlgaeTraits through the online editing interface (Algaetraits.org), and expansion of this European database to a global level will be initiated. The AlgaeTraits editorial community will also need to report to the WoRMS steering committee. As the database expands, adding new traits or trait values can be considered under thorough consideration and discussion with the WoRMS steering committee and data management team.

For now, traits are included at the species level in AlgaeTraits. However, multiple traits can exhibit substantial intraspecific variation (Kattge et al., 2011). For example, morphological seaweed traits can differ among populations depending on underlying genetic patterns (Serisawa et al., 2003), or depending on environmental conditions such as wave exposure with rather smaller and more slender individuals in exposed than sheltered localities (Ruuskanen et al., 1999; Fowler-walker et al., 2006; Kim et al., 2022). But also, habitat preference, life-history (Araújo et al., 2011) or life-cycle traits can vary intraspecifically. Some seaweeds reproduce sexually under normal conditions but change to asexual reproduction under specific environmental conditions (Demes and Graham, 2011; Murúa et al., 2017) or at the limits of their distribution (e.i. geographic parthenogenesis: Oppliger et al., 2014; Hoshino et al., 2021). Intraspecific trait variation is thus caused by both genetic variation and phenotypic plasticity and can be a response to improve performance under specific environmental biotic or abiotic conditions (Kattge et al., 2011). At the moment, we considered intraspecific variation by assigning localities (or life stages) to the trait values when possible, or specifying detailed information in the note field. However, complementary approaches measuring trait information at specimen level (e.g., Mauffrey et al., 2020; Cappelatti

et al., 2019) are useful, especially for quantitative traits, to fully capture intraspecific trait variability and allow more in-depth analysis.

5. Data Availability

The data can be accessed from the AlgaeTraits portal, algaetraits.org, doi: https://doi.org/10.14284/574 (AlgaeTraits, 2022).

6. Conclusion

We provided a consolidated database of important traits of European seaweeds that is distinct in its completeness and taxonomic coverage. Because the database is standardised and fits within the broader framework of WoRMS that aims to include all taxa described, it serves not only as a significant resource for phycological research focusing on trait-based ecology or evolution, but also for general macro-ecological and macroevolutionary research in general. The database can help to explore ecological questions about relations among traits or help to unravel taxonomic and evolutionary patterns of traits in seaweeds. Because some trait values vary geographically and some traits values were documented at the genus level, the database may not always provide the highest variation at the species level. However, an active thematic editorial community is currently committed to further updating and improving the quality of this European database and expanding it to a global level to facilitate thorough and broad scale trait-based analysis.

Author contribution:

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Competing interests

The authors declare that they have no conflict of interest.

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593

 Appendix A

 Table A1 Trait definitions as applied in AlgaeTraits.

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
Morphology	Body shape	Branched	/	Forming main and lateral branches (and branchlets).	*Plumaria*
		Capitate	/	(1) Enlarged or swollen at tip; (2) Gathered into a mass at tip or apex.	*Penicillus*
		Crustose	/	Forming a thin crust on the substratum, appl. certain lichens, sponges, algae (Lawrence, 2005).	*Hydrolithon*
		Cushion-like	/	Approximating the shape of a cushion (Womersley, 1987).	*Cladophoropsis membranacea*
		Discoid	/	(1) Flat and circular; (2) Disc-shaped (Lawrence, 2005).	*Ulvella*, *Scytosiphon lomentaria* (sporophyte)
		Erect	/	Upright.	*Cystoseira*
		Filamentous	/	Existing out of a branched or unbranched row of cells joined end to end (Womersley, 1987).	*Antithamnionella*
		Filiform	/	resembling a filament.	/
		Flabellate	/	Fan-shaped, thallus usually expanding upward from a narrow base.	*Flabellia*
		Foliose	/	Leaf-like (Womersley, 1987).	*Palmaria*, *Halymenia*
		Mucilaginous	/	consisting of a slippery and slimy texture (Maggs and Hommersand, 1993)	/
		Pinnate	/	With laterals or branches arranged along each side of an axis or branch (Womersley, 1987).	*Haliptilon*
		Prostrate	/	Trailing on the ground or lying closely along a surface (Lawrence, 2005).	*Parviphycus*
		Saccate	/	Inflated, or sac-like (Womersley, 1987).	*Colpomenia*
		Spheric	/	Approximating the shape of a sphere (Womersley, 1987).	*Valonia*
		Stoloniferous	/	forming a prostrate axis, lying on or in the substrate, from which erect branches arise (Womersley, 1984).	*Caulerpa*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Tubular	/	In the form of a tube, having tubes, consisting of tubes (Lawrence, 2005).	*Chorda filum*
		Unreported	/	So far it has not been reported in literature what the body shape (thallus) is for this taxon.	
	Body Size	[numerical value]	/	A measurement of the size of the organism. The measurement used to express body size varies within taxonomic groups. For example, some disciplines measure diameter, others carapace length, total body length or wingspan. Also, body size can vary with gender and life stage.	*Caulerpa prolifera: 25cm maximum thallus length*
	Calcification	Calcified articulated	/	Algal thallus that is encrusted or impregnated with lime with non-calcified articulae rendering the thallus a segmented nature.	*Halimeda, Corallina*
		Calcified non-articulated	/	Algal thallus that is encrusted or impregnated with lime lacking non-calcified articulae.	*Hydrolithon*
		Non-calcified	/	Algal thallus not encrusted or impregnated with lime.	*Cladophora*
		Unreported	/	So far it has not been reported in literature whether the thallus is calcified.	
	Cytomorphology	Unicellular	/	Having only one cell or consisting of one cell.	
		Unicellular	siphonous	An algal growth form that is filamentous, tubular, multinucleate and with a few cross-walls, if any (Brodie et al., 2007).	*Acetabularia, Bryopsis, Caulerpa, Codium*
		Non-unicellular		Having more than one cell or consisting of more than one cell (adapted from Lawrence, 2005).	*Furcellaria*
		Non-unicellular	coenocytic	With cells being multinucleate.	*Cladophora, Dictyosphaeria, Valonia*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
Ecology	Distribution*		/	Species distributions documented as georegions. See www.MarineRegions.org for the full list of georegions.	/
	Environmental position	Endolithic	/	Growing within a rock or other hard inorganic or organic substratum (Lincoln et al., 1998).	*Porphyra* (*Conchocelis-stage*), *Ostreobium*
		Endophytic	/	Living within a plant tissue or macroalgal thallus and not deriving nourishment from it.	*Callocolax*
		Endozoic	/	Living within or passing through the body of an animal and not deriving nourishment from it.	*Callocolax*
		Epilithic	/	Growing on rocks or other hard inorganic or organic substrata (Lincoln et al., 1998).	*Acanthophora*
		Epiphytic	/	Living on the surface of a plant or alga and not deriving nourishment from it.	*Vertebrata lanosa*
		Epipsammic	/	growing in or on sand or other soft inorganic or organic substratum	/
		Epizoic	/	Living attached to the body of an animal used for a non-parasitic organism that lives attached to the outer surface of an animal.	*Polysiphonia carettia*
		Unattached	/	Growing without attachment to any type of substrate.	*Ulva*
	Environment*	Marine	/	Occuring at salinities higher than 30 ppt	
		Brackish	/	Occuring at a salinity range of 0.5–30 ppt	
		Freshwater	/	Occuring at a salinity range of 0–0.5 ppt	
		Terrestrial	/	Occuring on land	
	Macroalgal Blooming	Yes	/	The species has the potential to go through episodes of intense thallus growth, reproduction and mass proliferation under specific environmental conditions such as high nutrient and temperature conditions	*Rugulopteryx okamurae*, *Ulva* spp.

