Biogeography and distribution of marine macroalgae (seaweeds)

macroalgae grow in the marine littoral...
Biogeographic areas and distribution of taxa are primarily determined by water temperature.

seven phycogeographical areas of our planet
simplified scheme:
arctic/antarctic = < 10°C summer isotherm / < 0°C winter isotherm
cold temperate = < 15°C s.i. / < 10°C w.i.
warm temperate = < 25°C s.i. / < 20°C w.i.
tropical
Fig. 4 Major dinoflagellate biogeographic zones. A = tropical-temperate macrozone, B = subarctic North Pacific, C = subarctic North Atlantic, D = arctic zone, E = subantarctic zone, F = Antarctic zone, black areas = substantial seasonal upwelling, hatched areas = regions of mixed character. From Taylor (1987d).

Fig. 2. Biogeographic coccolithophore zones from the Atlantic and Pacific Oceans (from Winter et al. 1994). 1 - Subarctic, 2 - Temperate (Transitional), 3 - Subtropical (Central), 4 - Tropical (Equatorial), 5 - Subantarctic. Similar distribution patterns are found in foraminifera.
In many cases, temperature determined actual distribution of species...

**Fig. 1.9** Distribution of the kelp *Saccorhiza polyschides*. Circles represent presence (species is absent on North American coasts); distribution area is dotted (occurring, however, only along the coasts); 4°C-winter isotherm = northern lethal boundary; 15°C-winter isotherm = southern reproduction boundary; 22°C-summer isotherm = southern lethal boundary; 21°C-winter isotherm = southern growth boundary (not reached by the species). (From van den Hoek 1982b).

**Fig. 1.10** Distribution of the brown alga *Dictyota* spp. on both sides of the North Atlantic: *D. dichotoma* in northwestern Atlantic and *D. menstrualis* in northeastern Atlantic. 2°C-winter isotherm = northern lethal boundary (limiting in North America); 13°C-summer isotherm = northern growth and reproduction boundary (limiting in Europe). (From van den Hoek 1982a.)

**Fig. 1.11** Distribution of the red alga *Chondrus crispus* at both sides of the North Atlantic. 24°C-summer isotherm = southern lethal boundary (limiting on both sides of the Atlantic); 17°C-winter isotherm = southern reproduction boundary (additionally limiting in North Africa); 7°C-summer isotherm = northern growth boundary (limiting on both sides of the Atlantic). A southern growth and reproduction boundary (23°C-winter isotherm) is not reached by the species (From van den Hoek 1982a.)
But historical effects (glacials, fluctuations of the sea surface levels, etc.) still play a role...

-17500 y, last glacial maximum
Atlantic is much younger than Pacific; i.e. there are more groups radiating from the Pacific.

Fig. 2.2 Continental drift and formation of the Atlantic Ocean. (A) 100 Ma (phase 1, Cretaceous): North Pacific wide open to the early Arctic Ocean. (B) 60 Ma (phase 2, early Tertiary): North Pacific closed off from the early Arctic Ocean. Notes: (1) The
European coasts – cold and warm temperate regions

Fig. 2.45  Phytogeographical regions and provinces in the North Atlantic. A = warm temperate Carolina region; B = western Atlantic tropical region; C, D, E = warm temperate Mediterranean–Atlantic region (C = Canary province; D = Mediterranean province, E = Lusitania province); F, G = cold temperate North Atlantic region (F = eastern province; G = western province), H = Arctic region. (From van den Hoek 1975.)
character and importance of transition zones for the community structure
European cold temperate Atlantic region – northern Norway/Iceland to northern France

Due to warm north-Atlantic current many taxa migrated from NW Africa/Gibraltar area to the north after the last glacial. These taxa form a bulk of the today cold temperate European flora.

Northern limits: August 8°C isotherm and February 0°C isotherm; i.e. between Norway and Spitzbergen
However, Icelandic and north Norwegian flora already has a few typically Arctic taxa, such as *Devaleraea ramentacea*, which is otherwise abundant on Spitzbergen.

otherwise: Alaska, Greenland, Faroes, arctic Canada
North Atlantic supralittoral (spray zone) – characteristic genera *Prasiola* + *Rosenvingiella*

*Prasiola stipitata*

vertical zonation - Galicia
The eulittoral of the European north Atlantic area

upper-eulittoral – *Fucus spiralis, F. distichus* mid-eulittoral – *Ascophyllum nodosum, F. vesiculosus, Enteromorpha spp.*, *Porphyra umbilicalis* (summer aspect)
strong effects of vertical structure on distribution of taxa – tidal effects in the eulittoral
Desiccation stress *Fucus spiralis* in upper (HZ) and lower (LZ) intertidal

**Fig. 6** Maximum quantum yields $F_v/F_m$ normalized to initial values after 25 min re-submersion in seawater after 1, 2, 3, 4, 5, 9, and 24 h desiccation on a mesh screen. *F. spiralis* HZ (gray) and LZ (black). Combined measurements of October 2005 and April 2006 (means ± SE; $n = 6$ for 2, 3, 4, 5, and 9 h and 12 for 1 and 24 h, respectively. Significant differences are indicated with asterisk).

