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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 1745 European seaweed species of which more than half (56 %) of the records were documented at the species level, while the remaining 44 % were 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 are publicly accessible through the AlgaeTraits portal, <https://doi.org/10.14284/574> (AlgaeTraits, 2022).

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 (De Wreede and King, 1988; Bell, 1994) used to explain various evolutionary questions (Heesch et al., 2021). In the 1980s, Littler and Littler (1980) and Littler et al. (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 (Steenack 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), to understand 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 phyco-logical 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 1745 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; McGill et al., 2006) to include data on habitat, seasonality, morphology, life cycle, life history, and biogeographical range (Fig. 1, Table A1). In total, we describe 21 traits linked to taxonomic information, covering 9 of the 10 previously prioritised traits in Costello et al. (2015). These data are available on the *AlgaeTraits* data portal <https://doi.org/10.14284/574> (*AlgaeTraits*, 2022), which is a subregister of the World Register of Marine species (WoRMS, 2022; Marine Species Traits, 2022). Here we introduce *AlgaeTraits* by (i) presenting the methodologies used to collect data, (ii) highlighting trait coverage for the current and first version of the database, and (iii) exploring trait variability for a selected subset of traits.

2 Data

2.1 Trait collection

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

2.2 Trait data

We included 21 traits for marine seaweeds: 8 ecological traits, 4 morphological traits, 6 life cycle traits, and 3 life history related traits (Fig. 1, Table A1). Ecological traits relate to the habitat of the seaweed with respect to environment (marine, freshwater, brackish), tidal zonation, various degrees of wave exposure, environmental position (substrate), tolerance to organic pollutants, vertical space use, and seasonality. In the few instances where seaweed species are known for their potential to form blooms, this has been indicated as well (Fig. 1, Table A1). Morphological traits describe the thallus based on body shape, body size, calcification, and cytomorphology (Fig. 1, Table A1). Body size is the only quantitative trait included in *AlgaeTraits* and can be documented as a mean, maximum, or minimum value to describe the thallus length or diameter. Life-history-related traits describe patterns that influence demography and population dynamics, while life cycle traits relate to the various stages an organism undergoes from one stage in its development (e.g. fertilisation) to the same stage in the next generation (Albecker et al., 2021) (Fig. 1, Table A1). In addition to these 21 traits, species distributions were documented as ecoregions defined by Spalding et al. (2007) and can be used to subset the database according to geographic region. Moreover, WoRMS also displays species' occurrences of the Ocean Biodiversity Information System (OBIS; <https://www.obis.org>, last access: 2 March 2022) (Fig. 1). Contrary to the other traits, environment and distribution were not uploaded as traits (i.e. attributes) in the database system (Aphia; see further) but as environment flags and distributions. This implies that environment and distribution are slightly differently visualised on the *AlgaeTraits* data portal (<https://www.algaetraits.org>, last access: 10 September 2022).

2.3 Taxonomy

The total number of described seaweeds is estimated at 9250 species on a global scale (Appeltans et al., 2012; Guiry, 2012), of which at least 1800 species occur in Europe (Costello et al., 2022). The taxonomic classification of these species is not always straightforward and is continuously updated. To provide the best possible taxonomic accuracy, the trait data were implemented in WoRMS. WoRMS aims to provide a complete taxonomic authoritative list of all currently published names of marine species and is synchronised with *AlgaeBase*, the most complete database on global algal taxonomic information (Guiry and Guiry, 2022).

2.4 Metadata

Every trait value is linked to a source (expert or literature) and a note field that can be used to include relevant metadata related to specific trait values. As values for the traits asexual reproduction, macroalgal blooming, body size, and seasonality may display considerable geographic variation,

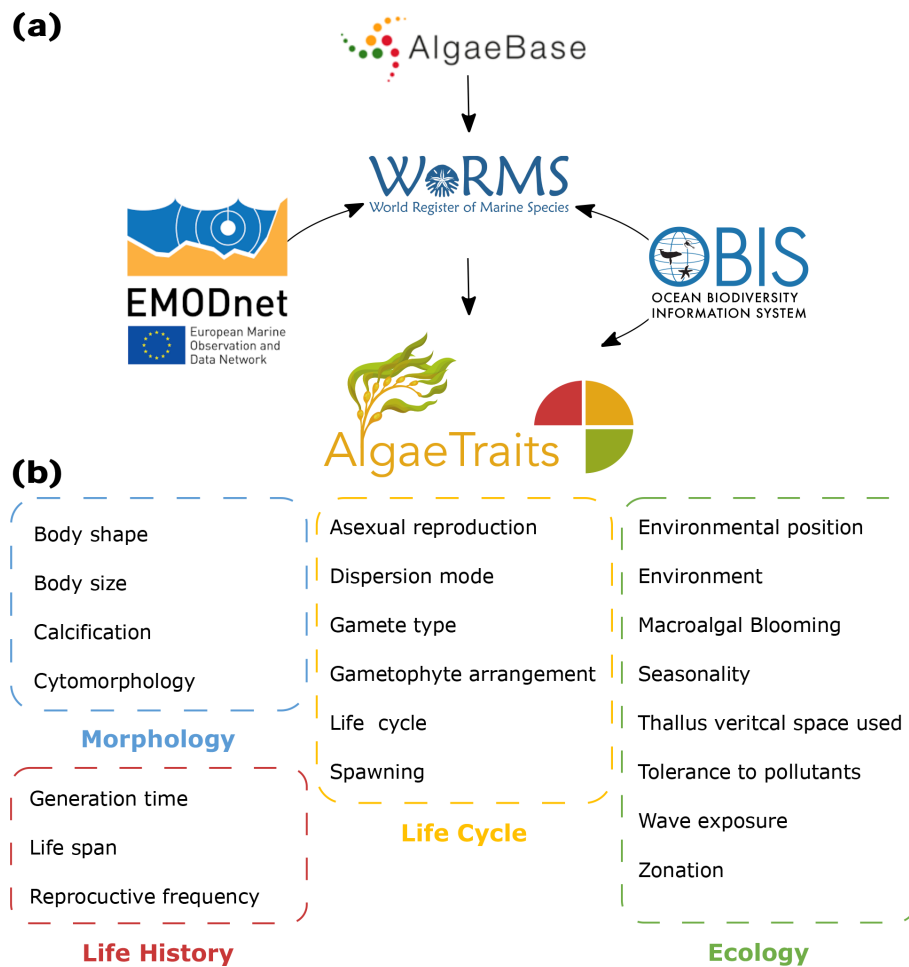


Figure 1. (a) Relation of AlgaeTraits to other databases. AlgaeTraits is a subregister of the World Register of Marine Species (WoRMS), which aims to provide a comprehensive authoritative list of all published names of marine organisms and other biological information including traits. AlgaeBase, the 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.

we assigned a specific locality to these trait values. Localities are defined as georegions obtained from the Marine Regions platform, which provides a hierarchical, standardised list of georeferenced marine regions and areas (<https://www.marineregions.org>, last access: 6 April 2022). As mentioned above, life cycles of seaweeds can be complex and often consist of different life stages with radically different morphological, physiological, and ecological characteristics (Fig. 2). When relevant, trait values are documented for the specific life cycle stage they apply to (i.e. sporophyte, gametophyte, microthallus, macrothallus).

2.5 Database structure and management

The AlgaeTraits database is a thematic subregister of WoRMS, part of the Aphia platform. The Aphia platform is an MS SQL (Microsoft Structured Query Language)

database specifically built to include taxonomic data and related information such as biological traits. In total, Aphia contains more than 400 data fields, which are maintained by more than 500 experts under guidance of the WoRMS steering committee, which takes the lead on setting priorities and future directions and coordination of the experts (Vandepitte et al., 2015, 2018). Both editors and database users are supported by a data management team that includes technical and scientific staff hosted at the Flanders Marine Institute (VLIZ) and can be contacted through info@marinespecies.org. This data management team is committed to safeguarding the integrity and online access of the database.