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		No	/	The species does not have the obvious potential to go through episodes of intense growth and mass proliferation of the thallus under specific environmental conditions such as high nutrient and temperature conditions	*Jania adhaerens*
	Seasonality	Spring	/	The organism can be observed in spring.	/
		Summer	/	The organism can be observed in summer.	/
		Autumn	/	The organism can be observed in autumn.	/
		Winter	/	The organism can be observed in winter.	/
		Unreported	/	Seasonality not reported in the literature.	/
	Vertical space	Canopy	/	Vegetation of macroalgae or plants partially blocking light penetration, thereby creating a shaded understory.	*Fucus, Laminaria, Saccorhiza*
		Encrusting	/	With a crustose growth form	*Hydrolithon*
		Sub-canopy	/	Forming a secondary cover, usually of 20 cm height maximum	*Dictyota, Halimeda*
		Turf	/	Vegetation dominated by macroalgae with limited vertical height, usually < 5 cm height	*Gelidium pusillum*
	Tolerance to organic pollutants	Clear waters	/	Occurring in waters where visibility is most of the time > 10 m.	/
		Eutrophic waters	/	Occurring in waters with high primary productivity; pertaining to waters rich in nutrients.	/
		Mesotrophic waters	/	Occurring in waters with intermediate levels of primary productivity; pertaining to waters having intermediate levels of the nutrients.	/
		Moderately turbid waters	/	Occurring in waters where visibility is most of the time > 1m and < 10m.	/
		Oligotrophic waters	/	Pertaining to waters with low levels of the nutrients resulting in low primary net productivity.	/

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Turbid waters	/	Occurring in waters where visibility is most of the time < 1m	/
		Water with variable turbidity	/	Occurring in waters where turbidity varies periodically.	/
	Wave exposure	Exposed	/	Occurring in habitats that are subject to high energy wave forces.	
		Exposed	High energy rock	Occurring on rocky substrate subject to high energy wave forces.	*Chondrus crispus*
		Features of rock	/	Specific characteristics of rocky substrate such as pools, caves, overhangs, surge gulleys, artificial hard substrata.	*Pylaiella littoralis*
		Semi-exposed	/	Occurring in habitats that are subject to moderate energy wave forces.	
		Semi-exposed	Moderate energy rock	Occurring on rocky substrate subject to moderate energy wave forces.	*Himanthalia elongata*
		Sheltered	/	Occurring in habitats that are subject to low energy wave forces.	
		Sheltered	Coarse sediments	Occurring on coarse sediments such gravel, pebbles, shingles and cobbles occurring at sheltered locations.	*Saccharina latissima*
		Sheltered	Low energy rock	Occurring on rocky substrate subject to low energy wave forces.	*Polysiphonia elongata*
		Sheltered	Macrophyte-dominated sediments	Sediments with a high cover of macroalgae or seagrasses.	*Laurencia caspica*
		Sheltered	Mud-dominated sediments	Sediments composed of a mixture of clay (< 2 um) and silt (4 - 62 um) typically deposited in a low energy environment.	*Chaetomorpha linum*
		Sheltered	Sand-dominated sediments	Sediments composed of a mixture of sand particles (0.074 - 4.75 mm) typically deposited in a low energy environment.	*Codium fragile*
		Unreported	/	Not been reported in literature in what type of wave exposure the species occurs.	/
	Zonation	Intertidal	/	The part of the shore between high and low tide.	

