Phaeophyceae
General characteristics

- ca 265 genera, 1500 - 2000 species
- multicellular thallus, attached to the surface
- marine, only 3-5 species in freshwater habitats
- rocky coastline – litoral, sublitoral (min. 0,6% of residual light – up to depth of 260 m, but most species are not shade-loving organisms)
- high primary production, DMS production
- economically and culturally important – aquacultures, seaweed art
Cell structure
Plastids

- chl a, c₁, c₂, β-carotene, fukoxanthin, violaxanthin, dinoxanthin, diadinoxanthin
- discoid plastids, 1 or more pyrenoids
- heterokont structure

(also Chrysophyceae)
Plastids

- 2layered plastid membrane
- chloroplast
- ER
- nucleus
- oil globules
Pyrenoid
Metabolism products

- storage products (chrysolaminaran, manitol)
- florotanins – stored in physodes, when oxidized, they case brown colour of water
- iodine (0.03 – 0.3% of weight)
- organobromids – destruction of ozone layer
- dimethylsulphopropionate – osmotic regulation production of DMS (in parallel to haptophytes)
Cell wall composition

• alginates – salts of Alginic acid (gelatinous)
  - Na-alginates – soluble
  - Ca-alginates – insoluble

• cell wall structure
  - fibrilar component – cellulose, Ca-alginates
  - amorphous component – soluble Na-alginates

• fucoidane – mucilage surrounding cell wall
  - against desiccation
  - environment for gamete fusion
Zoids features similar to other heterokont groups

- heterokont flagella, mastigonemata
- periplastidial reticulum
- four membranes, girdle lamella

Features typical for brown algae

- lateral flagella insertion
- flagella terminated by acronemates

photoreceptor
Zoids
Sexual reproduction

- diplohaplontic cell cycle, isomorphic and heteromorphic
- plurilocular zoidangia

- unilocular zoidangia
Thallus structure
Thallus structure

filament developmental patterns

Figure 3. Main developmental patterns observed in brown algae. (a) Primary growth. Localization and axes of cell division that are observed in brown algal development. Cell division occurs either in a terminal-apical position (blue), or in an intercalary position (green: either diffuse growth or localized growth: e.g. trichothallic growth). Cell division axes are either unidirectional (haplochotic, uni- or multi-axial, yellow), or multidirectional. In the latter, division occurs either in two steps (polystichous: orange; with or without secondary thickening of the axes in the Sphacelariales, the auxoecus and leptoecus construction modes, respectively, as defined by [104]) or simultaneously along different axes (parenchymatous: red). (b) Distribution of cell division patterns on the phylogenetic tree of brown algae. The cell division patterns (localization and axes) for each brown algal order are indicated by the color and style (defined or blurred) of the branches of the circular tree, in agreement with those indicated in (a). The haplochotic growth pattern is the most widely distributed. Note that Desmarestiales and Sporochnales develop haplochotic structures (unialgal in Desmarestiales and multi-axial in Sporochnales), which generate pseudo-parenchymes. Structures produced by a two-step cell division process (polystichous construction) with a terminal growth arose only once and are synapomorphic for the orders Syringodermatales, Sphacelariales, Dictyotales and Onkolaiales (SSDO). However, polystichous construction analogous to that in the SSDO group also appeared in Tilionidales (Tilotoperae, Cutleriaceae) and in numerous Ectocarpales, but as a result of intercalary growth rather than of terminal growth, such as that seen in the SSDO group. Parenchymatous growth appeared several times, and shows convergence in the most diversified brown algae (Fucales, Laminariales, Phyllophoraceae in Tilionidales and Ascosporiales) [1]. Interestingly, some distant orders comprise macroalgae with similar morphologies (e.g. Hymenostomum in the Desmarestiales and the kelps in Laminariales) [106] and, conversely, some closely related orders show different morphologies, as illustrated by the ‘crusts’ morphology observed in Nemodermatales (not shown), which are a sister order to Fucales, as well as in Petrodactyales, which are a sister family to Ishigeales (Ishigeales) and Lithodermatales within Sphacelariales. Photographs are displayed for brown algal orders containing at least three genera: Dictyotales, Dictyota linealis: Sphacelariales, Halopteris filicina: Desmarestiales, Desmarestia dressy: Sporochnales, Sporochroa pedunculata: Scytosiphonales, Spachnidium rugosum; Ectocarpales, Ectocarpus fasciculatus; Laminariales, Alaria esculenta: Raffiales, Ralfsia verrucosa; Tilotoperae, Tilotopera maritimi; Fucales, Fucus vesiculosus. Image reproduced, with permission, from AlgaeBase (M.D. Guiry; Spachnidium rugosum).
Utilization of brown algae

- Scandinavia, Faroe Islands – grazing by sheep
- fuel, composting, roofs
- production of soda, potash, iodine (1930s)
Utilization of brown algae - cultivation
Utilization of brown algae - food

kombu - *Laminaria*
Utilization of brown algae - food

wakame - *Undaria*
Utilization of brown algae - food

hiziki - *Hizikia*
Utilization of brown algae - alginates

Wet chopped seaweed → Sodium carbonate solution → Alkaline extract → Separation → Seaweed residue

Sodium alginate solution → Add calcium chloride → Calcium alginate fibres

Add acid → Alginic acid fibres

Add sodium carbonate → Sodium alginate

Add SODIUM CARBONATE → Dewatering alginic acid

Add SODIUM CARBONATE → Sodium alginate

Calcium alginate process → Alginic acid process

22 000 t/year
Utilization of brown algae - alginites
food industry
# Utilization of brown algae - alginites in the food industry

<table>
<thead>
<tr>
<th>Product</th>
<th>E number</th>
<th>Origin</th>
<th>Used as</th>
<th>Typical products</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alginites and various derivatives (e.g. Sodium alginate, Propylene glycol alginate)</td>
<td>E400-405</td>
<td>Large brown seaweeds such as <em>Laminaria hyperborea</em>, <em>Ascophyllum nodosum</em> and <em>Macrocystis</em> species</td>
<td>Emulsifier, suspending, stabiliser, gelling agent, thickener.</td>
<td>Ice-creams, milk shakes, instant desserts, custard tarts. Suspending agent in soft drinks. Spreads and many others.</td>
</tr>
<tr>
<td>Agar</td>
<td>E406</td>
<td>Mainly species of <em>Gelidium</em>, <em>Pterocladia</em>, and <em>Gracilaria</em></td>
<td>Emulsifier, stabiliser, gelling agent, thickener.</td>
<td>Ice-creams, tinned goods, glazes for meats, etc.</td>
</tr>
</tbody>
</table>
Utilization of brown algae - algginates

farmaceuticals, cosmetics
Utilization of brown algae - alginates

slim down diets – satiety
Utilization of brown algae - alginates
building materials
Utilization of brown algae - fucoidane

cell wall polysaccharides; used as dietary supplements
Utilization of brown algae seaweed baths
treatment of rheumatism and arthritis
Utilization of brown algae alginate batteries

Brown algae could help your smartphone keep its charge

Current battery electrodes are made from graphite, but it’s hoped by switching to silicon, larger capacity and longer life Li-ion batteries could be a reality. The only problem is that we need to find something that can bind effectively onto silicon electrodes. Current batteries use Polyvinylidene Fluoride (PVDF) which in addition to being toxic isn’t very good at binding to silicon.