**Fig. 8** Effective quantum yields $\Phi_{PSII}$ (%) of tufts (gray) compared to single fronds (black) of *F. spiralis* during desiccation lasting 1, 3, 5, and 10 h on a mesh screen exposed to the sun. Values normalized to initial yields (means ± SE; $n = 14$).
The lower eu-littoral – *F. serratus*, *Mastocarpus stellatus*, *Ch. crispus*, *C. officinalis*, *Scytosiphon lomentaria*
The sublittoral zone

upper sublittoral – still much influenced by waves

canopy brown algae: *Alaria esculenta, L. digitata, L. saccharina, Halidrys siliquosa*
... and the understorey algae: *C. officinalis, Ch. crispus, M. stellatus, Palmaria palmata*

sandy and muddy bottoms – *Zostera marina*

The mid-sUBLittoral zone

– from N Norway to mid Portugal: *L. hyperborea* dominates the kelp community (laminarian forest)
Nordsee – laminariacean „forest“ in the sublittoral with red algal epiphytes on stalks
The lower sublittoral zone (<5% penetrating light)

Scattered *L. hyperborea*, but no more canopy-forming. Laminarias grow extremely slowly and, consequently, often have a lot of epiphytes (such as *Membranipora membranacea*),
typical taxa: *Delesseria sanguinea*, *Phycodrys rubens*, *Desmarestia ligulata*, *Polysiphonia urceolata*

morphological adaptations to low light intensities and absence of major wave action
maerl vegetation – 3 to 25 meters, sandy bottoms (S Ireland, S Cornwall, Bretagne and elsewhere) dominated by *Phymatolithon calcareum, Lithothamnion corallioides*

loose lying, encrusted…
Brackish areas of the European cold temperate region – fjords, estuaries, Baltic Sea

eutrophication – *Enteromorpha* / *Ulva*
mesohaline conditions – *F. vesiculosus*, *F. serratus*, *Blidingia minima*, *Ulothrix*, *Ulva*, *Enteromorpha*

**Baltické moře**
-no tides = no eulittoral
- before 12000 years – freshwater lake; nowadays brackish; low seaweeds diversity
- *Prasiola*, *Cladophora* spp., *Ceramium tenuicorne*, *Monostroma* *grevillei*, *Bangia atropurpurea*, *Blidingia minima*, *Rhodomela confervoides*, *F. vesiculosus*

s. m.: 18 až 22°C, w.m.: -2 až 4°C
salinity gradients in major European brackish habitats

Fig. 2. The Baltic Sea (a), the Black Sea and the Sea of Azov (*) (b) and the Caspian Sea (c) with salinity zones according to the Venice system (zone border salinities as in Table 1). The salinity zone coloration as given in (a).

Paavola et al., 2005, Est Coast Shelf Sci 64: 738-750
- Baltic is the single largest brackish habitat in the world
- it is atidal, but there are non-periodic fluctuations
- anaerobic benthic zones
- eutrophication since 1950s
- occasional inflows of oceanic saltwater
- **brackish submergence**
- regular seasonal partial freezing
dominant marine landscapes of the Baltic sea

5 key vegetation types: Zostera
a) ulvophyceans
b) Fucus
c) stoneworts
d) Furcellaria

additional typical components:
a) brown epiphytes/ephemerals (Ectocarpus, Pilayella)
b) red epiphytes/ephemerals (Ceramium, Polysiphonia)
c) green epiphytes/ephemerals (Cladophora)
**Ice scraping** (= absence of perennial macroalgae in the upper sublittoral of northern Baltic shores)
upper sublittoral of central Baltic (the Fucus belt)
mid-sublittoral assemblages – Fucus belt in Baltic sublittoral – as result of brackish submergence
**Bodden habitats**
- coastal lagoons on southern shores,
- soft bottom, local salinity gradients, eutrophication

unique communities composed of plants and algae originating from both freshwater and marine ecosystems (*Ruppia maritima, Fucus vesiculosus, Furcellaria lumbricalis, Chara baltica, Myriophyllum spicatum*)
Charophyte gradients