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
			Littoral zone	The part of the shore covering the intertidal and the splash zone, with the upper limit marked by the top of the lichen zone and the lower limit marked by the top of the laminarian kelp zone.	*Ascophyllum nodosum*
		Subtidal	/	The part of the shore continuously covered by water, below the intertidal zone.	
			Lower infralittoral zone	The part of the infralittoral zone that supports scattered kelp plants.	*Bryopsis plumosa*
			Upper circalittoral zone	Dominated by animals with sparse foliose algae except where grazed. The part of the circalittoral subzone on hard substrata distinguished by the presence of scattered foliose algae amongst the dominating animals; its lower limit is the maximum limit of depth for foliose algae	*Corallina officinalis*
			Upper infralittoral zone	The region of the sublittoral which extends from the lower limit of the infralittoral to the maximum depth at which photosynthesis is still possible.	*Gracilaria gracilis*
		Unreported	/	unreported	/
Life cycle	Life cycle	Diplontic	/	Having a life cycle in which the direct products of meiosis act as gametes; only the gametes are haploid (Lincoln et al., 1998).	*Sargassum*
		Haplodiplontic	/	Having a life cycle with alternating free-living gametophyte and sporophyte phases (Womersley, 1987).	
		Haplodiplontic	Heteromorphic	Organisms with the gametophyte and sporophyte of different morphology and size (Womersley, 1987).	*Laminaria ochroleuca*
		Haplodiplontic	Isomorphic	Organisms with the gametophyte and sporophyte of similar morphology and size (Womersley, 1987).	*Dictyota dichotoma*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Haplodiplontic	Not applicable	It is not applicable whether this taxon is heteromorphic or isomorphic.	*Parvocaulis*
		Haplodiplontic	Unknown	According to literature it is unknown whether this organism is heteromorphic or isomorphic.	
		Haplodiplontic	Unreported	So far it has not been reported in literature whether this taxon is heteromorphic or isomorphic.	*Metapeyssonnelia*
		Haplontic	/	Having a life cycle in which meiosis occurs in the zygote to produce the haploid phase; only the zygote is diploid (Lincoln et al., 1998).	*Tolypella*
		Unknown	/	According to literature it is unknown what life cycle this organism has.	*Epicladia*
		Unreported	/	So far it has not been reported in literature what life cycle this taxon has.	*Hecatonema*
	Asexual reproduction	Asexual reproduction	/	Reproduction which does not involve fusion of gametes or meiosis and usually results in progeny with an identical genetic constitution to the parent and to each other. Asexual reproduction may amongst others occur by binary fission, budding, asexual spore formation or vegetative propagation.	
		Asexual reproduction	Asexual reproduction by an unknown mechanism	Asexual reproduction is detected, but the underpinning mechanism is unknown.	*Bryopsis hypnoides*
		Asexual reproduction	Asexual reproduction by direct development of spores	Reproduction by asexual spores resulting in a new individual of the same ploidy (exospore, endospore, monospore, bispore, paraspore, zoospore, aplanospore, autospore).	*Corallina officinalis*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Asexual reproduction	Asexual reproduction by fragmentation	Type of asexual reproduction in which the organism breaks up into smaller pieces, each of which can develop into a new individual, as in some algae (Lawrence, 2005).	*Caulerpa*
		Asexual reproduction	Asexual reproduction by parthenogenesis	Direct development of a new individual from an unfused gamete.	*Ulva prolifera*
		Asexual reproduction	Asexual reproduction by vegetative propagules	Asexual reproduction by development of a new individual from a vegetative propagule.	*Prasiola crispa*
		No asexual reproduction	/	The taxon does not reproduce asexually, which is reproduction which does not involve formation and fusion of gametes and results in progeny with an identical genetic constitution to the parent and to each other. Reproduction may occur by binary fission, budding, asexual spore formation or vegetative propagation. In asexual division in eukaryotic organisms, all cell divisions are by mitosis.	*Acanthophora*
		Unknown	/	According to literature it is unknown whether this organism reproduces asexually.	*Tolypella*
	Dispersion mode	Aplanospores	/	A non-motile, asexual spore.	*Cymopolia*
		Monospores	/	An undivided spore.	*Monosporus*
		Motile spores	/	Spores are flagellate and can therefore disperse.	*Ectocarpus*
		One motile gamete	/	Only the male gamete is flagellate and can therefore disperse.	*Chondracanthus*
		Two motile gametes	/	Both male and female gametes are flagellate and can therefore disperse.	*Colpomenia*, *Scytosiphon*
		Vegetative fragmentation	/	Type of asexual reproduction in which the organism breaks up into smaller pieces, each of which can develop into a new individual.	*Chaetomorpha*
		Vegetative fragmentation	Thallus fragmentation and drift	A part of the thallus can be lost and drift.	*Gracilaria*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Vegetative propagation	/	Vegetative reproduction by propagules that can also be used as a means of dispersal.	*Asparagopsis*
		Presence of buoyancy structures	/	Individuals exhibit gas-filled structures that favourise their floating.	*Sargassum*
		Species cultivated or sold in aquaria trade	/	The species is cultivated or sold in aquaria trade.	*Caulerpa taxifolia*
		Species growing on artificial substrate	/	The species is growing on artificial substrate such as harbour walls, boat hulls, piers, buoys.	*Undaria pinnatifida*
		Unknown	/	According to literature it is unknown which dispersion mode this organism has.	*Bornetia*
		Unreported	/	So far it has not been reported in literature which dispersion mode this taxon has.	*Herponema*
	Gamete type	Anisogamous	/	Having gametes of dissimilar size, shape or behaviour (Lincoln et al., 1998).	*Scytosiphon*
		Isogamous	/	Having gametes that are similar in size, shape and behaviour; having gametes (isogametes) not differentiated into male and female (Lincoln et al., 1998).	*Ectocarpus*
		Oogamous	/	Having a reproduction involving a large, non-motile female gamete (egg cell) and a small, motile male gamete (sperm cell or equivalent), except for red algae in which the male gamete is also non-motile (Womersley, 1987).	*Cryptonemia, Dictyota, Fucus*
		Not applicable	/	The attribute "gamete type" is not applicable for this taxon.	*Halothrix*
		Unknown	/	According to literature it is unknown which gamete type this organism has.	*Fosliea*
		Unreported	/	So far it has not been reported in literature what the gamete type is for this taxon.	*Rosenvingea*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
	Gametophyte arrangement	Dioecious	/	When male and female reproductive structures are formed on the separate individual and the sex is determined in diploid phase.	*Alaria esculenta*
		Dioicous	/	When male and female reproductive structures are formed on the separate individual and the sex is determined in haploid phase (Beukeboom and Perrin, 2014).	*Dasya elongata*
		Mixed	/	With individuals bearing only male or female reproductive structures and individuals bearing both male and female reproductive structures in one species.	*Griffithsia*
		Monoecious	/	When male and female reproductive structures are formed on same individuals and the sex is determined in diploid phase.	*Fucus distichus*
		Monoicous	/	When male and female reproductive structures are formed on same individuals and the sex is determined in haploid phase.	*Hydrolithon*
		Not applicable	/	The attribute "gametophyte arrangement" is not applicable for this taxon.	*Pedobesia*
		Unknown	/	According to literature it is unknown which gametophyte arrangement this organism has.	*Stilopsis*
		Unreported	/	So far it has not been reported in literature what the gametophyte arrangement is for this taxon.	*Chaetosiphon*
	Spawning	Fertilization in the water column	/	Fertilization with gametes released in the water column.	*Batophora*
		Fertilization on the female gametophyte	/	Female gamete retained on the female gametophyte (e.g. Rhodophyta).	*Atractophora hypnoides*
		Not applicable	/	The attribute "spawning" is not applicable for this taxon.	*Porphyridium purpureum*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Unknown	/	According to literature it is unknown which spawning mechanism this organism has.	*Chordaria*
		Unreported	/	So far it has not been reported in literature whether there is spawning for this taxon.	*Spongonema*
Life history	Generation time	1 to 3 months	/	Life cycle completed in 1 to 3 months in the lab.	*Ulva*
		3 to 12 months	/	Life cycle completed in 3 to 12 months in the lab.	*Cystoseira barbata*
		1 to 3 years	/	Life cycle completed in 1 to 3 years in the lab.	*Saccharina latissima*
		More than 3 years	/	Life cycle completed in more than 3 years in the lab.	*Furcellaria lumbricalis*
	Life span	Annual	/	(1) Appl. structures or growth features that are marked off or completed yearly; (2) living for a year only; (3) completing life cycle in a year from germination; (4) n. plant that completes its life cycle in a year. (Lawrence, 2005). Thallus which survives only one growing season (less than 1 year) (Womersley, 1987).	*Acrosymphyton purpuriferum*
		Annual	Ephemeral	(1) Short-lived; (2) taking place once only, appl. plant movements as expanding buds; (3) completing life cycle within a brief period; (4) n. a short-lived plant or animal species (Lawrence, 2005). Thallus which survives for only a few weeks (less than 1 month) (Womersley, 1987).	*Osmundea hybrida*
		Perennial	/	Plant which persists for several years (Lawrence, 2005).	
		Perennial	Long perennial	Thallus or part thereof with a lifespan exceeding 3 years (more than 3 years)	*Cystoseira barbata*
		Perennial	Short perennial	Thallus or part thereof with a lifespan exceeding 1 year but under 3 years.	*Undaria pinnatifida*

Trait group	Trait	Trait value	Trait child value	Definition	Genus or species Example
		Unreported	/	So far it has not been reported in literature which life span this organism has.	*Spatoglossum*
	Reproductive frequency	Throughout the year	/	Fertile individuals observed throughout the year.	*Codium fragile*
		One long period a year	/	A unique fertility period lasting more than 1 month.	*Pelvetia canaliculata*
		One short period a year	/	A unique fertility period lasting less than 1 month.	*Desmarestia viridis*
		Several long periods a year	/	Several distinct fertility periods lasting more than 1 month each.	*Ceramium virgatum*
		Several short periods a year	/	Several distinct fertility periods lasting less than 1 month each.	*Pyropia elongata*

596 *Not uploaded as traits or attributes in the Aphia database but as Distributions or Environmental flags

597

 Appendix B

 Table B1. Sources used in the database, ordered from most to least used.

Type	Source
literature	Bunker, F., Brodie, J. A., Maggs, C. A., & Bunker, A. R. (2017). Seaweeds of Britain and Ireland. Princeton University Press.
expert	Blanfuné, Aurélie. Institut Méditerranéen d'Océanologie. aurelie.blanfune-thibaut@mio.osupytheas.fr; Boudouresque, Charles-François. Institut Méditerranéen d'Océanologie. charles.boudouresque@mio.osupytheas.fr; Thibaut, Thierry. Institut Méditerranéen d'Océanologie. thierry.thibaut@mio.osupytheas.fr; Verlaque, Marc. Institut Méditerranéen d'Océanologie. marc.verlaque@mio.osupytheas.fr
expert	Rueness, Jan. University of Oslo. jan.rueness@ibv.uio.no
literature	Rodriguez-Prieto, C.; Ballesteros, E.; Boisset, F.; Afonso-Carrillo, J. (2013). Guía de las macroalgas y fanerógamas marinas del Mediterráneo occidental. Ediciones Omega. S.A., Barcelona.
expert	Krueger-Hadfield, Stacy A. University of Alabama at Birmingham. sakh@uab.edu
expert	Peña, Viviana. Universidad A Coruña. vpena@udc.es
expert	Criado, Ignacio Bárbara. Universidad A Coruña. barbara@udc.es
expert	Piñeiro-Corbeira, Cristina. Universidad A Coruña. c.pcorbeira@udc.es
literature	Guiry, M.D. & Guiry, G.M. (2022). AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. searched on YYYY-MM-DD.
expert	Le Gall, Line. Muséum National d'Histoire Naturelle. legall@mnhn.fr
expert	Kersen, Priit. Agriculture and Food Board. priit.kersen@gmail.com
expert	Leliaert, Frederik.
expert	Díaz-Tapia, Pilar. Universidad A Coruña. pdiaz@udc.es
expert	Sjøtun, Inga Kjersti. University of Bergen. Kjersti.Sjotun@bio.uib.no
literature	Brodie, J.; Maggs, C. A.; John, D. M. (2007). Green Seaweeds of Britain and Ireland. British Phycological Society.
expert	Smale, Dan. Marine Biological Association. dansma@MBA.ac.uk
literature	Maggs, C. A.; Hommersand, M. H. (1993). Seaweeds of the British Isles Volume 1 Rhodophyta Part 3A Ceramiales. British Museum (Natural History.
expert	de Reviers, Bruno. Muséum National d'Histoire Naturelle. reviers@mnhn.fr
expert	Vergés, Alba. Universitat de Girona. alba.verges@udg.edu
expert	De Clerck, Olivier.