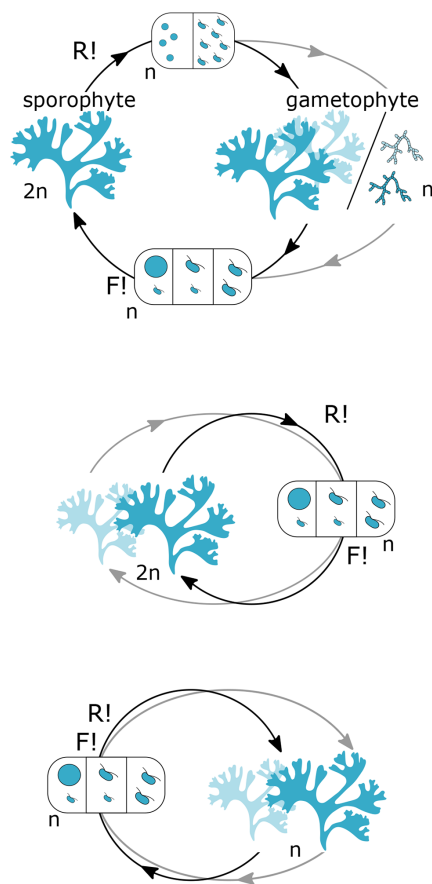


Figure 2. Life cycles of seaweeds. The sexual life cycle of seaweeds can be divided in three main categories: (1) biphasic haplodiplontic life cycle, (2) monophasic haplontic life cycle, or (3) monophasic diplontic life cycle. Male and female reproductive structures (haploid gametes) can be formed on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

3 Results

Twenty-one traits were documented resulting in 45 195 entries for 2830 accepted taxa according to AlgaeBase, among which 681 were at the genus level and 1742 at the species level. Fifty-six percent of the trait entries for species were inherited from the genus level. Environment and cytomorphology were the traits most documented for species, while the least information was provided for the traits that show substantial variation 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

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*

filaments (filamentous) or be leaf-like (foliose) or cushion-like (saccate). They can trail closely along the surface (prostrate), be upright (erect), or take many other shapes (Table A1, Fig. 4). Body shape had a high data coverage of 96 % (1678 species) at the species level (Figs. 3, 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 (Figs. 3, 5–7).

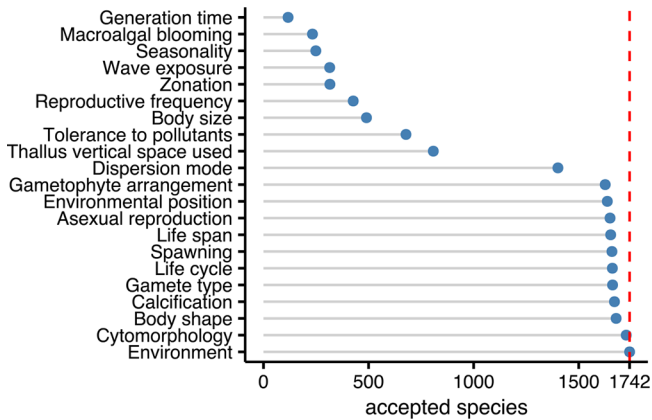


Figure 3. Number of taxonomically accepted species from Europe with trait information by trait. The dashed red line indicates the total number of accepted species (1742) according to AlgaeBase.

3.1.3 Calcification

Several species in different taxonomic groups have calcified thalli (Figs. 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) (Figs. 4a, 9). Calcification in various forms is present in four European orders of red seaweeds: in the Corallinales and Sporolithales as calcite in the cell walls (Figs. 4d, 10), whereas the Peyssonneliales and Nemaliales deposit aragonite (Pentecost, 1980). Calcification had a high data coverage of 96 % (1670 species) on a European level (Figs. 3, 5–7).

3.1.4 Cytomorphology

Cytomorphology was the trait best documented on a European level and reached a data coverage of 99 % (1726 species) (Figs. 4, 5–7). Although the trait which distinguishes unicellular 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 % (1636 species) (Figs. 3, 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 (Figs. 3, 5–7). Notorious examples of blooming species include *Ulva prolifera*, *Cladophora glomerata*, *Caulerpa cylindracea*, and holopelagic *Sargassum* and *Rugulopteryx okamurae*, and events have been often linked to eutrophication (Charlier et al., 2008; Pierucci et al., 2019; 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) (Figs. 3, 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) (Figs. 3, 5–7).

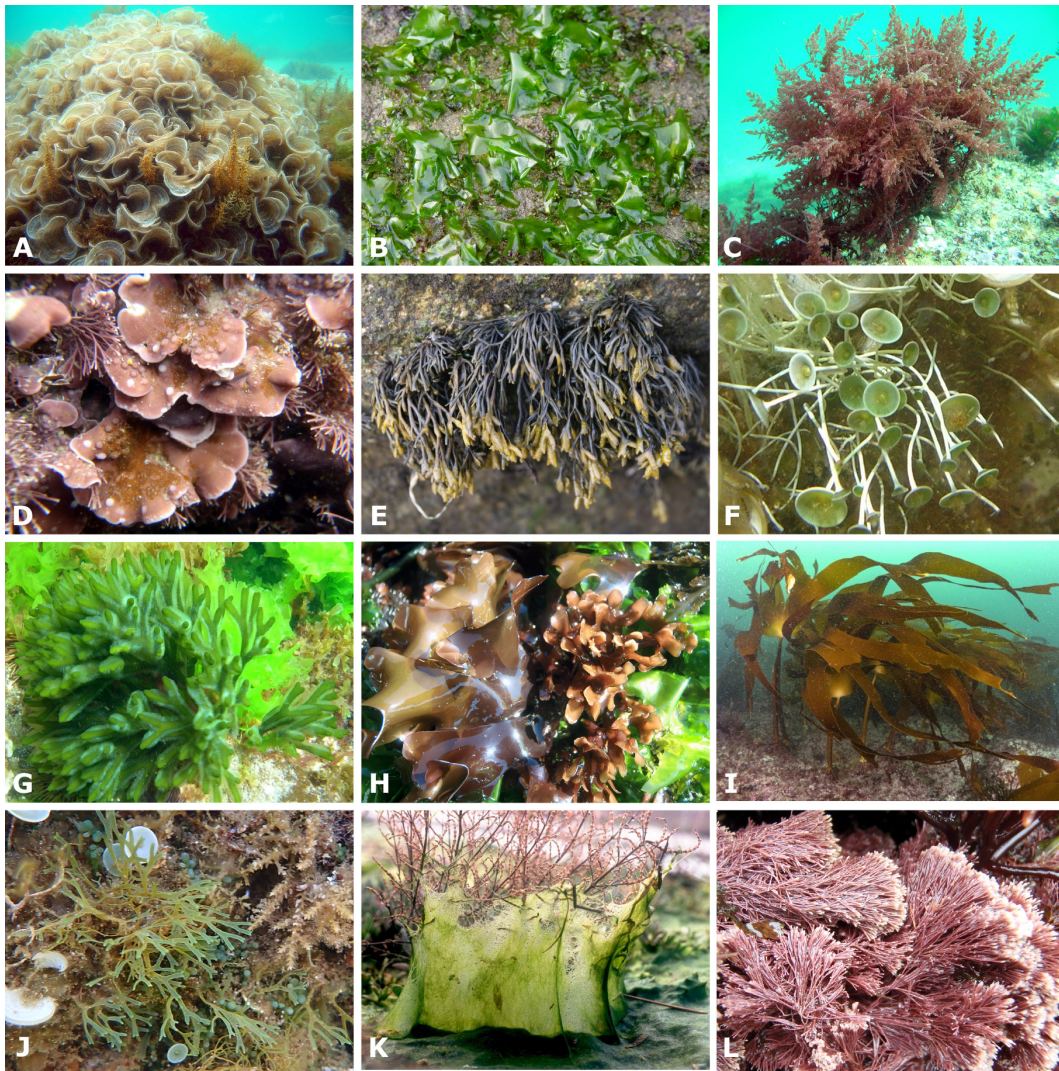


Figure 4. Morphological body shape diversity of seaweeds. (a) Flabellate and calcified *Padina*, (b) foliose *Ulva*, (c) branched *Asparagopsis*, (d) crustose and calcified *Mesophyllum*, (e) branched *Pelvetia*, (f) siphonous and calcified *Acetabularia*, and (g) branched and siphonous *Codium*. (h) *Chondrus* (left) and *Mastocarpus* (right) (i) erect *Laminaria*, (j) dichotomously branched *Dictyota*, (k) filamentous *Rhizoclonium*, and (l) calcified and articulated *Jania*. Photo credits: (a–d), (f–h), (k–l): Ignacio Bárbara; (e, j): Olivier De Clerck; (i) Cristina Piñeiro-Corbeira.

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 (mesotrophic, eutrophic; Table A1). Tolerance to organic pollutants was covered for 39 % of European accepted seaweeds (678 species) (Figs. 3, 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 adrianae* 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) (Figs. 3, 5–7).