Luckily, they’ve found something that works better, and is substantially more environmentally friendly. Alginate is a polymer harvested from fast growing brown seaweed, and it’s more efficient than PVDF with both silicon and graphite. The way it works is that the alginate forms a protective film on top of the silicon electrode to stop the electrolyte solvent from washing onto the surface of silicon particles, preventing the battery from decomposing.
seaweed art
(belongs to the land-art styles)
Systematics and diversity

- class Phaeophyceae, syn. Fucophyceae
- traditionally - ca 14 orders (van den Hoek 1995)
Phylogeny

- traditional concepts of phylogeny and taxonomy:

  Ectocarpaceae \(G,S,[iso]\)
  Sphacelariales \(G,S,iso\)
  Dictyotales \(G,S,iso\)
  Cutleriales \(G,S,hetero\)
  Laminariales \(S,hetero\)
  Fucales \(S,hetero\)
Fig. 4. Results of the ML-based ancestral character state estimation for six non-molecular characters on the chronogram topology of the Fig. 2. The six characters, traditionally considered as the most relevant in the field of brown algal systematics, are: A. type of life history; B. type of fertilization; C. growth of macroscopic thallus; D. architecture of macroscopic thallus; E. number of plastids; F. occurrence and structure of pyrenoid. The ML procedure provides a probabilistic assessment of the ancestral states; these probabilities are reflected in branch colors and pie diagrams at nodes. Each character state has been assigned a color and intermediate colors indicate uncertainty about the character state. For details, see the color caption associated with each tree.
DISCOSPORANGIOPHYCIDAE
Discosporangiales

ISHIGEOPHYCIDAE
Ishigeales

DICTYOTOPHYCIDAE
Dictyotales *
Onslowiales
Sphacelariales *
Syringodermatales

FUCOPHYCIDAE
Ascoseirales
Asterocladales
Desmarestiales *
Ectocarpales **
Fucales **
Laminariales **
Nemodermatales
Phaeosiphoniellales
Ralfsiales
Scytothamnales
Sporochnales
Tilopteridales *

Silberfeld et al., 2014, Crypt. Algol. 35
the traditional view of the life cycle evolution in Phaeophyceae

Figure 1. The classical interpretation of the sexual life cycle in Phaeophyta. This way of representing the life cycle, as a series of linked cycles, was introduced by Bell (1994).

Figure 5. How the balance of haploid and diploid growth varies with the disparity in gamete size. Diploid dominance is expressed as log (diploid size/haploid size), and gamete dimorphism as log (macrogamete size/microgamete size).

Primitive state is isomorphic alternation of filamentous individuals with isogametic sexuality

Advanced state is heteromorphic alternation of gametophytic microthallus with sporophytic macrothallus; anisogametic or oogametic sexuality
Time calibration of phaeophycean phylogenetic history

Fig. 3. Time tree derived from relaxed molecular clock method implemented in MCMCTREE in PAML 4.7 (Yang 2007). Horizontal bars indicate 95% credible intervals of divergence time estimates. Asterisks on nodes correspond to calibration points. Asterisks 1 and 2 indicate calibration points with fossils (Parker and Dawson 1965 and Rajanikant 1989, respectively), and minimum time constraints used for nodes were 13 and 99.6 Ma, respectively. Asterisk 3 shows calibration point based on previous molecular clock study (Brown and Sorhannus 2010), and maximum (267 Ma) and minimum (124 Ma) time constraints used on node. Estimated ages and their 95% credible intervals are listed in Table 2 with node numbers.

Kawai et al., 2015, J. Phycol.
**Discosporangium**  
(Discosporangiales)  
- epiphytic filaments, up to 4 cm  
- apical growth  
- numerous discoid plastids  
- plurilocular zoidangia form single-layered plate of locules

Subtropics, tropics (Mediterranean, Australia)
Ishige okamurae
(Ishigeales)

- irregular dichotomous branching
- thalli up to 20 cm
- unilocular and plurilocular sporangia
- presumably isomorphic life cycle

occurs in temperate and subtropical W Pacific

Lee et al., 2012, Mar. Biol.
Fig. 3 Geographical distribution of *Ishige okamurae* haplotypes. Shaded areas in light gray color are continental shelves that would have been covered by ice sheet during the Pleistocene glaciation. Letters correspond to the code in Table 1.
*Petroderma maculiforme* (Ishigeales)

- lichen photobiont – *Verrucaria tavaresiae* as a mycobiont

occurs in supralittoral / eulittoral of temperate and boreal seas (incl. European coasts – Baltic, North Sea, Atlantic)

two other species in subtropics/tropics
Dictyotales

- fan-shaped, parenchymatic thallus (2-3 layers of cells)
- diplohaplontic cell cycle, isomorphic, always oogamy
Dictyotales

Dictyota dichotoma

- true dichotomy, growth by division of apical cell
- temperate, cosmopolitan species
♀ gametophyte

dark brown sorus – oogonia (unilocular gametangia)

♂ gametophyte

light brown sorus – antheridia (plurilocular gametangia)

sporophyte

unilocular sporangia = tetrasporangia
Phylogenetic species structure of *Dictyota* in Europe

psbA based phylogeny of European species

*Tronholm et al., 2010, J Phycol 46: 1301-1321*
Dictyota cyanoloma

Dictyota dichotoma

Dictyota implexa
Fig. 2. Distribution maps of European Dictyota species. Dots represent DNA-confirmed distribution records; shaded areas indicate the estimated distribution range.
Dictyopteris

Dictyopteris polypodioides

shade-loving species, mesotrophic, moderately disturbed habitats
Lobophora variegata
Padina

- fan-shaped, slightly calcified thalli
Padina pavonica is an abundant Mediterranean species, typically found in shallow eutrophicated habitats.
Sphacelariales

- branching multiseriate filaments
- diplohaplontic cell cycle, isomorphic or slightly heteromorphic
- iso-, aniso- and oogamy
Sphacelariales
Sphacelaria rigidula

- tiny brown tufts
- cosmopolitan, on rocks or epiphytic
- triradiate asexual propagules
**Halopteris filicina**
abundant Mediterranean species

**Sphacelaria arctica**
cold water, slowly growing, deep sea species
Baltic – lower sublittoral
Fucales

- only macrothallus (S)
- diplont cell cycle, mostly oogamy
- conceptacula – cavities in thallus, containing gametangia
spermatophyte (♀)
receptacula
♀ conceptacula

♀ oogonium (♀ gametophyte)

♂ antheridium (♂ gametophyte)
→ analogy to flowering plants
Fucales

*Fucus* – conceptacula

Concepticle

Oogonia

Antheridia
Fucales

\textit{Fucus vesiculosus} – in tidal oceanic zones (eulittoral), cold seas, Baltic - sublitoral
Fucales

*Fucus serratus* – serrated margins of fyloidies
Adaptation of *Fucus serratus* to decreasing salinity in brackish waters


Fig. 2. Depth range of *Fucus serratus* in five regions of the Baltic proper based on 105 SCUBA diving transects.

Fig. 3. Number of non-reproductive *Fucus serratus* plants (juveniles) (mean ± S. E.) per reproductive plant (adult) in Sites 1 to 4.

Fig. 4. Proportion of fertilised *Fucus serratus* eggs after 15 h and germination of zygotes (%) cultured at different salinities in natural seawater. The material from Näsbys (Site 2) and Öland (Site 3) is included.
Microspeciation of *Fucus* in the Baltic

Bergström et al., 2005, *J Phycol* 41: 1025-1038

F. radicans

F. vesiculosus
BUT - probable parallel speciation of *F. radicans* from *F. vesiculosus* in the Baltic Sea

Pereyra et al., 2013, *J. Evol. Biol.*
Clonality (= genetic homogeneity) of *Fucus* population in relation to decreased salinity in the Baltic.