Type	Source
literature	Dixon, P. S. I. L. M. (1977). Seaweeds of the British Islands, vol. 1, Rhodophyta. British Museum, London.
literature	Fletcher, R. L. (1987). Seaweeds of the British Isles: Volume 3. Part 1 Fucophyceae (Phaeophyceae). Natural History Museum: London. ISBN 0-11-310003-5. 359 pp.
expert	Rindi, Fabio. Università Politecnica delle Marche. f.rindi@univpm.it
expert	Peters, Akira. Station Biologique de Roscoff. akirapeters@gmail.com
expert	Destombe, Christophe. Station Biologique de Roscoff. destombe@sb-roscoff.fr; Valero, Myriam. Station Biologique de Roscoff. valero@sb-roscoff.fr
literature	Irvine, L.M. (1983). Seaweeds of the British Isles. Vol. 1: Rhodophyta. Part 2A: Cryptonemiales (sensu stricto) Palmariales, Rhodymeniales. British Museum (Natural History) London, p. 115 pp.
literature	Cormaci, M.; Furnari, G.; Catra, M.; Alongi, G.; Giaccone, G. (2012). Flora marina bentonica del Mediterraneo: Phaeophyceae. Bollettino dell'Accademia Gioenia. 45: 1-508.
literature	Womersley, H. B. S. (1987). The marine benthic flora of southern Australia. Part II. Adelaide: South Australian Government Printing Division. Adelaide: South Australian Government Printing Division, pp. 481, 169 figs, 1 table, 8 plates, 4 maps.
literature	Bartsch, Inka. Alfred-Wegener-Institute. inka.bartsch@awi.de; Herbst, Anne. University Rostock. anne.herbst2@uni-rostock.de; Karez, Rolf. State Agency for Agriculture. Environment and Rural Areas. Rolf.Karez@llur.landsh.de; Kuhlenkamp, Ralph. Phycomarin. ralph.kuhlenkamp@phycomarin.de; Schubert, Hendrik. University Rostock. hendrik.schubert@uni-rostock.de
literature	Brodie, J. A. I. L. M. (2003). Seaweeds of the British Isles. Vol. 1: Rhodophyta. Part 3B: Bangiophycidae. Intercept Ltd, Hampshire SP10 1YG, United Kingdom.
literature	Irvine, L.M.; Chamberlain, Y.M. (1994). Seaweeds of the British Isles: Rhodophyta, Part 2B. Corallinales, Hildenbrandiales. Seaweeds of the British Isles, 1. Natural History Museum: London. ISBN 0-11-310016-7. 276 pp. Part of: Seaweeds of the British Isles. ISSN 8769-8522
literature	Athanasiadis, A. (1996). Morphology and classification of the Ceramioideae (Rhodophyta) based on phylogenetic principles. Opera Botanica, 128, 216 pp.
literature	Womersley, H. B. S. (1994). The marine benthic flora of southern Australia - Rhodophyta - Part III A: Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales sensu lato). Australian biological resources study, Canberra.
literature	Carpenter, K. E.; Niem, V. H. (1998). The living marine resources of the Western Central Pacific. Volume 1. Seaweeds, corals, bivalves and gastropods. FAO Species Identification Guide for Fishery Purposes. FAO: Rome. ISBN 92-5-104051-6. XIV, 686 pp.