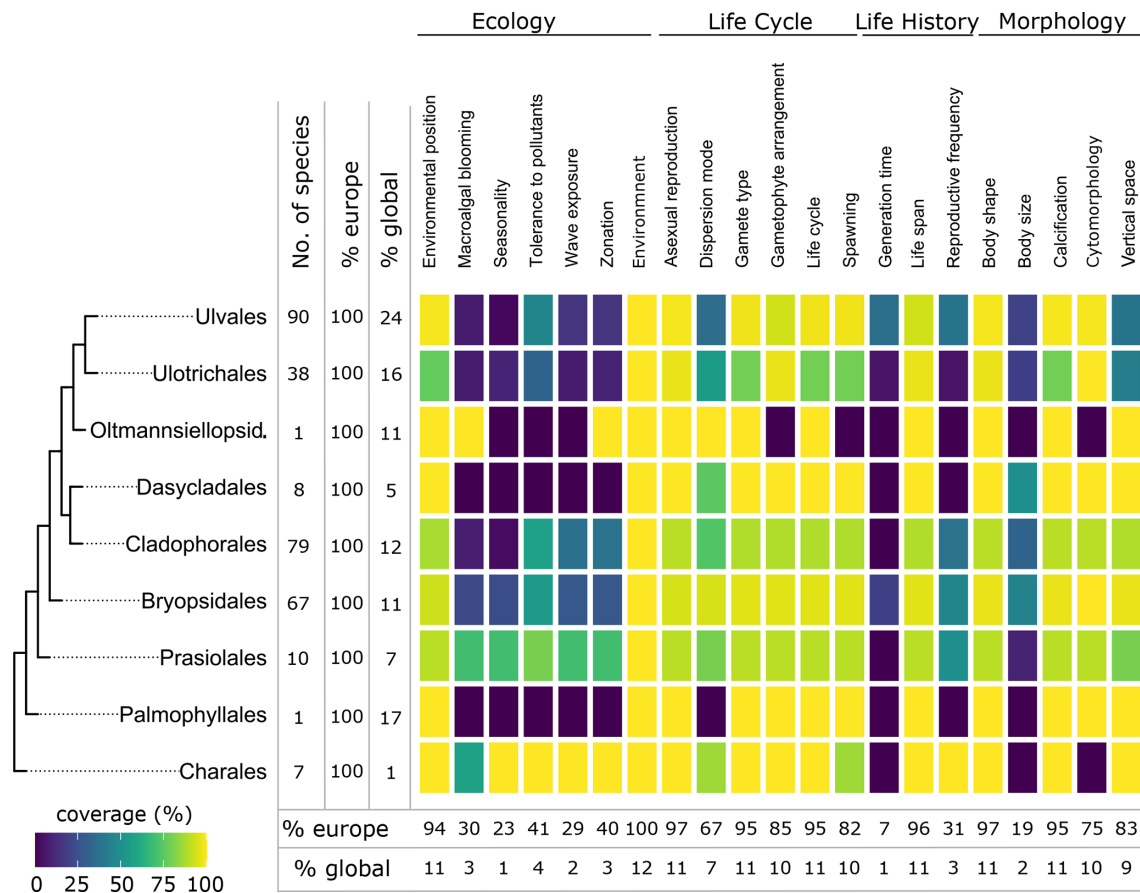


Figure 5. Data coverage for green seaweeds. The taxonomic coverage is restricted to marine representatives. The order Charales is included to accommodate a limited number of species that occur in brackish habitats. The left side shows a phylogenetic tree at the ordinal level. Next to the tree the number 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. Oltmannsiellopsid. refers to Oltmannsiellopsidales.

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) (Figs. 3, 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 (1660 species) (Figs. 3, 5–7). Many seaweeds have a biphasic or haplodiplontic life cycle in which a diploid sporophytic and a haploid gametophytic life phase al-

ternate. These can have a similar (isomorphic; e.g. *Chondrus crispus*) or distinct (heteromorphic) body shape (e.g. Lamnariales) (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

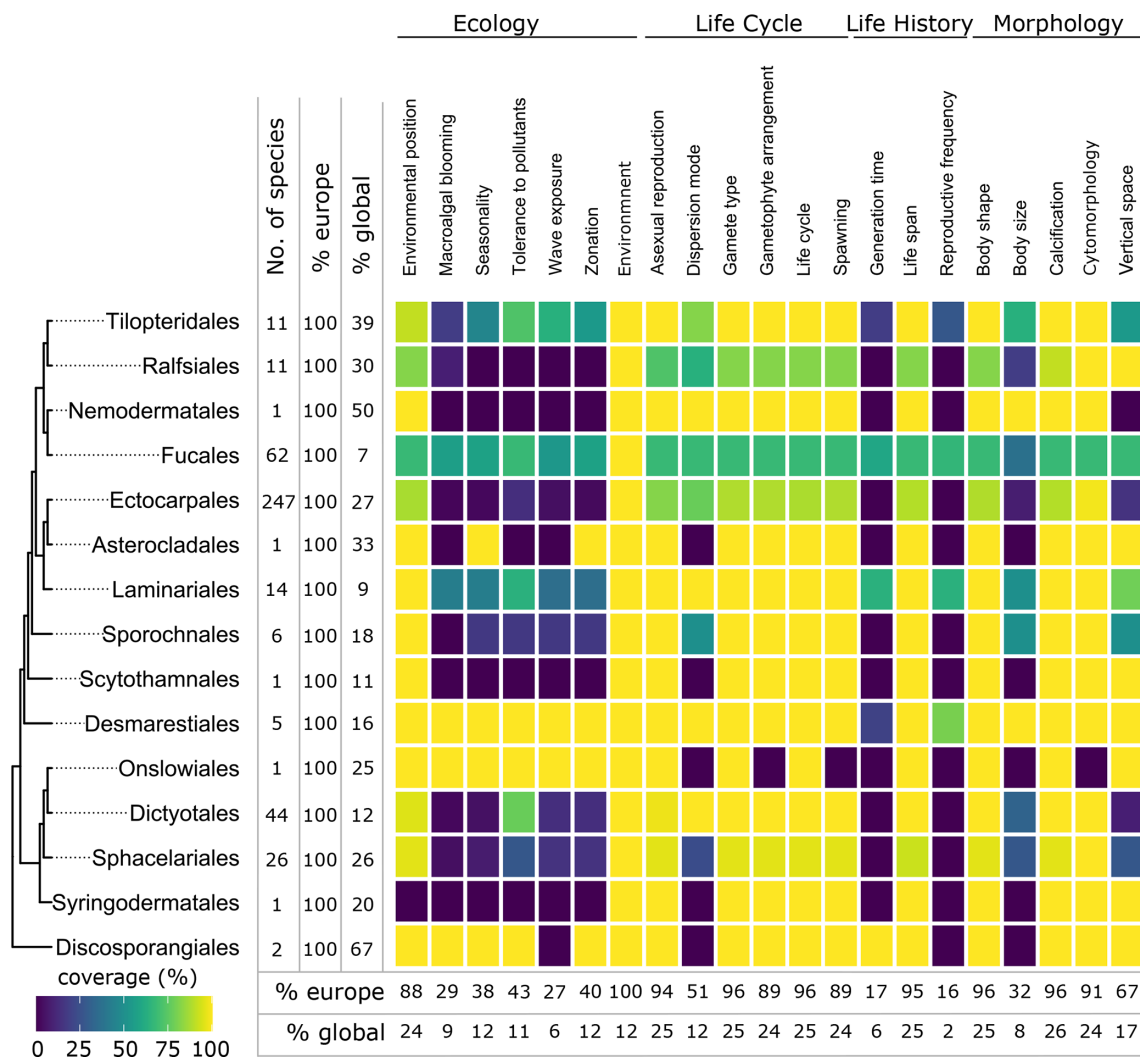


Figure 6. Data coverage for brown seaweeds (Phaeophyceae). The left side shows a phylogenetic tree at the ordinal level. Next to the tree the number of species with trait information available in the database is indicated as the total number (no. of species), the percentage relative to the total number 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.

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 (Figs. 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 (1649 species) (Figs. 3, 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 dis-

persal 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 (1401 species) (Figs. 3, 5–7).