**Table 1.** Sampled locations, salinities, and number of thalli genotyped for two Baltic fucoxid species, *Fucus radiicans* and *F. vesiculosus.*

<table>
<thead>
<tr>
<th>Sample</th>
<th>Region</th>
<th>Locality</th>
<th>Coordinates</th>
<th>Year</th>
<th>June salinity (PSU)</th>
<th>No. of thalli genotyped</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>W Sweden</td>
<td>Kristineberg</td>
<td>58°14' N, 11°27' E</td>
<td>2003</td>
<td>&gt;20.0</td>
<td>Absent 42</td>
</tr>
<tr>
<td>B</td>
<td>E Sweden</td>
<td>Öland</td>
<td>57°21' N, 17°03' E</td>
<td>2003</td>
<td>6.7</td>
<td>Absent 43</td>
</tr>
<tr>
<td>C</td>
<td>E Sweden</td>
<td>Öregrund</td>
<td>60°39' N, 18°26' E</td>
<td>2003</td>
<td>5.0</td>
<td>Absent 48</td>
</tr>
<tr>
<td>D</td>
<td>E Sweden</td>
<td>Djursten</td>
<td>60°29' N, 18°24' E</td>
<td>2007</td>
<td>5.0</td>
<td>Present 49</td>
</tr>
<tr>
<td>E</td>
<td>NE Sweden</td>
<td>Bornhöved</td>
<td>62°53' N, 18°19' E</td>
<td>2007</td>
<td>5.8</td>
<td>Present 54</td>
</tr>
<tr>
<td>F</td>
<td>NE Sweden</td>
<td>Jarlsholm</td>
<td>63°29' N, 19°40' E</td>
<td>2003</td>
<td>3.5</td>
<td>Absent 48</td>
</tr>
<tr>
<td>G</td>
<td>W Finland</td>
<td>Hallikaisa</td>
<td>63°25' N, 20°57' E</td>
<td>2007</td>
<td>4.0</td>
<td>Absent 50</td>
</tr>
<tr>
<td>H</td>
<td>W Finland</td>
<td>Södra Väling</td>
<td>63°09' N, 21°19' E</td>
<td>2007</td>
<td>4.3</td>
<td>Present 50</td>
</tr>
<tr>
<td>I</td>
<td>W Finland</td>
<td>Mariestad</td>
<td>62°51' N, 21°40' E</td>
<td>2007</td>
<td>5.2</td>
<td>Present 50</td>
</tr>
<tr>
<td>J</td>
<td>W Finland</td>
<td>Sääksjärvi</td>
<td>62°19' N, 21°10' E</td>
<td>2007</td>
<td>5.5</td>
<td>Not sampled 44</td>
</tr>
<tr>
<td>K</td>
<td>Estonia</td>
<td>Putho Panki</td>
<td>58°56' N, 22°58' E</td>
<td>2006</td>
<td>5.6</td>
<td>Present 15</td>
</tr>
<tr>
<td>L</td>
<td>Estonia</td>
<td>Tröögi</td>
<td>58°52' N, 22°43' E</td>
<td>2006</td>
<td>5.8</td>
<td>Absent 25</td>
</tr>
<tr>
<td>M</td>
<td>Estonia</td>
<td>Köögaste</td>
<td>58°22' N, 22°58' E</td>
<td>2006</td>
<td>5.2</td>
<td>Absent 23</td>
</tr>
</tbody>
</table>

June salinities are averaged over 10 years (see text for details). PSU, practical salinity units.

**Fig. 2.** Relationship between salinity and clonal richness of populations of *Fucus radiicans* (crosses, dotted trend line, $R^2 = 0.62, P = 0.007$) and *F. vesiculosus* (diamonds, broken trend line, $R^2 = 0.34, P = 0.17$).

Johannesson et al., 2011, J. Phycol.
Evolutionary geographic origins of *Fucus* and their phylogeny

**Fig. 1.** Species distributions and sampling locations. Panels on the left show the ranges of each species of *Fucus* examined (adapted from Lüning, 1990). Panels on the right indicate approximate location of samples collected for this study. Distinction among *F. distichus*, *F. evanescens*, and *F. gardneri* in the northeastern Pacific remains unclear.
Fig. 2. Bayesian phylogenetic tree based on mtDNA 23S sequences. Numbers above and below the line are Bayesian posterior probability and MP bootstrap values (1000 replications), respectively.
F. distichus infraspecific diversity indicated Pacific origin of that group (lineage 1)
fine-grained phylogeny illustrates isolation effect of geographical regions
rapid diversification related to cold (glacial) phases of Tertiary climatic history
Ecological niche differentiation between sympatric *Fucus* species

**Fig. 1.** Distribution of *Fucus serratus* and *Fucus vesiculosus* in the Bay of Kuggeboda, central Baltic Sea. The dotted area indicates areas without well-developed *Fucus* belts. The gray area indicates well-developed *F. vesiculosus* belts down to 2 m and occasional *F. serratus* plants in the same depth interval. The hatched area indicates well-developed separate *F. vesiculosus* and *F. serratus* belts. Numbers 1 to 6 are the sites visited in the population investigation. The comparative investigation of reproductive allocation was made at site 7.

**Fig. 2.** Number of *Fucus vesiculosus* and *Fucus serratus* individuals at different depths at sites 1 to 6. Each bar shows the number of plants in 20-cm-depth sections along the depth transects. Lf, maximum local fetch (wave exposure).

Fig. 4. Effective photochemical yield (ΔF/Fm') (mean ± SE) of apical tissue of *Fucus serratus* and *Fucus vesiculosus*, subjected to +4°C, −5°C, and −15°C in darkness for 1 or 3 h.

Fig. 5. Daily egg release per receptacle (mean ± SE) for (a) *Fucus vesiculosus* and (b) *Fucus serratus*. Temperature (°C), salinity (psu), and day length (hours of light) are given for the study period.
additional Fucales

*Ascophyllum nodosum* – pesticides (against nematodes)
additional Fucales
*Sargassum* – warm temperate to tropical waters

*S. vulgare*
additional Fucales

*Sargassum* – benthic and pelagic species (Sargasso sea)
**Hizikia** belongs to **Sargassum** (subgenus **Bactrophycus**)

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**Stiger et al., 2003, Phycol. Res.**
Turbinaria – a tropical genus

often grows in coral ecosystems
Durvillaea

Fig. 3. Maximum-likelihood phylogeny of Durvillaea based on mitochondrial (COI) data. Durvillaea lineages are identified by colored strips, with colors corresponding to those used in Fig. 1. Branches show Bayesian PP values (above the line) and ML bootstraps (>50%, below the line). The relationship of Durvillaea to the outgroup genera is shown (inset, upper left). Leaf-node images illustrate some of the important morphological differences among Durvillaea taxa (stylized drawings or photographs).
Fig. 1. Geographic range of each Durvillaea species recognized by Hay (1994), as well as the 'cape' form of D. antarctica (South and Hay, 1979; Fraser et al., 2006a). The general path of the Antarctic Circumpolar Current (ACC) is indicated on the global projection. Inset: New Zealand and NZ subantarctic region, where most diversity within the genus is found.

Fig. 6. Maximum likelihood phylogeny of Durvillaea based on concatenated (combined COI, rbcL, 18S and 28S) data. Durvillaea 'species' are identified by colored strips, with colors corresponding to those in Fig. 1. Branches show Bayesian PP values (above the line) and ML bootstraps (<100, below the line), with those calculated by PhyML in parentheses. The relationship of Durvillaea to the outgroup genera is shown (inset, upper left). Leaf-node images illustrate some of the important morphological differences among Durvillaea taxa (stylized drawings or photographs). The presence/absence of stipitate lateral blades (a key diagnostic feature) is indicated on the far right.