Type	Source
literature	Womersley, H. B. S. (1996). The marine benthic flora of southern Australia - Rhodophyta - Part III B. In: Flora of Australia, supplementary series, number 5. Australian biological resources study Canberra, p. 392 pp.
literature	Barcelo Marti, M.; Gallardo Garcia, T.; Gomez Garreta, A.; Perez Ruzafa, I.; Ribera Siguan, M.; Rull Luch, J. (2001). Flora Phycologica Iberica, vol 1: Fucales. Universidad de Murcia.
literature	Taylor, W. R. (1985). Marine algae of the eastern tropical and subtropical coasts of the Americas. The University of Michigan press, Michigan.
literature	Abbott, I. A. (1999). Marine red algae of the Hawaiian Islands. Bishop Museum Press, Hawaii, Honolulu.
literature	Burrows, E.M. (1991). Seaweeds of the British Islands, vol. 2 Chlorophyta. Natural History Museum Publications London, p. 238 pp.
literature	Womersley, H. B. S. (2003). The marine benthic flora of southern Australia - Rhodophyta - Part III D (Ceramiales, Delesseriaceae, Sarcomeniaceae, Rhodomelaceae). In: Flora of Australia, supplementary series, number 18. Australian biological resources study and the State Herbarium of South Australia Canberra, pp. 533 pp., ill.
literature	Stegenga, H.; Anderson, R. J.; Bolton, J. J. (2000). Notes on Ceramiaceae (Rhodophyta) from the eastern Cape Province, South Africa. III. New records from the Tsitsikamma coastal park, with the description of *Scageliopsis tsitsikammae*. Blumea. 45, 485-494.
literature	Wang, W. J.; Zhu, H. Y.; Xu, P.; Xu, J. R.; Lin, X. Z.; Huang, C. K. (2008). Characterization of the life history of *Bangia fuscopurpurea* (Bangiaceae, Rhodophyta) in connection with its cultivation in China. Aquaculture. 278, 101-109.
literature	Womersley, H.B.S. (1984). The marine benthic flora of southern Australia. Part I: Chlorophyta. Woolman, Government Printer, South Australia, Adelaide.
literature	Womersley, H.B.S. (1998). The marine benthic flora of Southern Australia. Rhodophyta. Part III C: Rhodophyceae, Ceramiaceae, Dasyaceae. State Herbarium, South Australia.
literature	Schnetter, R.; Brück, B.; Gerke, K.; Seibold, G. (1990). Notes on heterokaryotic life cycle phases in some Dasycladales and Bryopsidales (Chlorophyta). In: Cell Walls and Surfaces, Reproduction, Photosynthesis. Springer, pp. 124-133.
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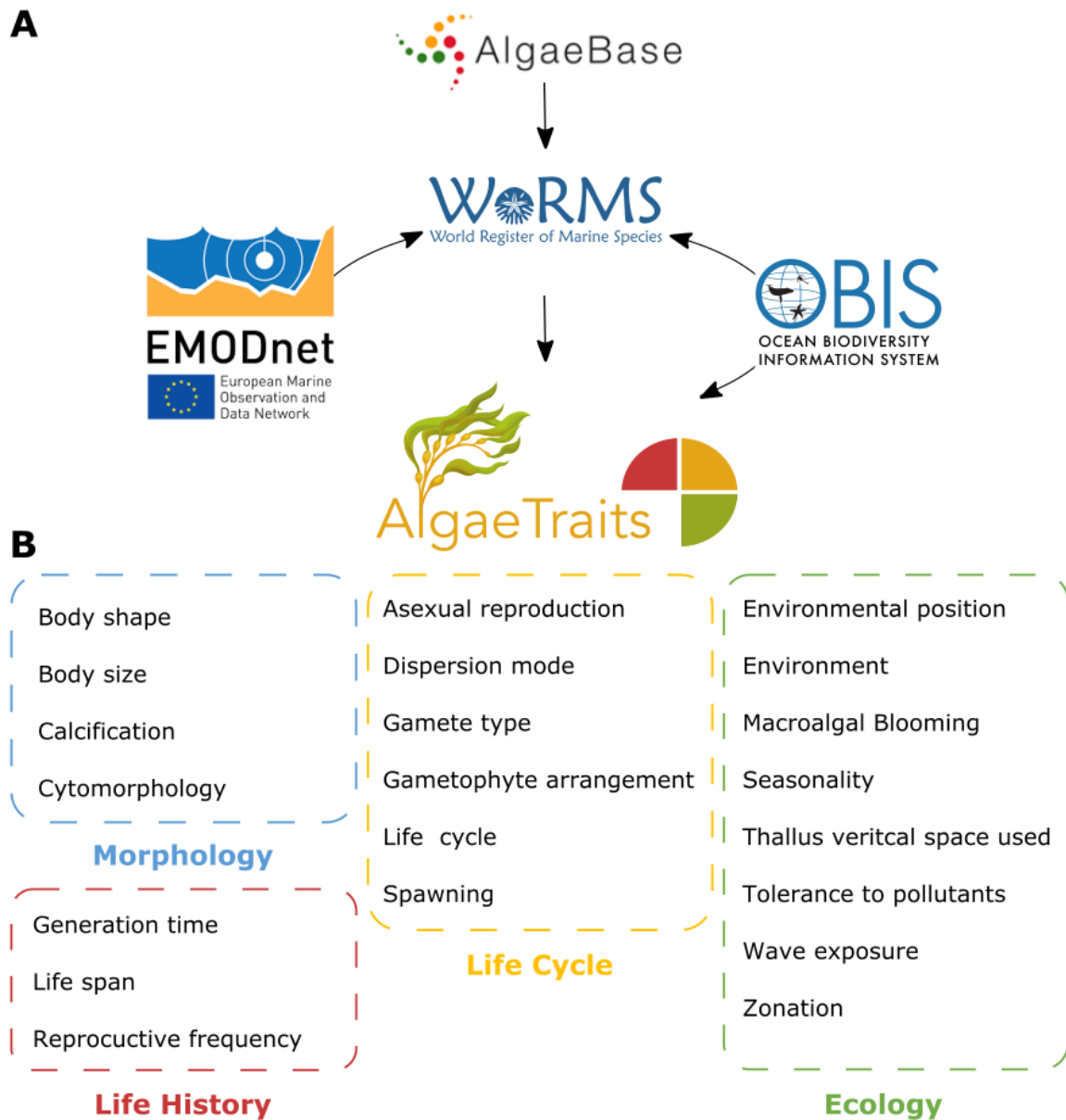
Figure 1. A) Relation of AlgaeTraits to other databases. AlgaeTraits is a subregister of the World Register of Marine Species (WoRMS), which aims to provide an comprehensive authoritative list of all published names of marine organisms and other biological information including traits. AlgaeBase, the most complete list on global algal taxonomy, is used as the main source for algal taxonomy in WoRMS. WoRMS and AlgaeTraits display OBIS occurrence data. All traits included in WoRMS and AlgaeTraits were collected under the EMODnet project. B) All 21 traits currently included in AlgaeTraits can be categorised under 'Morphology', 'Life History', 'Life Cycle' and 'Ecology'.

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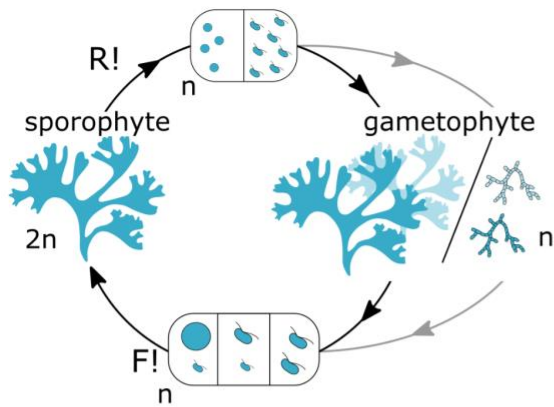
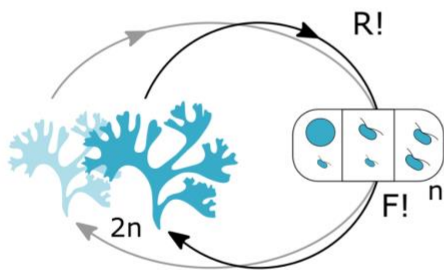
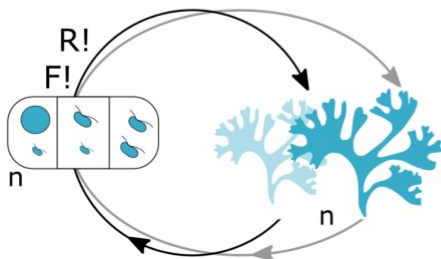

Haplodiplontic

a biphasic life cycle with free living haploid gametophytic and diploid sporophytic phases that both undergo mitosis. The gametophytic and sporophytic phase can be similar in size and morphology (isomorphic) or different (heteromorphic). Here, sex determination happens in the haploid phase.
E.g. isomorphic monoicous: *Dermocorynus*; heteromorphic monoicous: *Atractophora*, *Gloiosiphonia*; isomorphic dioicous: *Gracilaria*; heteromorphic dioicous: *Cutleria*, *Derbesia*, *Laminariales (kelps)*

Diplontic

a monomorphic life cycle where mitosis only happens in the diploid phase, the haploid phase is restricted to the unicellular gametes. Here, sex determination happens in the diploid phase. E.g. *Fucus*, *Cystoseira*

Haplontic

a monomorphic life cycle where mitosis only happens in the haploid phase. Here, sex determination happens in the haploid phase. E.g. *Chara*, *Tolypella*, *Rhodophysema*, *Pantoneura*

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612 **Figure 2. Life cycles of seaweeds. The sexual life cycle of seaweeds can be divided in three main categories: (1) biphasic**
613 **haplodiplontic life cycle or (2) a monophasic haplontic or (3) monophasic diplontic life cycle. Male and female**
614 **reproductive structures (haploid gametes) can be formed on the same or separate thalli (mono- vs. di-; light blue**
615 **indicates production of male and female gametes on separate individuals), and sex determination can happen in both**
616 **the haploid and diploid life phase (-oicous vs. -oecious). The form of the gametes can be (1) identical in size and**
617 **morphology (isogamous), (2) different in size but both motile with flagella (anisogamous), or (3) different in morphology**
618 **and size with a bigger non-motile female gamete lacking a flagella and smaller motile male gametes with flagella**
619 **(oogamous), except for red algae in which the male gamete is also non-motile. n = haploid, 2n = diploid, F!= fertilisation,**
620 **R! = meiosis**