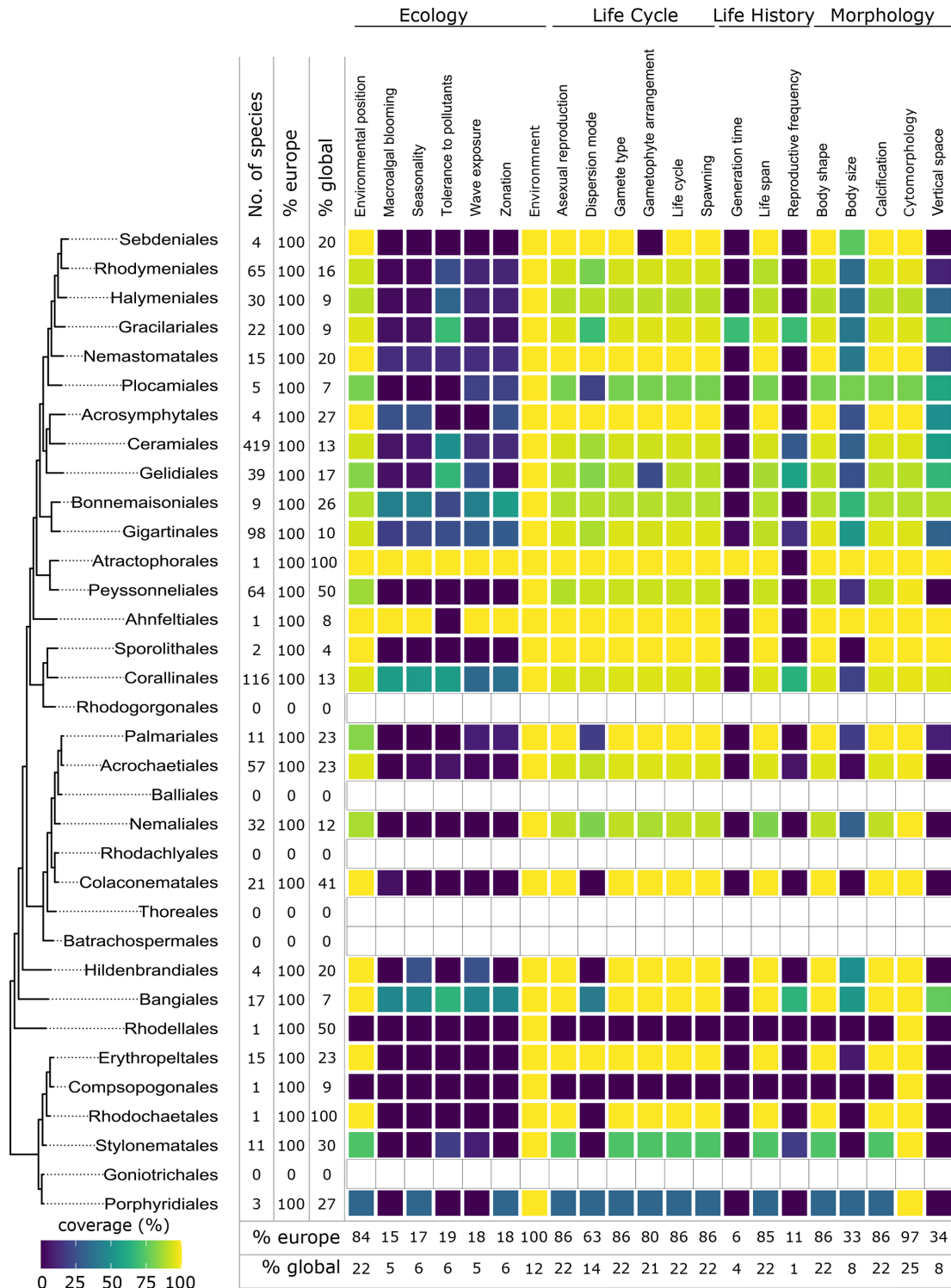


Figure 7. Data coverage for red seaweeds (Rhodophyta). The left side shows a phylogenetic tree at the ordinal level. Next to the tree the number of species with trait information available in the database is indicated as the total number (no. of species), the percentage relative to the total number of 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.

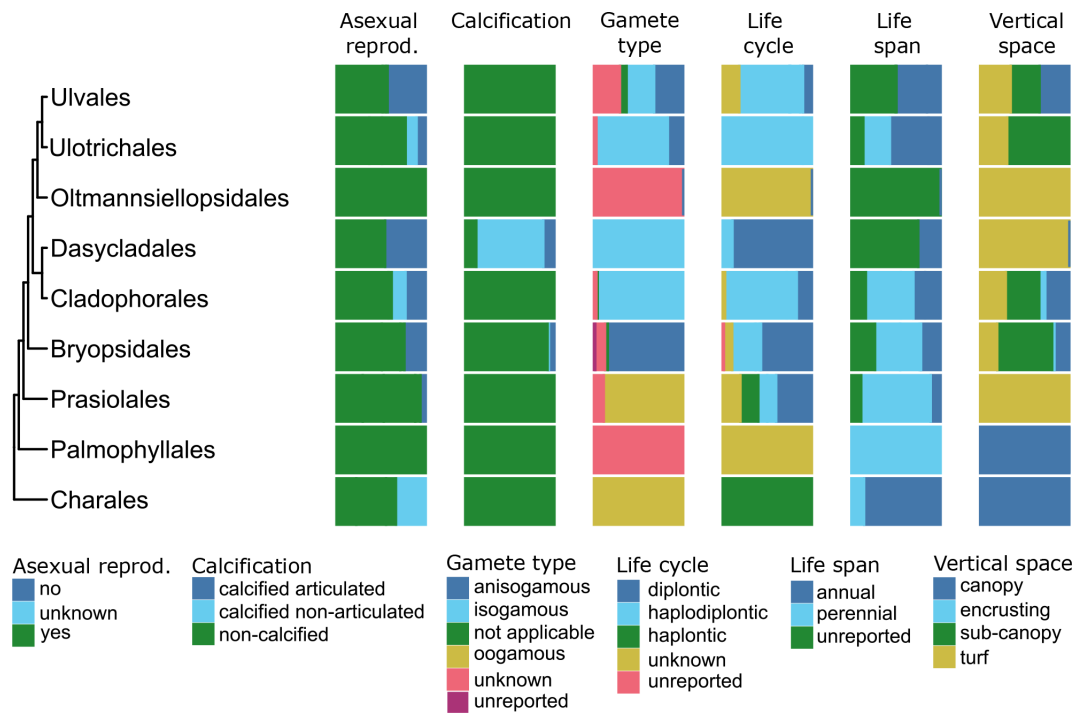


Figure 8. Trait variability for a selected set of traits (asexual reproduction, calcification, gamete type, life cycle, life span, vertical space) for European green seaweeds. The left side shows a phylogenetic tree at the ordinal level. On the right stacked bar plots indicate trait variability as the proportion of species exhibiting a certain trait value by order and by trait.

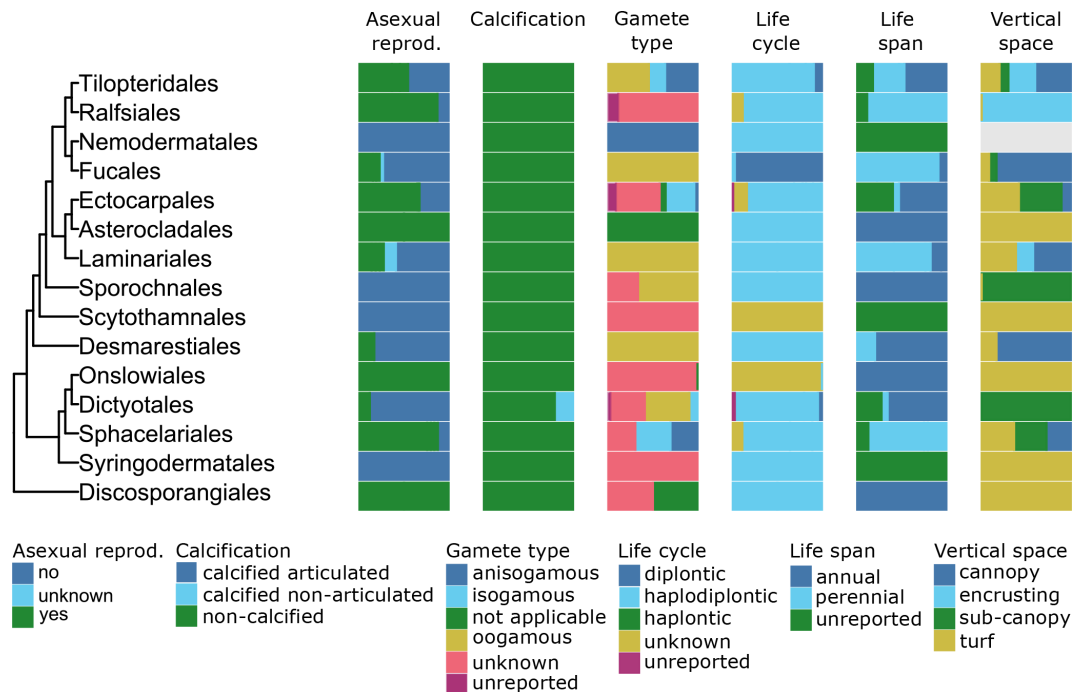


Figure 9. Trait variability for a selected set of traits (asexual reproduction, calcification, gamete type, life cycle, life span, vertical space) for European brown seaweeds (Phaeophyceae). The left side shows a phylogenetic tree at the ordinal level. On the right stacked bar plots indicate trait variability as the proportion of species exhibiting a certain trait value by order and by trait. Grey bars indicate missing data.