**Fucus vesiculosus** depth distribution dynamics

**Furcellaria** dominated communities
distribution limits of selected marine taxa
distribution limits of selected freshwater taxa
The effect of salinity gradients
the case study of *Furcellaria lumbricalis* – possible speciation due to salinity gradient and geographic isolation

**Fig. 1** Sixteen *Furcellaria lumbricalis* populations from the Atlantic Ocean and Baltic Sea included in the study. The names of the populations and additional sampling site information are given in Table 1

**Fig. 4** Bayesian estimates of population structure of *Furcellaria lumbricalis* based on EST-derived microsatellites in a five populations grouped together as cluster A (populations 1–3 and 5 from the Atlantic Ocean and population 6 from the west coast of Sweden) in the first round of STRUCTURE analysis, and in b six populations grouped together as cluster B (populations 7–9 and 13–15 from the Baltic Sea). Each shade represents one of the clusters formed in the analysis ($K = 3$ in analysis (a) and $K = 2$ in analysis (b)). All populations examined using EST-derived microsatellites grouped to either cluster A or B. Results are based on ten replicate runs.
Probable parallel speciation of *F. radicans* from *F. vesiculosus* in the Baltic Sea

Fig. 3 Plot of two morphological variables in *Fucus radicans* and *F. vesiculosus*. Results from a principal component analysis based on two morphological variables with five measurements. Abbreviations from

Fig. 4 Overall genetic differentiation between *Fucus* species in the Baltic Sea. (a) Combined histogram of Bayesian individual assignment test to illustrate the overall genotypic clustering of both species from all the sampling localities. Bars represent individual assignment probability into different genetic clusters depicted with colours, as in Fig. 2. (b) Neighbour-joining microsatellite-based population tree calculated with Cavalli-Sforza genetic distances. Out-group locations are indicated in Fig. 4c. (c) Map of the Baltic Sea with a superimposed gene flow network identifying the genetic sources among species and populations. Arrow thickness is proportional to the amount of gene flow to the indicated direction. Numbers 1 and 2 correspond to cut groups *Fucus vesiculosus* from Eggholmen, Norway and Fiskebäckskil, west Sweden, respectively.
Baltic water blooms
- mostly formed by Cyanobacteria
- develops in summer (2\textsuperscript{nd} half of July, August)
- non-periodic development (depends on combination of temperature and salinity)
- leads to extensive anoxic benthic zones

summer 2010

Aphanizomenon/Anabaena

Nodularia spumigena
phytoplankton in W Baltic (2006)

typically two seasonal maxima:

**spring** diatoms/dictyocha bloom + **late summer** cyanobacteria/diatom bloom

(dominants may include even the phototrophic ciliates (*Mesodinium*), dinoflagellates, dictyoches, haptophytes or euglenoids)
European / NW African warm temperate Mediterranean-Atlantic region

from 10°C w.i. near western Ireland/Brittany to 25°C s.i. near Cape Verde

three phycogeographic provinces: **Lusitania province, Canary province, Mediterranean**

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Lusitania province

*Alaria esculenta* and *L. digitata* do not reach below W Ireland/Bretagne; but additional cold temperate seaweeds reach up to mid Portugal (e.g., *L. hyperborea, Saccharina latissima*).

Typical ancestral species: *Saccorhiza polyschides, L. ochroleuca*.

(They mix with the cold temperature species on Bretagne coast.)
southern species reaching the northern limits in Lusitanian province

*Codium bursa, Bifurcaria bifurcata, Cystoseira spp., Padina pavonica, Halopteris filicina, Dictyopteris membranacea, Dictyota dichotoma*
many species - distributional gap along the French Atlantic coast south of the Loire to north Spain (e.g. *L. saccharina*, *F. seratus*, *A. nodosum*, *Ch. crispus*) substratum…

but on Basque coast: 22°C in August (as in Mediterranean and Morocco); too much for laminariacean cold temperate species

Basque coast: *Cystoseira tamariscifolia*, *Gelidium sesquipedale*, *C. officinalis*  
*F. spiralis*
northern Spain – many cold temperate species again (*L. hyperborea*, *L. saccharina*)
	northwestern Spain – upwelling area – cold water (in August max. 18-19°C)
	e.g., *L. hyperborea, L. saccharina, Fucus vesiculosus, F. spiralis, F. serratus, Ch. crispus*
	southern Portugal - 20°C s.i., 15°C w.i. - end of cold temperate kelps… (*Saccharina latissima* and *L. hyperborea* gametophytes cannot mature…)

about 20 tropical species reach northern limit here (e.g. *Valonia utricularis*)