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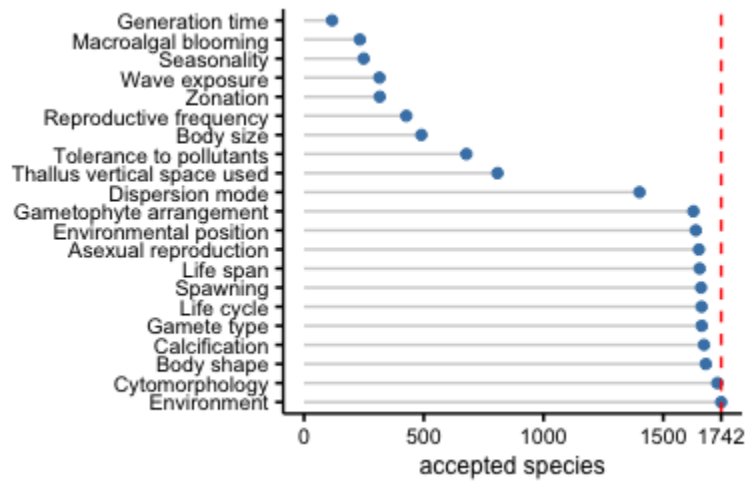
Figure 3. Number of taxonomically accepted species from Europe with trait information by trait. The dashed red line indicates the total number of accepted species (1742) according to Algaebase.

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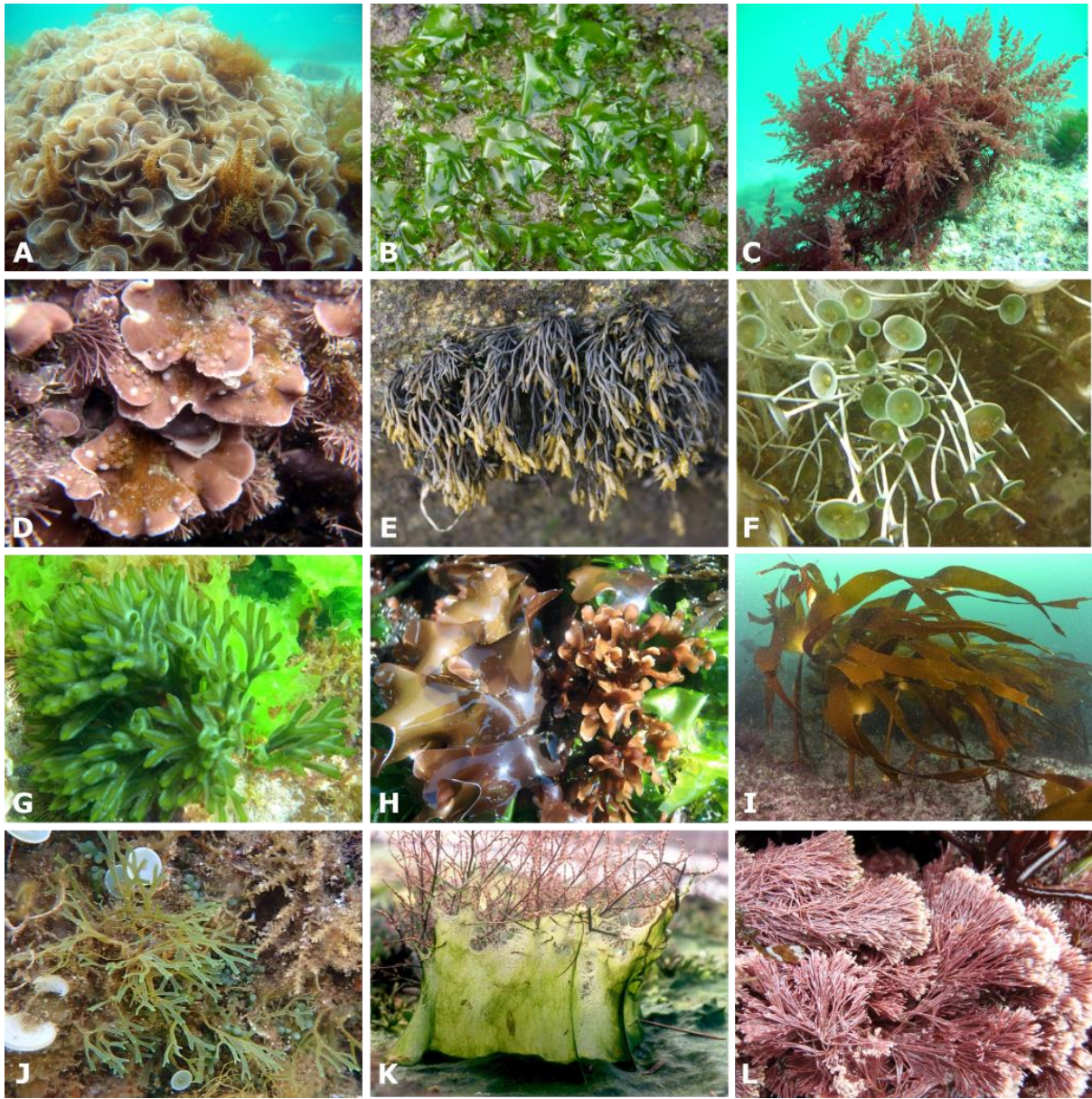
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627 **Fig. 4 Morphological Body Shape diversity of seaweeds. A) flabellate and calcified** *Padina,* **B) foliose** *Ulva***, C) branched**
628 *Asparagopsis***, D) crustose and calcified** *Mesophyllum,* **E) branched** *Pelvetia***, F) siphonous and calcified** *Acetabularia***, G)**
629 **branched and siphonous** *Codium***. H)** *Chondrus* **(left) and** *Mastocarpus* **(right) I) erect** *Laminaria***, J) dichotomously**
630 **branched** *Dictyota***, K) filamentous** *Rhizoclonium***, L) calcified and articulated** *Jania.* **Photo credits: A-D, F-H, K-L:**
631 **Ignacio Bárbara; E,,J: Olivier De Clerck, I: Cristina Piñeiro-Corbeira**

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635 **Figure 5: Data coverage for green seaweeds. The taxonomic coverage is restricted to marine representatives. The order**
636 **Charales is included to accommodate a limited number of species that occur in brackish habitats. The left side shows**
637 **a phylogenetic tree at the ordinal level. Next to the tree the number of species with trait information available in the**
638 **database is indicated as the total number (No. of species), the percentage relative to the total number of European**
639 **species (% europe), and the percentage relative to the total number of global species (% global). The heatmap indicates**
640 **the percentage of trait coverage relative to the total number of European species per order per trait included in the**
641 **database. At the bottom of the figure, average species coverage per trait is presented as a percentage of the total number**
642 **of European (% europe) and global (% global) species. Oltmannsiellopsid. refers to Oltmannsiellopsidales.**