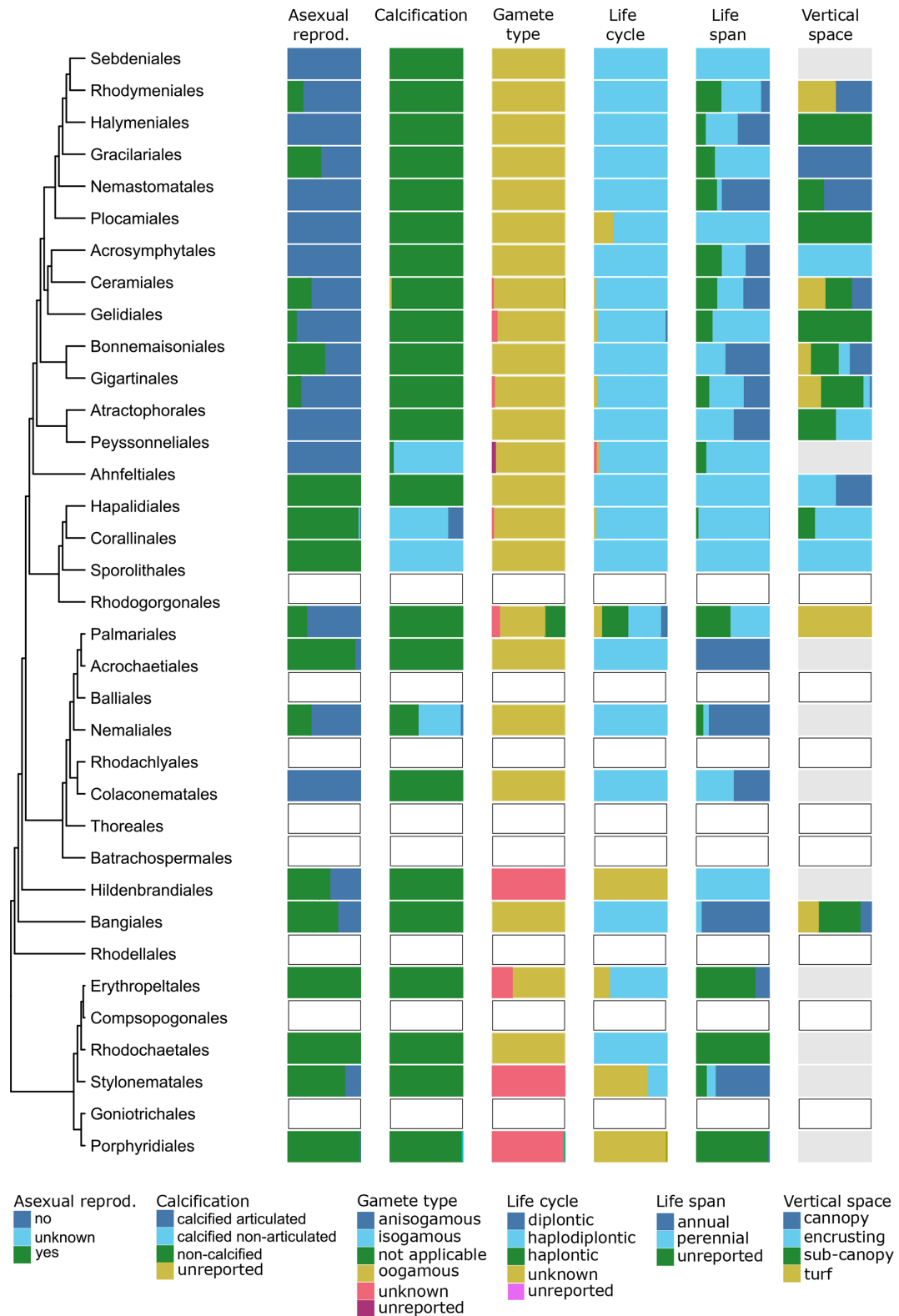


Figure 10. Trait variability for a selected set of traits (asexual reproduction, calcification, gamete type, life cycle, life span, vertical space) for European red seaweeds. The left side shows a phylogenetic tree at the ordinal level. On the right stacked bar plots indicate trait variability as the proportion of species exhibiting a certain trait value by order and by trait. Orders with blank bars are not present in European marine waters, and grey bars indicate missing data.

3.3.4 Gamete type

Gamete type varies among and within orders of green and brown seaweeds (Figs. 8, 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 (1661 species) (Figs. 3, 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) (Figs. 3, 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 (1658 species) (Figs. 3, 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) (Figs. 3, 5–7).

3.4.2 Life span

Life span varies within and among European green, brown, and red seaweeds (Figs. 8–10). Perennial macroalgae can live up to multiple years such as for several years. Many kelp species such as Laminariales or *Gracilaria gracilis* can live for more than 50 years (Engel et al., 2001); *Ascophyllum nodosum* 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 % (1652 species) (Figs. 3, 5–7).

3.4.3 Reproductive frequency

Data coverage was limited for reproductive frequency, with data available for only 25 % for the European species (427 species) (Figs. 3, 5–7).

4 Discussion

AlgaeTraits includes 21 traits and 1742 European seaweed species, and it is structured within a general framework and ontology aiming to describe all marine species (Costello et al., 2015). With a mean coverage of $\sim 60\%$ 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; Esmaili 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), can 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 service 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 it is limited to only 30 seaweed species. SeaTraIn (2022) covers around 10 traits, of which 2 traits overlap with AlgaeTraits, and includes 96 seaweed species. As to taxonomic coverage (1742 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 30 trained thematic editors who actively update the trait information on a voluntary basis through the online editing inter-

face (<https://www.algaetraits.org>, lastaccess:10/09/2022) and gradually work on the expansion of this European database to a global database. 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 (i.e. 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, <https://doi.org/10.14284/574> (AlgaeTraits, 2022).

6 Conclusions

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 phylogenetic 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.