Fig. 7. Bayesian maximum-clade consensus phylogeny of Durvillaea species and outgroup genera. This analysis is based on sequence data from three markers: COI, rbcL, and 28S. Outgroups have been removed from the tree for clarity, but are indicated schematically in the inset (upper left) with red stars showing the positions of calibrated nodes. Horizontal bars and associated number ranges show the 95% posterior probability of the age of each node. The scale bar indicates time in millions of years (Ma) from present.
Fig. 1. Phylogeographic relationships within *D. antarctica* based on COI data. The phylogenetic tree (lower right corner) indicates haplotype relationships, with Bayesian PP values above branches and ML bootstraps below. Outgroup taxa have been removed for clarity. “NZ subantarctic” refers to the Snares, Auckland, Campbell, and Antipodes Islands. The morphologically and genetically distinct “cape” form of *D. antarctica*, recently identified by Fraser et al. (25) from southeastern NZ, is indicated by an asterisk. The global projection shows haplotype distributions and proportions at each locality. Diversity in the southern New Zealand region is illustrated at higher magnification (Inset, upper right). Green arrows show major surface currents.
Fig. 2. Haplotype network diagrams for the “subantarctic” clade of *D. antarctica* for both mtDNA (COI) and chloroplast (rbcL) datasets. Circle size is scaled according to haplotype frequency. Black dots represent hypothetical haplotypes not detected in the current study.

Fraser et al., 2009, PNAS

Fig. 3. Positions of the subantarctic islands in relation to present-day conditions and reconstructed LGM oceanographic features, including LGM WSI extent, modified from Gersonde et al. (13). Dot points indicate sediment core sites used to reconstruct LGM sea ice cover (after ref. 13): yellow dots contained no evidence of sea ice-associated diatoms, green dots indicate (minimal) evidence, and blue dots indicate high proportions of ice-indicator diatoms. Regions demarcated by question marks lack core data (13). Based on *D. antarctica* genetic data, red labels indicate “recolonized” islands putatively affected by LGM ice scour, whereas blue labels indicate putative “refugial” islands. The LGM 4 °C isotherm has been identified as a feature roughly equivalent, in terms of water properties and gradients, to the modern APF (13).
Cystoseiraceae – a Mediterranean fucalean lineage

upper sublittoral; stable, pristine, climax habitats
**Recent decline of subtropical Fucales in the Mediterranean?**

### Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Abundance</th>
<th>Feldmann (1937a,b)</th>
<th>Gros (1978)</th>
<th>This study</th>
<th>Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. barbata</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. caespitosa</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>R</td>
<td>Decrease</td>
</tr>
<tr>
<td>C. compressa f. compressa</td>
<td>VA</td>
<td>VA</td>
<td>VA</td>
<td>VA</td>
<td>–</td>
</tr>
<tr>
<td>C. crinita</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. elegans</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>VR</td>
<td>Nearly</td>
</tr>
<tr>
<td>C. foeniculacea f. latirostris</td>
<td>R</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. foeniculacea f. temiramoides</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. fusiformis</td>
<td>R</td>
<td>R</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. mediterranea</td>
<td>VA</td>
<td>VA</td>
<td>A</td>
<td>A</td>
<td>Decrease</td>
</tr>
<tr>
<td>C. samuiziana</td>
<td>R</td>
<td>VR</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. spinosa var. compressa</td>
<td>A</td>
<td>A</td>
<td>VR</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. spinosa var. spinosa</td>
<td>R</td>
<td>?</td>
<td>VR</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>C. zosteroides</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>R</td>
<td>Decrease</td>
</tr>
<tr>
<td>S. achardii</td>
<td>?</td>
<td>R</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>S. hornechuchii</td>
<td>?</td>
<td>F</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
<tr>
<td>S. vulgaris</td>
<td>R</td>
<td>F</td>
<td>–</td>
<td>–</td>
<td>Extinct</td>
</tr>
</tbody>
</table>

A: abundant, F: frequent, R: rare, VA: very abundant, VR: very rare, ?: unknown; –: not reported.

**Fig. 1.** The Alberes coast.

**Fig. 2.** Map of the study area.

**Fig. 3.** Cystoseira compressa

**Fig. 4.** Cystoseira barbata

Thibaut et al., 2005, Mar Pollut Bull 50: 1472-1489
Fig. 1. Map of Menorca (Balearic islands) showing location and type of the study sites (triangle: north, round: very sheltered, cross: south, square: harbour). Urban areas and main roads are represented and the most important harbours are indicated.

Fig. 4. Distance-based redundancy analysis showing direction of increasing abundances of different species along the study sites. CaStr: Cystoseira amentacea var. amentacea, C. compressa var. compressa, C. crassifolia, C. thuretii, C. blanda, C. atenuata var. balanacea, C. algarvensis, C. compressa var. pustulata, C. pinnatifida var. tenerrima, C. amentacea var. pustulata, C. fimbriata var. tenerrima. Axis I explains 63.8% variation out of the fitted model and 38.4% of the total variation, while axis II explains respectively 26.9% and 16.2% of the variation.
C. barbata, S. vulgare, C. compressa
profound seasonal phenological cycles
Laminariales

- reduced microthallus (G) + foliose macrothallus (S)
- diplohaplontic cell cycle, heteromorphic, oogamy, no plurilocular zoidangia
current phylogenetic concept of the Laminariales includes three major lineages (and Chordaceae)

Fig. 5. Bayesian consensus tree from the combined total alignment (nuclear, RUBISCO, and 2nd codon positions from the nad6 region of the mitochondrion) both (a) with, and (b) without *Egregia menziesii* included in the analysis. The removal of *E. menziesii* from the data set changes the topology from a Type II to a Type I under Bayesian analyses. Support values are presented in the same order as Fig. 3 (Bayes/NJ/pars). *100% support and “.” indicates < 50% support for each analysis. Support values in bold indicate major clades.
The 11 world regions used for the biogeographical analysis (adapted from the system of Spalding et al. 2007, see text) (TNEP temperate Northeast Pacific, ALSK Alaska, ARCT Arctic, TNWA temperate Northwest Atlantic, TNEA temperate Northeast Atlantic, OKHO Okhotsk Sea, JAPK Japan, Korea, TSAM temperate South America, SOCE Southern Oceans, TSAF temperate South Africa, AUST Australasia)

![Map of world regions](image)

Table 3 Numbers of species in each kelp family in each of 11 world marine regions (for explanation of region codes, see Table 2)

<table>
<thead>
<tr>
<th>Family</th>
<th>OKHO</th>
<th>JAPK</th>
<th>ALSK</th>
<th>TNEP</th>
<th>ARCT</th>
<th>TNWA</th>
<th>TNEA</th>
<th>TSAM</th>
<th>SOCE</th>
<th>TSAF</th>
<th>AUST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Akkeshiophycaceae</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chordaceae</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pseudochordaceae</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Alariaceae</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>4</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Costariaceae</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Laminariaceae</td>
<td>19</td>
<td>14</td>
<td>13</td>
<td>16</td>
<td>7</td>
<td>7</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Lessoniaceae</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Total species</td>
<td>29</td>
<td>37</td>
<td>25</td>
<td>29</td>
<td>14</td>
<td>10</td>
<td>11</td>
<td>9</td>
<td>7</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>% Age of world species</td>
<td>25.9</td>
<td>33.0</td>
<td>22.3</td>
<td>25.9</td>
<td>12.5</td>
<td>8.9</td>
<td>9.8</td>
<td>8.0</td>
<td>6.3</td>
<td>3.6</td>
<td>6.3</td>
</tr>
</tbody>
</table>