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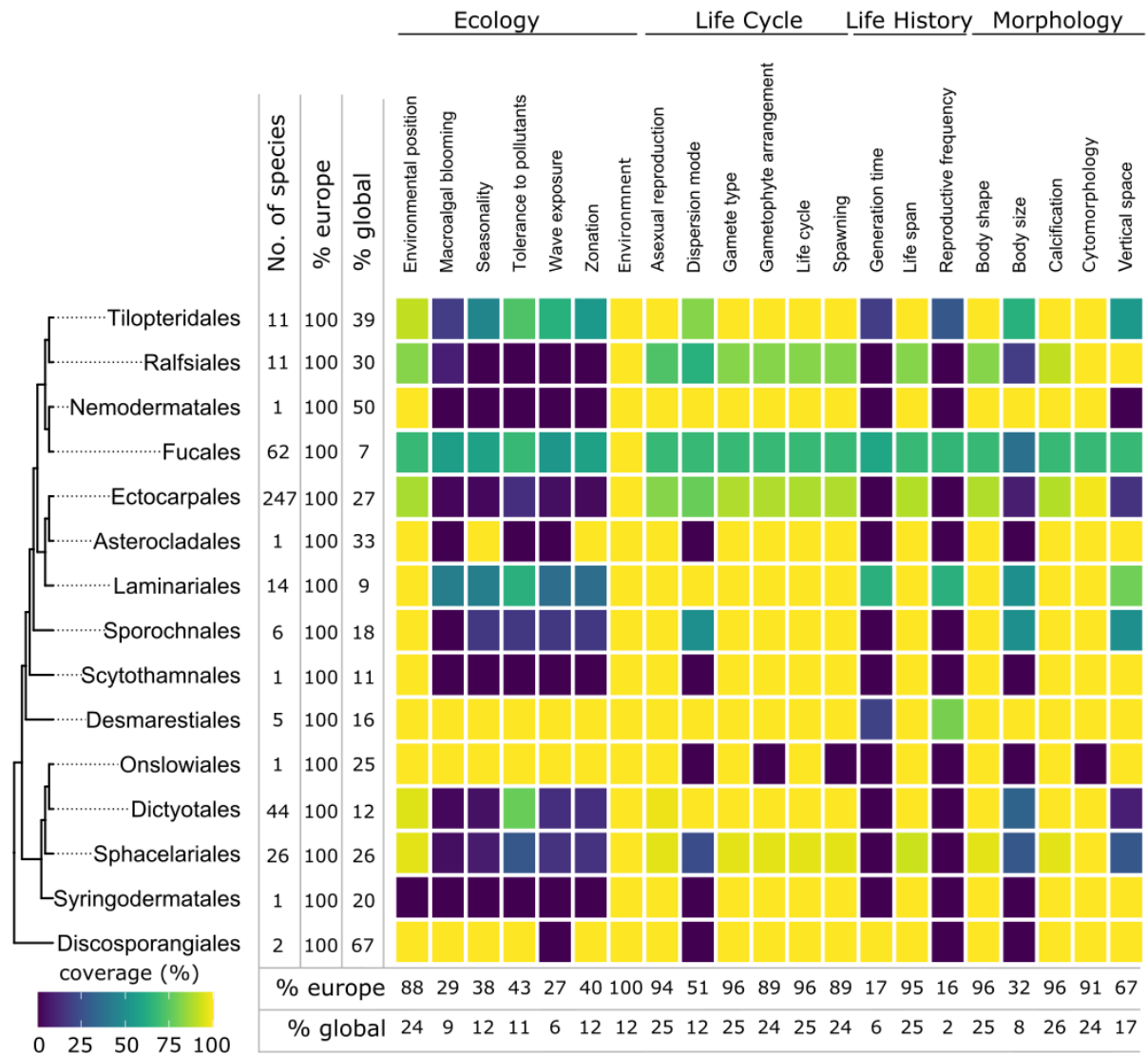
Figure 6: Data coverage for brown seaweeds (Phaeophyceae). The left side shows a phylogenetic tree at the ordinal
level. Next to the tree the number of species with trait information available in the database is indicated as the total
number (No. of species), the percentage relative to the total number of European species (% europe), and the percentage
relative to the total number of global species (% global). The heatmap indicates the percentage of trait coverage relative
to the total number of European species per order per trait included in the database. At the bottom of the figure,
average species coverage per trait is presented as a percentage of the total number of European (% europe) and global
(% global) species.

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Figure 7: Data coverage for red seaweeds (Rhodophyta). The left side shows a phylogenetic tree at the ordinal level. Next to the tree the number of species with trait information available in the database is indicated as the total number (No. of species), the percentage relative to the total number of European species (% europe), and the percentage relative to the total number of global species (% global). The heatmap indicates the percentage of trait coverage relative to the total number of European species per order per trait included in the database. At the bottom of the figure, average species coverage per trait is presented as a percentage of the total number of European (% europe) and global (% global) species. Orders with blank bars are not present in European marine waters.

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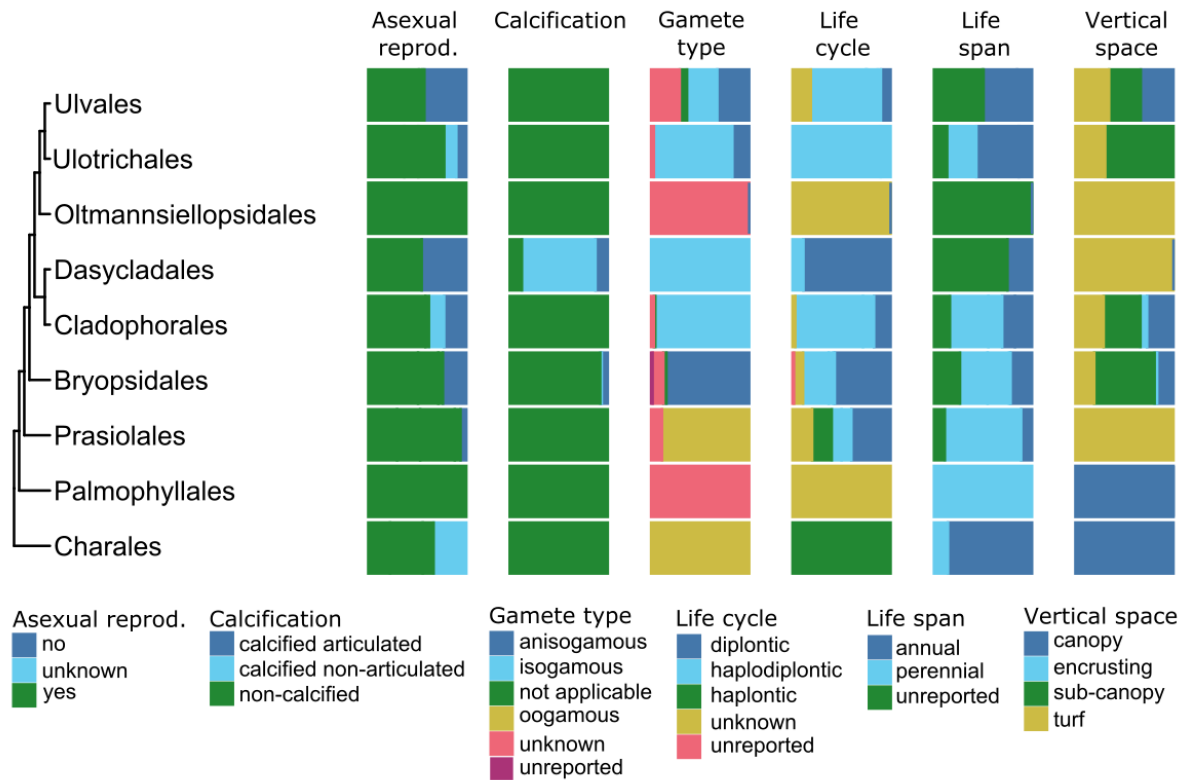
Figure 8 Trait variability for a selected set of traits ('Asexual reproduction', 'Calcification', 'Gamete type', 'Life cycle', 'Life span', 'Vertical space') for European green seaweeds. The left side shows a phylogenetic tree at the ordinal level. On the right stacked barplots indicate trait variability as the proportion of species exhibiting a certain trait value by order and by trait.