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). | <i>Plumaria</i> |
| | | Capitate | – | (1) Enlarged or swollen at tip; (2) gathered into a mass at tip or apex. | <i>Penicillus</i> |
| | | Crustose | – | Forming a thin crust on the substratum, applicable to certain lichens, sponges, and algae (Lawrence, 2005). | <i>Hydrolithon</i> |
| | | Cushion-like | – | Approximating the shape of a cushion (Womersley, 1987). | <i>Cladophoropsis membranacea</i> |
| | | Discoid | – | (1) Flat and circular; (2) disc-shaped (Lawrence, 2005). | <i>Ulvella</i> , <i>Scytosiphon lomentaria</i> (sporophyte) |
| | | Erect | – | Upright. | <i>Cystoseira</i> |
| | | Filamentous | – | Existing out of a branched or unbranched row of cells joined end to end (Womersley, 1987). | <i>Antithamnionella</i> |
| | | Filiform | – | Resembling a filament. | – |
| | | Flabellate | – | Fan-shaped, thallus usually expanding upward from a narrow base. | <i>Flabellia</i> |
| | | Foliose | – | Leaf-like (Womersley, 1987). | <i>Palmaria</i> , <i>Halymenia</i> |
| | | 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). | <i>Haliptilon</i> |
| | | Prostrate | – | Trailing on the ground or lying closely along a surface (Lawrence, 2005). | <i>Parviphycus</i> |
| | | Saccate | – | Inflated, or sac-like (Womersley, 1987). | <i>Colpomenia</i> |
| Spheric | – | Approximating the shape of a sphere (Womersley, 1987). | <i>Valonia</i> | | |
| Stoloniferous | – | Forming a prostrate axis, lying on or in the substrate, from which erect branches arise (Womersley, 1984). | <i>Caulerpa</i> | | |
| Tubular | – | In the form of a tube, having tubes, consisting of tubes (Lawrence, 2005). | <i>Chorda filum</i> | | |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait child value | Definition | Genus or species example |
|-------------|------------------------|---------------------------|--|--|---|
| | | Unreported | – | So far it has not been reported in the 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. | <i>Caulerpa prolifera</i> : 25 cm maximum thallus length |
| | Calcification | Calcified articulated | – | Algal thallus that is encrusted or impregnated with lime with non-calcified joints rendering the thallus a segmented nature. | <i>Halimeda</i> , <i>Corallina</i> |
| | | Calcified non-articulated | – | Algal thallus that is encrusted or impregnated with lime lacking non-calcified joints. | <i>Hydrolithon</i> |
| | | Non-calcified | – | Algal thallus not encrusted or impregnated with lime. | <i>Cladophora</i> |
| | | Unreported | – | So far it has not been reported in the 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). | <i>Acetabularia</i> , <i>Bryopsis</i> , <i>Caulerpa</i> , <i>Codium</i> |
| | | Non-unicellular | Having more than one cell or consisting of more than one cell (adapted from Lawrence, 2005). | <i>Furcellaria</i> | |
| | | Non-unicellular | Coenocytic | With cells being multinucleate. | <i>Cladophora</i> , <i>Dicetyosphaeria</i> , <i>Valonia</i> |
| Ecology | Distribution* | – | Species distributions documented as georegions. See https://www.marineregions.org (last access: 26 August 2022) for the full list of georegions. | – | |
| | Environmental position | Endolithic | – | Growing within a rock or other hard inorganic or organic substratum (Lincoln et al., 1998). | <i>Porphyra</i> (Conchocelis stage), <i>Ostreobium</i> |
| | | Endophytic | – | Living within a plant tissue or macroalgal thallus and not deriving nourishment from it. | <i>Callocolax</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|-------------|---------------------|-------------|-------------|-------|---|--|
| | | Endozoic | – | | Living within or passing through the body of an animal and not deriving nourishment from it. | <i>Callocolax</i> |
| | | Epilithic | – | | Growing on rocks or other hard inorganic or organic substrata (Lincoln et al., 1998). | <i>Acanthophora</i> |
| | | Epiphytic | – | | Living on the surface of a plant or alga and not deriving nourishment from it. | <i>Vertebrata lanosa</i> |
| | | 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. | <i>Polysiphonia caretia</i> |
| | | Unattached | – | | Growing without attachment to any type of substrate. | <i>Ulva</i> |
| | Environment* | Marine | – | | Occurring at salinities higher than 30 ppt | |
| | | Brackish | – | | Occurring at a salinity range of 0.5–30 ppt | |
| | | Freshwater | – | | Occurring at a salinity range of 0–0.5 ppt | |
| | | Terrestrial | – | | Occurring 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 | <i>Rugulopteryx okamurae</i> , <i>Ulva</i> spp. |
| | | 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 | <i>Jania adhaerens</i> |
| | 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. | – |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|-------------|---------------------------------|-------------------------------|------------------|-------|---|---|
| | | Unreported | – | | Seasonality not reported in the literature. | – |
| | Vertical space | Canopy | – | | Vegetation of macroalgae or plants partially blocking light penetration, thereby creating a shaded understory. | <i>Fucus</i> , <i>Laminaria</i> , <i>Saccorhiza</i> |
| | | Encrusting | – | | With a crustose growth form | <i>Hydrolithon</i> |
| | | Sub-canopy | – | | Forming a secondary cover, usually of 20 cm height maximum | <i>Dictyota</i> , <i>Halimeda</i> |
| | | Turf | – | | Vegetation dominated by macroalgae with limited vertical height, usually < 5 cm height | <i>Gelidium pusillum</i> |
| | 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 > 1 and < 10 m. | – |
| | | Oligotrophic waters | – | | Pertaining to waters with low levels of the nutrients resulting in low primary net productivity. | – |
| | | Turbid waters | – | | Occurring in waters where visibility is most of the time < 1 m | – |
| | | 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. | <i>Chondrus crispus</i> |
| | | Features of rock | – | | Specific characteristics of rocky substrate such as pools, caves, overhangs, surge gulleys, artificial hard substrata. | <i>Pylaiella littoralis</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait child value | Definition | Genus or species example |
|-------------|------------|--------------|--------------------------------|---|------------------------------|
| | | 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. | <i>Himantalia elongata</i> |
| | | 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. | <i>Saccharina latissima</i> |
| | | Sheltered | Low-energy rock | Occurring on rocky substrate subject to low-energy wave forces. | <i>Polysiphonia elongata</i> |
| | | Sheltered | Macrophyte-dominated sediments | Sediments with a high cover of macroalgae or seagrasses. | <i>Laurencia caspica</i> |
| | | Sheltered | Mud-dominated sediments | Sediments composed of a mixture of clay (< 2 µm) and silt (4–62 µm) typically deposited in a low-energy environment. | <i>Chaetomorpha linum</i> |
| | | Sheltered | Sand-dominated sediments | Sediments composed of a mixture of sand particles (0.074–4.75 mm) typically deposited in a low-energy environment. | <i>Codium fragile</i> |
| | | Unreported | – | Not been reported in the literature in what type of wave exposure the species occurs. | – |
| Zonation | Intertidal | – | | The part of the shore between high and low tide. | |
| | | | 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. | <i>Ascophyllum nodosum</i> |
| | | 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. | <i>Bryopsis plumosa</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait child value | Definition | Genus or species example |
|-------------|------------|----------------|--------------------------|--|------------------------------|
| | | | 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 | <i>Corallina officinalis</i> |
| | | | 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. | <i>Gracilaria gracilis</i> |
| | | 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). | <i>Sargassum</i> |
| | | 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). | <i>Laminaria ochroleuca</i> |
| | | Haplodiplontic | Isomorphic | Organisms with the gametophyte and sporophyte of similar morphology and size (Womersley, 1987). | <i>Dictyota dichotoma</i> |
| | | Haplodiplontic | Not applicable | It is not applicable whether this taxon is heteromorphic or isomorphic. | <i>Parvocaulis</i> |
| | | Haplodiplontic | Unknown | According to the literature it is unknown whether this organism is heteromorphic or isomorphic. | |
| | | Haplodiplontic | Unreported | So far it has not been reported in the literature whether this taxon is heteromorphic or isomorphic. | <i>Metapeyssonnelia</i> |
| | | 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). | <i>Tolypella</i> |
| | | Unknown | – | According to the literature it is unknown what life cycle this organism has. | <i>Epicladia</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait child value | Definition | Genus or species example |
|-------------|----------------------|-------------------------|--|---|------------------------------|
| | | Unreported | – | So far it has not been reported in the literature what life cycle this taxon has. | <i>Hecatonema</i> |
| | 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. | <i>Bryopsis hypnoides</i> |
| | | 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, bipore, paraspore, zoospore, aplanospore, autospore). | <i>Corallina officinalis</i> |
| | | 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). | <i>Caulerpa</i> |
| | | Asexual reproduction | Asexual reproduction by parthenogenesis | Direct development of a new individual from an unfused gamete. | <i>Ulva prolifera</i> |
| | | Asexual reproduction | Asexual reproduction by vegetative propagules | Asexual reproduction by development of a new individual from a vegetative propagule. | <i>Prasiola crispa</i> |
| | | 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. | <i>Acanthophora</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|-------------|-----------------|---|---------------------------------|-------|--|---|
| | | Unknown | – | | According to the literature it is unknown whether this organism reproduces asexually. | <i>Tolypella</i> |
| | Dispersion mode | Aplanospores | – | | A non-motile, asexual spore. | <i>Cymopolia</i> |
| | | Monospores | – | | An undivided spore. | <i>Monosporus</i> |
| | | Motile spores | – | | Spores are flagellate and can therefore disperse. | <i>Ectocarpus</i> |
| | | One motile gamete | – | | Only the male gamete is flagellate and can therefore disperse. | <i>Chondracanthus</i> |
| | | Two motile gametes | – | | Both male and female gametes are flagellate and can therefore disperse. | <i>Colpomenia</i> , <i>Scytosiphon</i> |
| | | Vegetative fragmentation | – | | Type of asexual reproduction in which the organism breaks up into smaller pieces, each of which can develop into a new individual. | <i>Chaetomorpha</i> |
| | | Vegetative fragmentation | Thallus fragmentation and drift | | A part of the thallus can be lost and drift. | <i>Gracilaria</i> |
| | | Vegetative propagation | – | | Vegetative reproduction by propagules that can also be used as a means of dispersal. | <i>Asparagopsis</i> |
| | | Presence of buoyancy structures | – | | Individuals exhibit gas-filled structures that favour their floating. | <i>Sargassum</i> |
| | | Species cultivated or sold in aquaria trade | – | | The species is cultivated or sold in aquaria trade. | <i>Caulerpa taxifolia</i> |
| | | Species growing on artificial substrate | – | | The species is growing on artificial substrate such as harbour walls, boat hulls, piers, buoys. | <i>Undaria pinnatifida</i> |
| | | Unknown | – | | According to the literature it is unknown which dispersion mode this organism has. | <i>Bornetia</i> |
| | | Unreported | – | | So far it has not been reported in the literature which dispersion mode this taxon has. | <i>Herponema</i> |
| | Gamete type | Anisogamous | – | | Having gametes of dissimilar size, shape, or behaviour (Lincoln et al., 1998). | <i>Scytosiphon</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|-------------|-------------------------|----------------|-------------|-------|--|---|
| | | Isogamous | – | | Having gametes that are similar in size, shape and behaviour; having gametes (isogametes) not differentiated into male and female (Lincoln et al., 1998). | <i>Ectocarpus</i> |
| | | 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). | <i>Cryptonemia</i> , <i>Dictyota</i> , <i>Fucus</i> |
| | | Not applicable | – | | The attribute gamete type is not applicable for this taxon. | <i>Halothrix</i> |
| | | Unknown | – | | According to the literature it is unknown which gamete type this organism has. | <i>Fosliea</i> |
| | | Unreported | – | | So far it has not been reported in the literature what the gamete type is for this taxon. | <i>Rosenvingea</i> |
| | Gametophyte arrangement | Dioecious | – | | When male and female reproductive structures are formed on the separate individual and the sex is determined in diploid phase. | <i>Alaria esculenta</i> |
| | | 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). | <i>Dasya elongata</i> |
| | | Mixed | – | | With individuals bearing only male or female reproductive structures and individuals bearing both male and female reproductive structures in one species. | <i>Griffithsia</i> |
| | | Monoecious | – | | When male and female reproductive structures are formed on same individuals and the sex is determined in diploid phase. | <i>Fucus distichus</i> |
| | | Monoicous | – | | When male and female reproductive structures are formed on same individuals and the sex is determined in haploid phase. | <i>Hydrolithon</i> |
| | | Not applicable | – | | The attribute gametophyte arrangement is not applicable for this taxon. | <i>Pedobesia</i> |
| | | Unknown | – | | According to the literature it is unknown which gametophyte arrangement this organism has. | <i>Stilopsis</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|--------------|-----------------|---|-------------|-------|--|-----------------------------------|
| | | Unreported | – | | So far it has not been reported in the literature what the gametophyte arrangement is for this taxon. | <i>Chaetosiphon</i> |
| | Spawning | Fertilisation in the water column | – | | Fertilisation with gametes released in the water column. | <i>Batophora</i> |
| | | Fertilisation on the female gametophyte | – | | Female gamete retained on the female gametophyte (e.g. Rhodophyta). | <i>Atractophora hypnoides</i> |
| | | Not applicable | – | | The attribute spawning is not applicable for this taxon. | <i>Porphyridium purpureum</i> |
| | | Unknown | – | | According to the literature it is unknown which spawning mechanism this organism has. | <i>Chordaria</i> |
| | | Unreported | – | | So far it has not been reported in the literature whether there is spawning for this taxon. | <i>Spongonema</i> |
| Life history | Generation time | 1 to 3 months | – | | Life cycle completed in 1 to 3 months in the lab. | <i>Ulva</i> |
| | | 3 to 12 months | – | | Life cycle completed in 3 to 12 months in the lab. | <i>Cystoseira barbata</i> |
| | | 1 to 3 years | – | | Life cycle completed in 1 to 3 years in the lab. | <i>Saccharina latissima</i> |
| | | More than 3 years | – | | Life cycle completed in more than 3 years in the lab. | <i>Furcellaria lumbricalis</i> |
| | Life span | Annual | – | | (1) Applicable to 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) plant that completes its life cycle in a year. (Lawrence, 2005). Thallus which survives only one growing season (less than 1 year) (Womersley, 1987). | <i>Acrosymphyton purpuriferum</i> |
| | | Annual | Ephemeral | | (1) Short-lived; (2) taking place once only, applicable to plant movements as expanding buds; (3) completing life cycle within a brief period; (4) a short-lived plant or animal species (Lawrence, 2005). Thallus which survives for only a few weeks (less than 1 month) (Womersley, 1987). | <i>Osmundea hybrida</i> |