Values with more than 20% of the world's species are highlighted

Table 4 Numbers of species in the most species-rich kelp genera in each of 11 world marine regions (for explanation of region codes, see Table 2)

<table>
<thead>
<tr>
<th>Genera</th>
<th>OKHO</th>
<th>JAPK</th>
<th>ALSK</th>
<th>TNEP</th>
<th>ARCT</th>
<th>TNWA</th>
<th>TNEA</th>
<th>TSAM</th>
<th>SOCE</th>
<th>TSAF</th>
<th>AUST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaria (15)</td>
<td>6</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Laminaria (22)</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Saccharonia (20)</td>
<td>6</td>
<td>10</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ecklonia (7)</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Eisenia (9)</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lessoniella (9)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

![DECORANA analysis of world temperate marine regions](image)

Fig. 4 DECORANA analysis of 11 world temperate marine regions, based on the kelp species that occur in them (Eigenvalues: Axis 1, 0.9414; Axis 2, 0.6482). Region codes as in Fig. 1

Laminariales

*Laminaria*

- several very common species, kelp forests of N Hemisphere
- alginate industry
- biodiversity centre – NW Pacific coast (Alaska – California)
sporophyte
(fyloid, cauloid, haptera with rhizoides)

♀ gametophyte
oogonia
(unilocular gametangia)

♂ gametophyte
antheridia
(unilocular gametangia)

sori
unilocular sporangia
(+) paraphyses
Most frequent European members of traditional *Laminaria*

- **S. latissima**
- **L. hyperborea**
- **L. digitata**
Laminariales

*Laminaria hyperborea* – canopy species of European kelp forests
Table 1. Current concept of species within the genera *Laminaria* Lamouroux and *Saccharina* Stackhouse

<table>
<thead>
<tr>
<th>Species name</th>
<th>Most recent synonym(s)</th>
<th>Region of occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. abyssalis</em> Joly et Oliveira 1967</td>
<td></td>
<td>S Atlantic: deep-water off Brazil</td>
</tr>
<tr>
<td><em>L. appretirhiza</em> Petrov et Vozhinskaya 1970&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td>NW Pacific: Sea of Okhotsk</td>
</tr>
<tr>
<td><em>L. brasiliensis</em> Joly et Oliveira 1967&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>S Atlantic: deep-water off Brazil</td>
</tr>
<tr>
<td><em>L. complanata</em> (Setchell et Gardner) Muenscher 1917&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
<td>NE Pacific: restricted occurrence in Washington and British Columbia</td>
</tr>
<tr>
<td><em>L. digitata</em> (Hudson) Lamouroux 1813</td>
<td></td>
<td>N Atlantic</td>
</tr>
<tr>
<td><em>L. ephemera</em> Setchell 1901</td>
<td></td>
<td>NE Pacific</td>
</tr>
<tr>
<td><em>L. farlowii</em> Setchell 1893</td>
<td></td>
<td>NE Pacific</td>
</tr>
<tr>
<td><em>L. gurjanovae</em> Zinova 1964&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td>NW Pacific: Kamchatka, Sakhalin</td>
</tr>
<tr>
<td><em>L. kyperborea</em> (Gunnerus) Foslie 1884</td>
<td></td>
<td>NE Atlantic</td>
</tr>
<tr>
<td><em>L. inclinatorhiza</em> Petrov et Vozhinskaya 1970&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>NW Pacific: Sea of Okhotsk</td>
</tr>
<tr>
<td><em>L. longipes</em> Bory de Saint-Vincent 1826&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
<td>NE Pacific</td>
</tr>
<tr>
<td><em>L. multiplicata</em> Petrov et Suchovejeva 1976&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td>NW Pacific: Sea of Okhotsk</td>
</tr>
<tr>
<td><em>L. nigripes</em> Agardh 1868&lt;sup&gt;2, e&lt;/sup&gt;</td>
<td></td>
<td>N Atlantic: Arctic</td>
</tr>
<tr>
<td><em>L. ochroleuca</em> Bachelot de la Pylaie 1824</td>
<td></td>
<td>NE Atlantic, Mediterranean Sea</td>
</tr>
<tr>
<td><em>L. pallida</em> Greville 1848&lt;sup&gt;b&lt;/sup&gt;</td>
<td><em>L. schinzii</em> Foslie 1893</td>
<td>S Atlantic</td>
</tr>
<tr>
<td><em>L. philippinensis</em> Petrov et Suchovejeva 1973&lt;sup&gt;3, i&lt;/sup&gt;</td>
<td></td>
<td>NW Pacific: deep water off Philippines</td>
</tr>
<tr>
<td><em>L. rodriguezii</em> Bornet 1888</td>
<td></td>
<td>Mediterranean Sea</td>
</tr>
<tr>
<td><em>L. sacholinensis</em> (Miyabe) Miyabe 1933</td>
<td></td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>L. setchelli</em> Silva 1957</td>
<td></td>
<td>NE Pacific</td>
</tr>
<tr>
<td><em>L. sinclairii</em> (Harvey ex Hooker et Harvey) Farlow, Anderson et Eaton 1878</td>
<td></td>
<td>NE Pacific</td>
</tr>
<tr>
<td><em>L. solidungula</em> Agardh 1868</td>
<td></td>
<td>N Atlantic: Arctic</td>
</tr>
<tr>
<td><em>L. yezoensis</em> Miyabe 1902</td>
<td></td>
<td>N Pacific</td>
</tr>
<tr>
<td><em>S. angustata</em> (Kjellman) Lane, Mayes, Druehl et Saunders 2006</td>
<td><em>L. angustata</em> Kjellman 1885</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. dichroroides</em> (Miyabe) Lane, Mayes, Druehl et Saunders 2006&lt;sup&gt;d&lt;/sup&gt;</td>
<td><em>L. dichroroides</em> Miyabe 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. coriacea</em> (Miyabe) Lane, Mayes, Druehl et Saunders 2006&lt;sup&gt;e&lt;/sup&gt;</td>
<td><em>L. coriacea</em> Miyabe 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. sculpa</em> (Miyabe) Lane, Mayes, Druehl et Saunders 2006</td>
<td><em>Kjellmaniella crassifolia</em> Miyabe 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. dentigera</em> (Kjellman) Lane, Mayes, Druehl et Saunders 2006</td>
<td><em>L. dentigera</em> Kjellman 1889</td>
<td>NE Pacific: Alaska</td>
</tr>
<tr>
<td><em>S. diabolica</em> (Miyabe) Lane, Mayes, Druehl et Saunders 2006&lt;sup&gt;2, l&lt;/sup&gt;</td>
<td><em>L. diabolica</em> Miyabe 1902</td>
<td>NW Pacific: Japan</td>
</tr>
</tbody>
</table>