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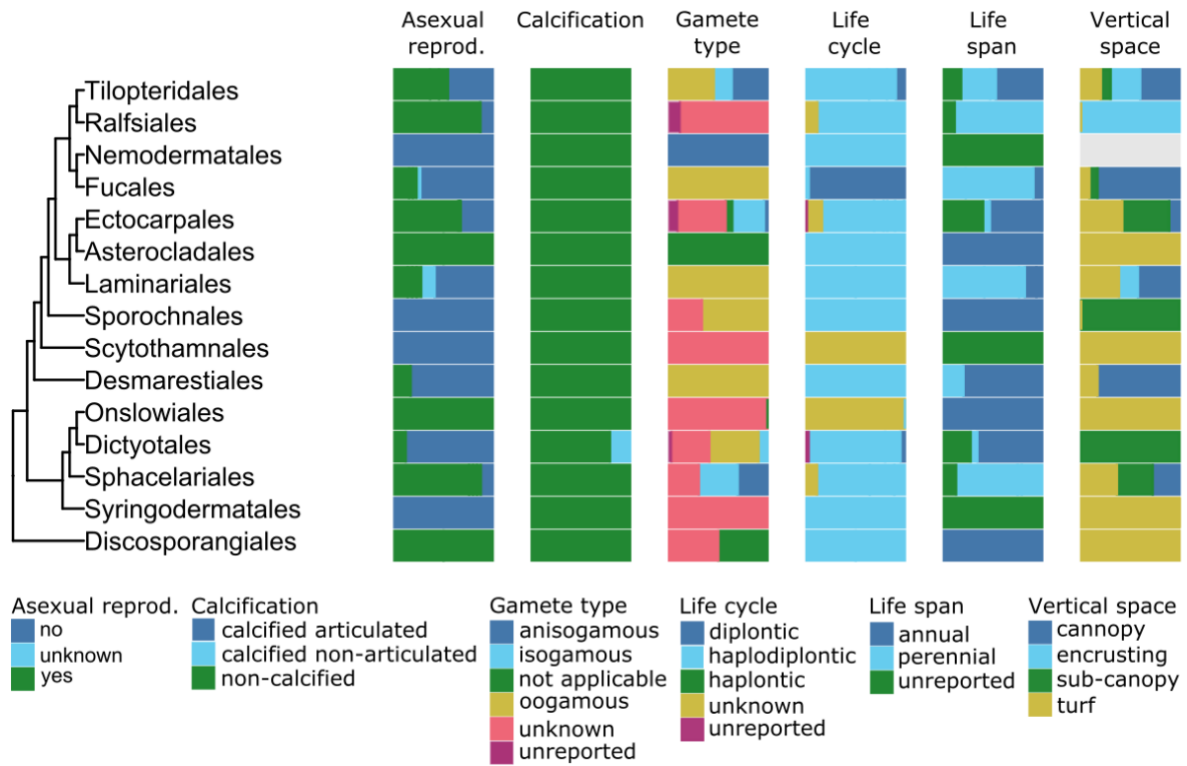
Figure 9 Trait variability for a selected set of traits ('Asexual reproduction', 'Calcification', 'Gamete type', 'Life cycle', 'Life span', 'Vertical space') for European brown seaweeds (Phaeophyceae). The left side shows a phylogenetic tree at the ordinal level. On the right stacked barplots indicate trait variability as the proportion of species exhibiting a certain trait value by order and by trait. Grey bars indicate missing data.

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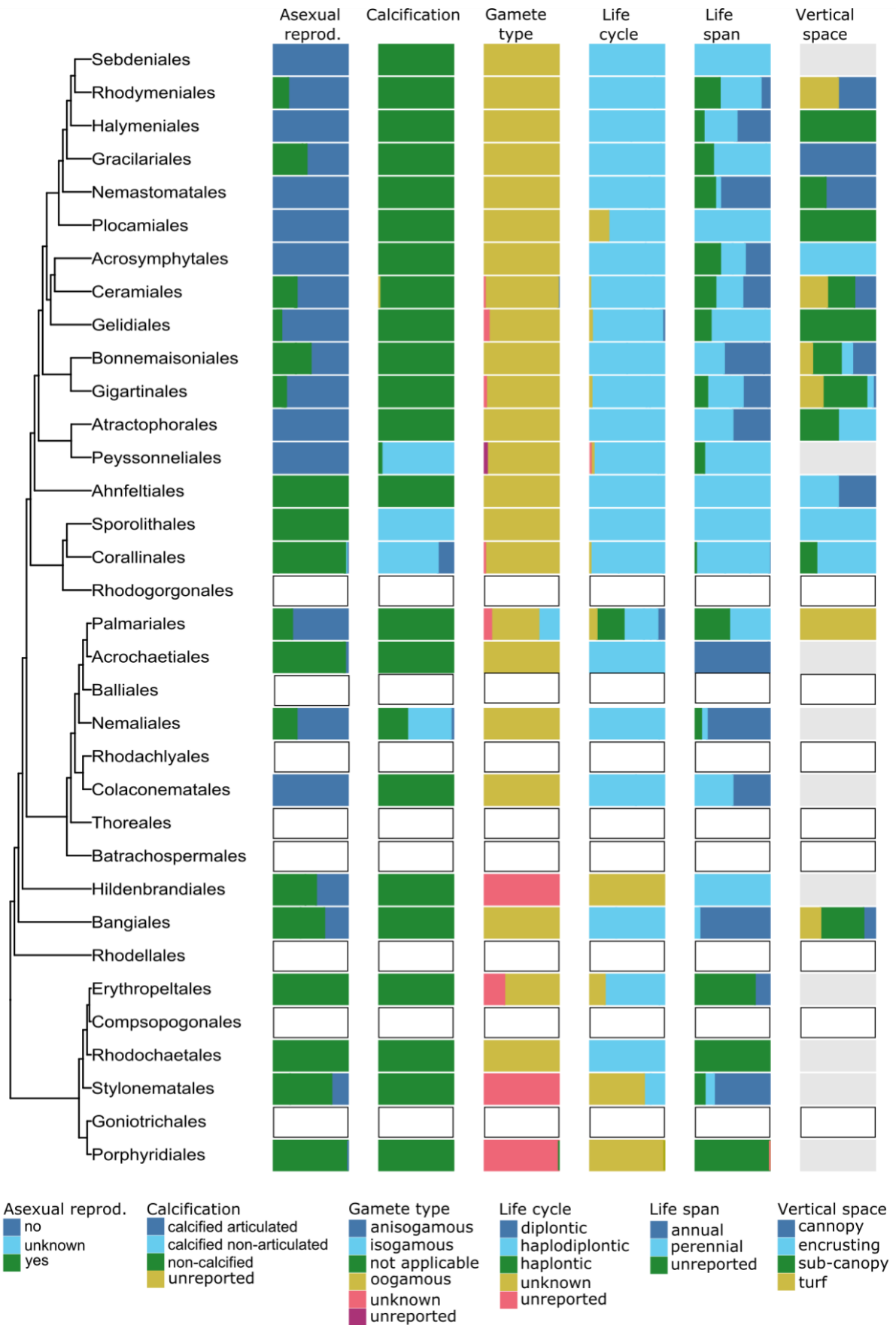
Figure 10 Trait variability for a selected set of traits ('Asexual reproduction', 'Calcification', 'Gamete type', 'Life cycle', 'Life span', 'Vertical space') for European red seaweeds. The left side shows a phylogenetic tree at the ordinal level. On the right stacked barplots indicate trait variability as the proportion of species exhibiting a certain trait value

677 **by order and by trait. Orders with blank bars are not present in European marine waters and grey bars indicate**
678 **missing data.**

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