Table A1. Continued.

| Trait group | Trait | Trait value | Trait value | child | Definition | Genus or species example |
|-------------|------------------------|------------------------------|-------------|-----------|--|------------------------------|
| | | 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) | <i>Cystoseira barbata</i> |
| | | Perennial | Short | perennial | Thallus or part thereof with a lifespan exceeding 1 year but under 3 years. | <i>Undaria pinnatifida</i> |
| | | Unreported | – | | So far it has not been reported in the literature which life span this organism has. | <i>Spatoglossum</i> |
| | Reproductive frequency | Throughout the year | – | | Fertile individuals observed throughout the year. | <i>Codium fragile</i> |
| | | One long period a year | – | | A unique fertility period lasting more than 1 month. | <i>Pelvetia canaliculata</i> |
| | | One short period a year | – | | A unique fertility period lasting less than 1 month. | <i>Desmarestia viridis</i> |
| | | Several long periods a year | – | | Several distinct fertility periods lasting more than 1 month each. | <i>Ceramium virgatum</i> |
| | | Several short periods a year | – | | Several distinct fertility periods lasting less than 1 month each. | <i>Pyropia elongata</i> |

* Not uploaded as traits or attributes in the Aphia database but as distributions or environmental flags.

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.blanfuné-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 Mediterraneo 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. frederik.leliaert@meisebotanicgarden.be |
| Expert | Díaz-Tapia, Pilar. Universidad A Coruña. pdiaz@udc.es |
| Expert | Sjötun, 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 Reviere, Bruno. Muséum National d’Histoire Naturelle. reviere@mnhn.fr |
| Expert | Vergés, Alba. Universitat de Girona. alba.verges@udg.edu |
| Expert | De Clerck, Olivier. Olivier.declerck@ugent.be |

Table B1. Continued.

| 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 Floridophyceae (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. |

Table B1. Continued.

| 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 (Ceramiaceae, Delesseriaceae, Sarcmeniaceae, 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 <i>Scageliopsis tsitsikammae</i> . 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 <i>Bangia fuscopurpurea</i> (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, Dasycladaceae. 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. |
| Literature | Díaz-Tapia, P.; Bárbara, I. (2013). Seaweeds from sand-covered rocks of the Atlantic Iberian Peninsula. Part 1. The Rhodomelaceae. (Ceramiaceae, Rhodophyta). Cryptogamie Algologie. 34(4): 325-422. |
| Literature | Van Reine, W. P. (1982). A taxonomic revision of the European Sphacelariaceae: (Sphacelariales, Phaeophyceae). Brill Archive. |
| Literature | Coppejans, E. (1995). Flore algologique des côtes du Nord de la France et de la Belgique. In: Scripta botanica Belgica, p. 454. |

Table B1. Continued.

| Type | Source |
|------------|---|
| Literature | Harper, J. T.; Saunders, G. W. (2002). A re-classification of the Acrochaetiales based on molecular and morphological data, and establishment of the Colaconematales ord. nov. (Florideophyceae, Rhodophyta). <i>European Journal of Phycology</i> . 37(3): 463-476. |
| Literature | South, G. R.; Hooper, R. G.; Irvine, L. M. (1972). The life history of <i>Turnerella pennyi</i> (Harv.) Schmitz. <i>Brit Phycol J.</i> 7, 221-233. |
| Literature | Denizot, M. (1968). Les algues floridees encroutantes (a l'exursion des Corallinales). Laboratoire Cryptogamie, Muséum National d'Histoire Naturelle, Paris, 310 pp. |
| Expert | Vranken, Sofie. Ghent University. sofievranken@gmail.com |
| Literature | De Clerck, O.; Anderson, R. J.; Bolton, J. J.; Robertson-Andersson, D. (2002). <i>Schimmelmannia elegans</i> (Gloiosiphoniaceae, Rhodophyta): South Africa's first introduced seaweed?. <i>Phycologia</i> . 41(2): 184-190. |
| Literature | Maggs, C. A.; Ward, B. A. (1996). The genus <i>Pikea</i> (Dumontiaceae, Rhodophyta) in England and the North Pacific: comparative morphological, life history, and molecular studies. <i>J Phycol.</i> 32, 176-193. |
| Expert | Robuchon, Marine. Muséum National d'Histoire Naturelle. marine.robuchon@mnhn.fr |
| Literature | Kraft, G. T. (2007). <i>Algae of Australia: Marine Benthic Algae of Lord Howe Island and the Southern Great Barrier Reef, 1: Green Algae</i> . ABRS–CSIRO Publishing, Canberra Melbourne. [i-iv], v-vi, 1-347. |
| Literature | Leliaert, F.; Coppejans, E. (2007). Morphological re-assessment of the <i>Boodlea composita</i> – <i>Phyllocladion anastomosans</i> species complex (Siphonocladales: Chlorophyta). <i>Australian Systematic Botany</i> . 20, 161-185. |
| Literature | Edelstein, T. (1970). The life history of <i>Gloiosiphonia capillaris</i> (Hudson) Carmichael. <i>Phycologia</i> . 9, 55-59. |
| Literature | Peters, A. F.; Novacek, I.; Müller, D. G.; Mclachlan, J. (1987). Culture studies on reproduction of <i>Sphaerotrichia divaricata</i> (Chordariales, Phaeophyceae). <i>Phycologia</i> . 26, 457-466. |
| Literature | Hillis-Colinvaux, L. (1980). Ecology and taxonomy of <i>Halimeda</i> : Primary producer of coral reefs. <i>Advances in Marine Biology Volume 17</i> . 1-327. |
| Literature | Vroom, P. S.; Smith, C. M.; Coyer, J. A.; Walters, L. J.; Hunter, C. L.; Beach, K. S. et al. (2003). Field biology of <i>Halimeda tuna</i> (Bryopsidales, Chlorophyta) across a depth gradient: comparative growth, survivorship, recruitment, and reproduction. <i>Hydrobiologia</i> . 501, 149-166. |
| Literature | Peters, A. (1998). Ribosomal DNA sequences support taxonomic separation of the two species of <i>Chorda</i> : reinstatement of <i>Halosiphon tomentosus</i> (Lyngbye) Jaasund (Phaeophyceae, Laminariales). <i>Eur. J. Phycol.</i> 33, 65-71. |