(continued)
<table>
<thead>
<tr>
<th>Species name</th>
<th>Most recent synonym(s)</th>
<th>Region of occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. groenlandica</em> (Rosevinge) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;6&lt;/sup&gt;</td>
<td><em>L. groenlandica</em> Rosenvinge 1893 (sensu Druelh, 1968)</td>
<td>NE Pacific: California to British Columbia</td>
</tr>
<tr>
<td><em>S. gyrate</em> (Kjellman) Lane, Mayes, Druelh &amp; Saunders 2006</td>
<td><em>L. bongardiana</em> Postels &amp; Ruprecht 1840&lt;sup&gt;8&lt;/sup&gt;</td>
<td>N Pacific: Alaska, Commander Islands</td>
</tr>
<tr>
<td><em>S. japonica</em> (Areschoug) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;1&lt;/sup&gt;</td>
<td><em>Kjellmaniella gyrate</em> (Kjellman) Miyake 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. kurilensis</em> (Miyabe &amp; Nagai) Lane, Mayes, Druelh &amp; Saunders 2006</td>
<td><em>L. japonica</em> Areschoug 1851</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. latissima</em> (Linnaeus) Lane, Mayes, Druelh &amp; Saunders 2006</td>
<td><em>L. fragilis</em> Miyake 1902</td>
<td>NW Pacific: Kuril Islands</td>
</tr>
<tr>
<td><em>S. longipes</em> (Bachelot de la Pylaie) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Cymathaeae japonica</em> Miyabe et Nagai 1940</td>
<td>NW Pacific: Kuril Islands</td>
</tr>
<tr>
<td><em>S. longipes</em> (Okamura) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;4&lt;/sup&gt;</td>
<td><em>L. saccharina</em> (Linnaeus) Lamouroux 1813</td>
<td>NE Atlantic and N Pacific</td>
</tr>
<tr>
<td><em>S. longipes</em> (Miyabe) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;5&lt;/sup&gt;</td>
<td><em>L. feroxens</em> (Borgesen) Borgesen 1902&lt;sup&gt;6&lt;/sup&gt;</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Miyabe) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;5&lt;/sup&gt;</td>
<td><em>L. agardhii</em> Kjellman 1877&lt;sup&gt;6&lt;/sup&gt;</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Bachelot de la Pylaie) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>L. groenlandica</em> Rosenvinge 1893 (NW Atlantic form)&lt;sup&gt;6&lt;/sup&gt;</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Okamura) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;4&lt;/sup&gt;</td>
<td><em>L. longipes</em> Okamura 1896</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Miyabe) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;5&lt;/sup&gt;</td>
<td><em>L. longipes</em> Miyake 1902</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Bachelot de la Pylaie) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>L. longipes</em> Miyake 1902</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Okamura) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;4&lt;/sup&gt;</td>
<td><em>L. longipes</em> Miyake 1902</td>
<td>NW Atlantic: Canada</td>
</tr>
<tr>
<td><em>S. longipes</em> (Miyabe) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;5&lt;/sup&gt;</td>
<td><em>L. religiosa</em> Miyake 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. religiosa</em> (Miyabe) Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;6&lt;/sup&gt;</td>
<td><em>S. religiosa</em> Miyake 1902</td>
<td>NW Pacific: Japan</td>
</tr>
<tr>
<td><em>S. sessilis</em> (Agardh) Kuntze 1891</td>
<td><em>Hedophyllum sessile</em> (Agardh) Setchell 1901</td>
<td>NE Pacific and Kamchatka</td>
</tr>
<tr>
<td><em>S. subimplex</em> (Setchell &amp; Gardner) Widdowson, Lindstrom &amp; Gabrielson 2006&lt;sup&gt;6&lt;/sup&gt;</td>
<td><em>L. subimplex</em> (Setchell &amp; Gardner) Miyabe et Nagai 1933</td>
<td>NE Pacific and Kamchatka</td>
</tr>
<tr>
<td><em>S. yendoana</em> Lane, Mayes, Druelh &amp; Saunders 2006&lt;sup&gt;4&lt;/sup&gt;</td>
<td><em>L. yendoana</em> Miyabe 1936</td>
<td>NE Pacific and Kamchatka</td>
</tr>
</tbody>
</table>

All names listed have been in use since Kain (1979); doubtful earlier taxa are excluded. For an overview of synonymized and doubtful taxa and more taxonomic references see www.algaebase.org. Distribution extracted from Kain (1979), L"uning (1990) and Guiry & Guiry (2007). Species considered to be currently valid are in bold type.

<sup>a</sup> Taxonomic position unclear.<sup>b</sup>Similar to *L. digitata*; spongiangia on one side only, mucilage ducts medially placed and widely spaced (Olga Selivanova, pers. comm. Algaebase version 4.2, 13 Nov 2006). <sup>c</sup>Relationship between *L. abyssalis* and *L. brasilienis* unclear; it seems probable that just one species is involved due to the restricted occurrence of both. <sup>d</sup>For distribution see also Druelh (1969); he assumes affinity to Arctic *L. digitata f. complanata* but basionym is *L. saccharina f. complanata* Setchell et Gardner (Algaebase, vers. 4.2). <sup>e</sup>Petrov (1972) included *L. groenlandica* in his concept of *L. bongardiana*; L"uning & De Dieck (1990) supported this idea, suggesting similarities to N Atlantic *L. digitata* which were not corroborated by hybridization studies (De Dieck, 1992; Gabrielson et al. 2006) synonomized *L. bongardiana* and *L. groenlandica* with *Saccharina subimplex*; Lane et al. (2006) transferred NE Atlantic *L. groenlandica* to *S. groenlandica*. <sup>f</sup>Molecular data from a population outside the currently recognized range for the species (San Juan Island) indicate a closer relationship to *Laminaria* than to *Saccharina* (Lane, pers. comm.); although this needs confirmation, the transfer to the genus *Saccharina* proposed by Lane et al. (2006) is not followed here. <sup>g</sup>Close relation to *L. digitata* (Kain, 1979), but taxonomic position still unclear. <sup>h</sup>Conspecificity with *L. schizii* was suggested by Stegenga et al. (1997) as *L. pallida* and *L. schizii* were interfertile (Fl generation) (tom Dieck & De Oliveira, 1993). <sup>i</sup>First published in Petrov et al. (1973); deep-water population. <sup>j</sup>Lane et al. (2006) assume conspecificity with *S. latissima* due to identical ITS sequences. <sup>k</sup>Lane et al. (2006) assume conspecificity with *S. japonica* due to identical ITS sequences. <sup>l</sup>According to Yotsukura et al. (2006), *S. japonica*, *S. religiosa*, *S. ochotensis* and *S. diabolica* are considered to be one biological species. <sup>m</sup>Taxonomic relationship between N Atlantic and N Pacific plants unclear (Druelh, 1969); N Atlantic *L. groenlandica* has been synonymized with *L. canefolia* and then with *L. saccharina* (Wolfe, 1960; Kain, 1979), a concept which is followed here; N-Pacific plants differ by frequent fingering of the blade (Druelh, 1968). <sup>n</sup>According to partial LSU rDNA, ITS rDNA and AFLP data *L. feroxens* has a sub-species status to *L. saccharina* (Ertig et al., 2004); Kain (1979) also suggested it to be a ‘generic strain’. <sup>o</sup>According to Chapman (1975), who discounted duct anatomy as taxonomic character; Kain (1979) and later Bhattacharyya et al. (1991) suggest conspecificity with *L. longipes* and *L. saccharina*. <sup>o</sup>There is much evidence (Kain,1979: duct and stipe anatomy; L"uning et al., 1978: hybridization studies; Bhattacharyya et al., 1991: 18S rDNA, rDNA (LSU), Cho et al., 2000: RuBiCo spacer; Lane et al., 2006: ITS) that *S. longipes* is conspecific with *S. latissima*. <sup>g</sup>According to Lane et al. (2006), there is only one base pair difference in ITS sequence between *S. ochotensis*, *S. religiosa* and *S. japonica*. <sup>g</sup>Yoon et al. (2001) suggest conspecificity of *S. religiosa* with *S. japonica* due to identical RuBiCo spacer sequences. <sup>g</sup>Druelh et al. (1963) state close morphological relationship of *S. yendoana* to *C. cichorioides* which, in turn, has identical ITS sequences to *S. latissima* (Lane et al., 2006).
Growth of sporophytes
light saturation: 20 -100 µmol m^{-2} s^{-1}
minimal annual light requirement: 40-96 mol photons m^{2} y^{-1}
optimum temperatures: 5 – 15 °C
nutrients modulate growth, but are not triggers