Table B1. Continued.

| Type | Source |
|------------|---|
| Literature | Schneider, C. W. S. J. S. (1991). Seaweeds of the southeastern United States. Duke University Press, Durham, London. |
| Literature | Kim, M. S.; Lee, I. K. (1999). <i>Neosiphonia flavimarina</i> gen. et sp. nov. with a taxonomic reassessment of the genus <i>Polysiphonia</i> (Rhodomelaceae, Rhodophyta). Phycol Res. 271-281. |
| Literature | Maggs, C. A. (1989). <i>Erythrodermis allenii</i> Batters in the life history of <i>Phyllophora traillii</i> Holmes ex Batters (Phylloporaceae, Rhodophyta). Phycologia. 28, 305-317. |
| Literature | Peña, V.; Bárbara, I. (2010). New records of crustose seaweeds associated with subtidal maerl beds and gravel bottoms in Galicia (NW Spain). Bot Mar. 53, 41-61. |
| Literature | Littler, D. S. L. M. M. (2000). Caribbean reef plants. OffShore Graphics, Inc. Washington. |
| Literature | Sanson, M.; Martin, M. J.; Reyes, J. (2006). Vegetative and reproductive morphology of <i>Cladosiphon contortus</i> , <i>C. occidentalis</i> and <i>C. cymodoceae</i> sp. nov. (Ectocarpales, Phaeophyceae) from the Canary Islands. Phycologia. 45, 529-545. |
| Literature | Saunders, G. W.; Lane, C. E.; Schneider, C. W.; Kraft, G. T. (2006). Unraveling the <i>Asteromenia peltata</i> species complex with clarification of the genera <i>Halichrysis</i> and <i>Drouetia</i> (Rhodymeniaceae, Rhodophyta). Botany. 84, 1581-1607. |
| Literature | Breeman, A. M.; Ten Hoopen, A. (1981). Ecology and distribution of the subtidal red alga <i>Acrosymphyton purpuriferum</i> (J. AG.) Sjöst. (Rhodophyceae, Cryptonemiales). Aquatic Botany. 11: 143-166. |
| Literature | Draisma, S. G.; Prud'homme Van Reine, W. F.; Kawai, H. (2010). A revised classification of the Sphacelariales (Phaeophyceae) inferred from a <i>psbC</i> and <i>rbcL</i> based phylogeny. Eur. J. Phycol. 45, 308-326. |
| Literature | McCarthy, P.M., Huisman, J. & Kraft, G.T. (2006). Algae of Australia: Nemaliales. Australian Government - SCIRO publishing, Canberra. |
| Literature | Schneider, C. W.; Searles, R. B. (1997). Notes on the marine algae of the Bermudas. 2. Some Rhodophyta, including <i>Polysiphonia tongatensis</i> and a discussion of the <i>Herposiphonia secunda/tenella</i> complex. Cryptogamia, algol. 2, 187-210. |
| Literature | Kawai, H.; Sasaki, H. (2004). Morphology, life history, and molecular phylogeny of <i>Stschapovia flagellaris</i> (Tilopteridales, Phaeophyceae) and the erection of the Stschapoviaceae fam. nov. Journal of Phycology. 40(6): 1156-1169. |
| Literature | Breeman, A. M. (1979). The caryological phases in the life history of <i>Acrosymphyton purpuriferum</i> (J. Ag.) Sjöst. (Rhodophyceae, Cryptonemiales). Phycologia. 18(2): 146-148. |
| Literature | Wilce, R. T. (1969). <i>Papenfussiella callitricha</i> : new observations on a little-known endemic brown alga from southwest Greenland. J Phycol. 5, 173-180. |
| Literature | Bartsch, I.; Wiencke, C.; Bischof, K.; Buchholz, C. M.; Buck, B. H.; Eggert, A. (2008). The genus <i>Laminaria</i> sensu lato: recent insights and developments. Eur. J. Phycol. 43, 1-86. |
| Literature | Maggs, C. A.; Pueschel, C. M. (1989). Morphology and development of <i>Ahnfeltia plicata</i> (Rhodophyta): proposal of Ahnfeltiales ord. nov. J Phycol. 25, 333-351. |

Table B1. Continued.

| Type | Source |
|------------|---|
| Literature | De Jong, Y. S. D. M.; Prud'homme van Reine, W. F.; Lokhorst, G. M. (1997). Studies on Dasyaceae. II. A revision of the genera <i>Eupogodon</i> and <i>Dipterocladia</i> gen. nov. (Ceramiales, Rhodophyta). <i>Botanica Marina</i> . 40(1-6): 421-450. |
| Literature | Mathieson, A. C.; Dawes, C. J.; Wallace, A. L.; Klein, A. S. (2006). Distribution, morphology, and genetic affinities of dwarf embedded <i>Fucus</i> populations from the Northwest Atlantic Ocean. <i>Botanica Marina</i> . 49(4): 283-303. |
| Literature | Wynne, M. J.; Leliaert, F. (2001). <i>Pedobesia simplex</i> (Kützting) comb. nov. (Chlorophyta), a new name for <i>P. lamourouxii</i> and its first report from the Indian Ocean. <i>Cryptogam. Algol.</i> 22, 3-14. |
| Literature | Mineur, F., Verlaque, M. & Johnson, M.P. (2005 (unpublished)). Traits of invasive macroalgae found in Europe. Results of the ALIENS (Alien Introductions to European Shores) project. |
| Literature | Rodríguez-Prieto, C.; De Clerck, O. (2009). <i>Leptofauchea coralligena</i> (Faucheaceae, Rhodophyta), a new species from the Mediterranean Sea. <i>European Journal of Phycology</i> . 44: 107-121. |
| Literature | Abbott, I. A.; Ballantine, D. L.; O'Doherty, D. C. (2010). Morphological relationships within the genus <i>Lophocladia</i> (Rhodomelaceae, Rhodophyta) including a description of <i>L. kuesteri</i> sp. nov. from Hawaii. <i>Phycologia</i> . 49(4): 390-401. |
| Literature | Pedersen, P.M. (1984). Studies on primitive brown algae (Fucophyceae). <i>Opera botanica</i> , 74, 5-76. |
| Literature | Bergström, A.; Tatarenkov, A.; Johannesson, K.; Jonsson, R. B.; Kautsky, L. (2005). Genetic and morphological identification of <i>Fucus radicans</i> sp. nov. (Fucales, Phaeophyceae) in the brackish Baltic Sea. <i>Journal of Phycology</i> . 41: 1025-1038. |
| Literature | Tabares, N.; Afonsocarrillo, A.-C. (1997). Morfología y distribución de <i>Thuretella schousboei</i> en las islas Canarias (Rhodophyta, Gloiosiphoniaceae). <i>Vieraea</i> . 26, 77-85. |
| Literature | Nam, K. W.; Choi, H. G. (2000). A detailed morphological study of the type species of <i>Osmundea</i> (Rhodomelaceae, Rhodophyta). <i>Bot Mar.</i> 43, 291-297. |
| Literature | Cecere, E.; Perrone, C. (2002). Morphology of <i>Acanthophora nayadiformis</i> (Ceramiales, Rhodophyceae). <i>Phycologia</i> . 41, 523-532. |
| Literature | Kim, S. H.; Peters, A. F.; Kawai, H. (2003). Taxonomic revision of <i>Sphaerotrichia divaricata</i> (Ectocarpales, Phaeophyceae), with a reappraisal of <i>S. firma</i> from the north-west Pacific. <i>Phycologia</i> . 42, 183-192. |
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| Type | Source |
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| Type | Source |
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| Type | Source |
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Table B1. Continued.

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Table B1. Continued.

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Competing interests. The contact author has declared that none of the authors has any competing interests.

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