Fertility:
gametophytes (optimum): 5-18 °C, 4-90 µmol photons m^{2} s^{-1}
sporophytes: 1 to 18 °C, 5-200 µmol photons m^{2} s^{-1}
Table 6. Reproductive period of selected *Laminaria* species worldwide

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Month</th>
<th>Remarks</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. angariata</em></td>
<td>Hokkaido, Japan</td>
<td>J: S; M: S</td>
<td>1-year plants</td>
<td>Hasagawa (1972)*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A: S; M: S</td>
<td></td>
<td>Kawashima (1983)</td>
</tr>
<tr>
<td><em>L. digitata</em></td>
<td>Calvados, France</td>
<td>J: S; M: S</td>
<td>2nd blade</td>
<td>Cosson (1976)</td>
</tr>
<tr>
<td></td>
<td>Wales, UK</td>
<td>J: S; M: S</td>
<td></td>
<td>Harries (1982)</td>
</tr>
<tr>
<td></td>
<td>Cape Cod, USA</td>
<td>J: S; M: S</td>
<td></td>
<td>Sears &amp; Wicke (1975)</td>
</tr>
<tr>
<td><em>L. farlowii</em></td>
<td>S, USA</td>
<td>J: S; M: S</td>
<td></td>
<td>McPeak (1981)</td>
</tr>
<tr>
<td></td>
<td>San Diego, USA</td>
<td>J: S; M: S</td>
<td></td>
<td>Dayton et al. (1999)</td>
</tr>
<tr>
<td><em>L. fragilis</em></td>
<td>Muroran and Hakodate, Japan</td>
<td>J: S; M: S</td>
<td></td>
<td>Miyabe (1957)</td>
</tr>
<tr>
<td><em>L. hyperborea</em></td>
<td>Isle of Man, UK</td>
<td>J: S; M: S</td>
<td></td>
<td>Calvin &amp; Ellis (1961)</td>
</tr>
<tr>
<td></td>
<td>Helgoland, Germany</td>
<td>J: S; M: S</td>
<td></td>
<td>Kain (1975)</td>
</tr>
<tr>
<td></td>
<td>Wales, UK</td>
<td>J: S; M: S</td>
<td></td>
<td>Liittine (1982)</td>
</tr>
<tr>
<td><em>L. japonica</em></td>
<td>Hokkaido, Japan</td>
<td>J: S; M: S</td>
<td>Young sporophytes</td>
<td>Harries (1982)</td>
</tr>
<tr>
<td><em>L. longicruris</em></td>
<td>Long Island Sound, USA</td>
<td>J: S; M: S</td>
<td>Soft from August onwards</td>
<td>Miyabe (1957)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A: S; M: S</td>
<td>2-year plants</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>J: S; M: S</td>
<td>3-year plants</td>
<td></td>
</tr>
<tr>
<td><em>L. ochotensis</em></td>
<td>Brittany, France</td>
<td>J: S; M: S</td>
<td>Sor begin to appear in August</td>
<td>Miyabe (1957)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A: S; M: S</td>
<td>Summer to autumn fertility</td>
<td>Saovagea (1982)</td>
</tr>
<tr>
<td><em>L. ocellata</em></td>
<td>Cape of Good Hope, South Africa</td>
<td>S: S; M: S</td>
<td>Summer to autumn fertility</td>
<td>Dieckmann (1980)</td>
</tr>
<tr>
<td><em>L. rodriguezi</em></td>
<td>Hokkaido, Japan</td>
<td>J: S; M: S</td>
<td></td>
<td>Abe et al. (1982)</td>
</tr>
<tr>
<td><em>L. saccharina</em></td>
<td>Mediterranean Sea</td>
<td>J: S; M: S</td>
<td></td>
<td>Huve (1955)</td>
</tr>
<tr>
<td></td>
<td>Argyll, UK</td>
<td>J: S; M: S</td>
<td></td>
<td>Park (1948)*</td>
</tr>
<tr>
<td></td>
<td>Wales, UK</td>
<td>J: S; M: S</td>
<td>Annual population</td>
<td>Lee &amp; Brinkhuis (1986)</td>
</tr>
<tr>
<td></td>
<td>Helgoland, Germany</td>
<td>J: S; M: S</td>
<td>Most plants vegetative during reproductive period</td>
<td>Sears &amp; Wicke (1975)</td>
</tr>
<tr>
<td></td>
<td>Long Island Sound, USA</td>
<td>J: S; M: S</td>
<td>Annual population</td>
<td>Liittine &amp; Hsiao (1982)</td>
</tr>
<tr>
<td></td>
<td>Cape Cod, USA</td>
<td>J: S; M: S</td>
<td></td>
<td>Druehl (1968), Klinger (1984)</td>
</tr>
<tr>
<td></td>
<td>British Columbia, Canada</td>
<td>J: S; M: S</td>
<td>Sor in the field restricted to dissected blade portion</td>
<td>Druehl (1968), Markham (1973)</td>
</tr>
<tr>
<td><em>L. setchellii</em></td>
<td>British Columbia, Canada</td>
<td>J: S; M: S</td>
<td>In spring sor at tips of 2-3 cm blades; in autumn on old blades</td>
<td>Druehl (1968), Markham (1973)</td>
</tr>
<tr>
<td><em>L. solidungula</em></td>
<td>Newfoundland, Canada</td>
<td>J: S; M: S</td>
<td>Space release next spring to summer</td>
<td>Hooper (1964)</td>
</tr>
</tbody>
</table>

Abbreviations: S: sori present; M: main fruiting period; s: sori present, but in relatively low quantity; -: no sori present or no information available.

*Cited by Liittine (1982).*

Table 4. Examples of deepest *Laminaria* populations

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Depth limits</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. abysinii/brasilienis</em></td>
<td>Off Brazilian coast</td>
<td>70–95 m</td>
<td>Joly &amp; de Oliveira Filho (1967)</td>
</tr>
<tr>
<td><em>L. hyperborea</em></td>
<td>Aran Islands, Ireland</td>
<td>32 m</td>
<td>Lüning (1990)</td>
</tr>
<tr>
<td><em>L. ocellata</em></td>
<td>Strait of Messina, Italy</td>
<td>60–95 m</td>
<td>Drew (1972), Giacone (1972)</td>
</tr>
<tr>
<td><em>L. philippinensis</em></td>
<td>Off the Philippines</td>
<td>85 m</td>
<td>Petrov et al. (1973)</td>
</tr>
<tr>
<td><em>L. rodriguezi</em></td>
<td>Corsica, France</td>
<td>95 m</td>
<td>Fredj (1972)</td>
</tr>
<tr>
<td><em>L. saccharina</em></td>
<td>Spitsbergen</td>
<td>25 m</td>
<td>Hanek (1998)</td>
</tr>
<tr>
<td><em>L. solidungula</em></td>
<td>Newfoundland, Canada</td>
<td>30 m</td>
<td>Whittick et al. (1982)</td>
</tr>
</tbody>
</table>
Phyllariopsis brevicops

Phyllariopsis purpurascens

Sacchorhiza dermatodea

Sacchorhiza polyschides

Undaria pinnatifida
How good are the species of *Laminaria*?

Fig. 1. Map showing the three main locations where the *Laminaria* species were collected (see also Table 1). Area 1 in

Laminariales

Saccharina
- separated from Laminaria
- circumboreal genus (*S. latissima, S. japonica*)

(kombu)

Chi et al., 2014, Acta Oceanol Sin
How good are the species of Laminaria?

ITS based phylogeny

Laminariales

*Alaria* – lanceolated fyloide
Laminariales

*Nereocystis* – annual plant, length up to 40 m
Laminariales

*Egregia menziesii* – „feather boa kelp“

http://natural-history.main.jp
Laminariales

Macrocystis – sublitoral, length up to 60m, weight 300 kg

NW USA, S America, Australia
Laminariales

Macrocystis pyrifera
Evolutionary geographic origins of the genus *Macrocystis*

Figure 1. Phylogenetic reconstruction of the *Macrocystis* genus under the Bayesian inference using a GTR+Γ mixture model. The numbers at the nodes are posterior probabilities, values higher than 0.5 are shown. The different circle colours indicate the four *Macrocystis* morphospecies: Blue = *Integrifolia*; Green = *pyrifera*; Yellow = *angustifolia*; and Red = *laevis*. MpIBlancaCh, MpFBulnesCh, and MpTeupaCh indicate new samples from this work / Reconstrucción filogenética del género *Macrocystis* bajo la inferencia Bayesiana usando el modelo 1 GTR+Γ. El número de los nodos son probabilidad posterior, se muestran los valores superiores a 0.5. Los diferentes círculos de colores indican las cuatro morfoespecies de *Macrocystis*: Azul = *Integrifolia*; Verde = *pyrifera*; Amarillo = *angustifolia*, y Rojo = *laevis*. MpIBlancaCh, MpFBulnesCh, y MpTeupaCh indican las nuevas muestras aportadas por este trabajo.

<table>
<thead>
<tr>
<th>Node</th>
<th>Northern Hemisphere</th>
<th>Southern Hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.88 ± 0.13</td>
<td>0.12 ± 0.13</td>
</tr>
<tr>
<td>2</td>
<td>0.99 ± 0.01</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>3</td>
<td>0.64 ± 0.22</td>
<td>0.36 ± 0.22</td>
</tr>
<tr>
<td>4</td>
<td>0.99 ± 0.01</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>5</td>
<td>0.01 ± 0.01</td>
<td>0.99 ± 0.01</td>
</tr>
</tbody>
</table>

Table 1. The probability values for each ancestral state of (A) Hemisphere, (B) Ocean, and (C) Morphology of *Macrocystis*. The probability values are reported with 10 times the standard error based on the BMCMC approach / Valores de probabilidad de cada estado ancestral para (A) Hemisferio, (B) Océano y (C) Morfología de *Macrocystis*. Los valores de probabilidad son reportados con 10 veces el error estándar basado en la aproximación BMCMC.
Laminariales
Undaria

originally an Asian (N Pacific) genus, 4 species

annual production of *U. pinnatifida* in aquacultures – cca 1.8 million tonnes; constituting possibly about 20% of total kelp production in agriculture

*U. pinnatifida* (wakame) – the single most successful laminarialean invasive species

---

**Figure 1** Different developmental stages of *Undaria pinnatifida* sporophytes (a–d). *Undaria pinnatifida* can be found growing in the subtidal and intertidal, as well as on natural and artificial substrates (e–g).

**Figure 2** Approximate distribution of *Undaria pinnatifida*. Global map: Green = native range, red = non-native range. Regional maps: Each point represents a distinct location but does not indicate precise position or entire extent. See Table S1 for more information and references.

**Figure 3** Thermal tolerances of the different life stages of *Undaria pinnatifida*. Lighter colors = life stage possible but may be limited. See text for references.

U. pinnatifida – wakame cultivation

En - Wakame, Fr - Wakamé, Es - Abeto marino

Production cycle

Global Aquaculture Production for species (tonnes)
Source: FAO FishStat

Laminariales

*Chorda filum* – 0.3 to 5 m long strands, filled by air

paraphyses (and hairs) cover the thallus

cold temperate/subarctic alga, ephemeral thalli, penetrates deep into the brackish water habitats
Desmarestiales

D. anceps

D. ligulata

Himantothallus grandifolius
Ectocarpales

- simple, uniseriate filaments
- diplohaplontic cell cycle, isomorphic or slightly heteromorphic
Ectocarpus siliculosus

- delicate, filamentous tufts
- very common, cosmopolitan species
Pylaiella littoralis

abundant cold water species, often in brackish waters, dominant as annual epiphyte in the Baltic
Pylaiella littoralis
♂ gametophyte

♀ gametophyte

plurilocular sporangia

plurilocular gametangia

unilocular sporangia
Colpomenia

invasive species, origin in NW Pacific

ephemeral thalli, saccate gametophytes, crustose sporophytes

Colpomenia peregrina
Figure 1  *Colpomenia sinusosa*: variable morphology and habit.
(A) Group Ia, Sasudong, Jeju, Korea (8 Jul. 2011); (B) group Ic, Punta Santa Ana, Magallanes, Chile (31 Oct. 2013); (C) group Ie, Prala Rasa, Búzios, Brazil (24 Oct. 2011); (D) group II, Heraklion, Crete Island, Greece (11 Jan. 2011); (E) group IIa, Daedonghae, Hainan, China (9 Mar. 2009); (F) group IIb, Bulusan, Philippines (3 Feb. 2010). Scale bars are 1 cm.

Figure 2  *Colpomenia sinusosa*: ML tree inferred from the phylogenetic analysis of cox3 sequences.
Values shown near branches are bootstrap values (1000 iterations) from the data (ML/MP). Only bootstrap values >50% are shown. Branch lengths are proportional to the number of substitutions per site.
Figure 4  Colpomenia sinuosa: distribution map of the cox3 haplotypes.
Circles indicate haplotypes, and boxes indicate locations in which more than two haplotypes were found. Different colors are given for group II and subgroups of group I and III, as indicated in Figure 5. Abbreviations explained in Table 1.

Figure 5  Colpomenia sinuosa: statistical parsimony network for 37 cox3 haplotypes.
Each circle represents a haplotype and circle size is proportional to strain frequency. Black solid lines delineate the three major groups (I, II, and III). Lines between haplotypes are single mutational steps; small black dots indicate missing haplotypes (either extinct or not sampled).
Fig. 10. Maximum likelihood tree for *Myelophybus* and relatives estimated from rbcL sequence data (GTR + I + Γ model, -Log likelihood = 9745.20; I = 0.5984; Γ = 0.9113; A ↔ C = 1.227, A ↔ G = 4.55; A ↔ T = 1.207; C ↔ G = 1.314; C ↔ T = 10.16; and G ↔ T = 1). Thicker branches represent the posterior probabilities (>95%) from Bayesian analysis. Bootstrap values (>50%) are given above (MP) and below (ME) branches. The alternative hypothetical topologies of the rbcL tree are shown with numbered arrows, indicating the constrained monophyly with *Myelophybus* for Shimodaira-Hasegawa test.
Scytosiphon lomentaria

Fig. 4. Diagrammatic illustrations of the life history of Azorean *Scytosiphon lomentaria* in culture. (A) Macrothallus with plurilocular sporangia. (B) Transverse section of a small portion of macrothallus with plurilocular sporangia. (C) Spore from the plurilocular sporangia (plurispore). (D) Crustose microthallus. (E) Crustose microthallus with erect blades and true hairs emerging. (F) Squashed microthallus with unilocular sporangia and paraphyses. (G) Spore from the unilocular sporangia (unispore). AS, ascocyst; MA, macrothallus; MI, microthallus; PH, paraphyses; PS, plurilocular sporangia; TH, true hair; US, unilocular sporangia.

Dictyosiphon foeniculaceus
Adenocystis

Adenocystis utricularis
Splachnidium

*S. rugosum*
freshwater brown algae

- *Pleurocladia*, *Heribaudiella*, [Ectocarpus]