Moroccan coast – southern limit of *F. vesiculosus, F. spiralis*
in upwellings – still Lusitanian species (*S. polyschides, B. bifurcata, L. ochroleuca*)

many tropical species have northern limit on Cape Blanc…
Canary province

80% of macroalgae here is common with Lusitanian and Mediterranean shores

some characteristic taxa are missing (B. bifurcata, S.polyschides) some are extremely rare (L. ochroleuca)

water temperature: 17-23°C, tropical elements are frequent - e.g. Valonia utricularis, Caulerpa spp., Galaxaura spp., Zonaria, Padina, Dictyota, Gelidium (endemic G. arbuscula, G. canariensis), Cystoseira abies-marina, Stypocaulon scoparium

Azores – more Lusitanian and less tropical species; amost none American taxa BUT: Asparagopsis armata!
Distribution of European kelp species I

- *Alaria esculenta*
- *Laminaria digitata*
- *Laminaria hyperborea*
- *Laminaria ochroleuca*
- *Laminaria rodriguezii*
- *Laminaria saccharina*
Distribution of European kelp species II

Phyllariopsis breviceps

Phyllariopsis purpurascens

Saccorhiza dermatodea

Saccorhiza polyschides

Undaria pinnatifida
Major kelp regions of the world
Mediterranean province in the Mesozoic – tropical Tethys Sea between Africe and Laurasia/Eurasia

Tertiary – open to both oceans
Miocene – tropical climate
early Miocene – Suezian strait closed

Messinian saline crisis – 5 to 6 mil years ago
Mediterranean transformed to a few hypersaline lakes, refugies for palaeomediterranean flora on the W shores
recent climate of the Mediterranean

- low tidal effects, but local tidal maxima exist (e.g., N Adriatic – ca 1 meter)
- salinity increases towards east (but the Black Sea is brackish)
- Seasonal temperature fluctuations are higher in N and E areas.
- Never freezes, but winter minima often limit distribution of taxa.
Mediterranean macroalgal flora 1: The (so called) tropical paleomediterranean element

Halimeda tuna, Udotea petiolata, Valonia utricularis, Anadyomene stellata, Acetabularia acetabulum, Amphiroa rigida, Wrangelia penicillata, Sargassum vulgare

most taxa from the Atlantic
very few Indo-Pacific taxa, because the connection was closed too early
Mediterranean macroalgal flora 2: The Lessepsian immigrants
migration slowed by hypersaline Bitter Lakes

*Caulerpa racemosa, Halophila stipulacea*

*C. racemosa* – in fact 3 microspecies (one of them from S Australia and highly invasive, two are non-invasive
Lessepsian immigrants

Mediterranean macroalgal flora 3: Messinian taxa – very few algae, if any

Mediterranean macroalgal flora 4: The cold water Atlantic element – glacial relicts
*F. virsoides, Plocamium cartilagineum, Desmarestia viridis, Laminariales*
Mediterranean macroalgal flora 5: Endemic taxa
(paleoendemites, neoendemites – after closing of the Suez strait in early Miocene)

paleoendemite red algal species – *Rissoella verruculosa* (W Mediterranean)

neoendemites – *Cystoseira* (2/3 taxa are Mediterranean endemites),
(in the Atlantic – up to S England)
*Phyllophora nervosa*

*C. amentacea*  
*C. compressa*  
*C. barbata*

Adriatic cystoseires
Mediterranean macroalgal flora 6: Introduced seaweeds

Asparagopsis armata from Australia, first in 1923 in Algeria, 1925 in Biarritz, 1973 up to Shetland

Bonnemaisonia hamifera from Japan, since early 20th centur in Europe, recently – from Canarias to Orkney, W Mediterranean from Connecticut to Newfoundland

Colpomenia peregrina from Japan, now temperate N/S hemispheres, by exchange of oyster cultures, „oyster thief“, ...
Structure [and invasion] of *Colpomenia sinuosa*

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

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.
Codium fragile from Japan, now warm temperate zones of both hemispheres, in Europe since early 20th century, first in the Netherlands.

Sargassum muticum from Japan, to America in 1940 (oyster aquaculturists), in 1973 oysters from British Columbia to France, now – the Atlantic European coast up to Skagerrak i.e., the northern most Sargassum…

Caulerpa taxifolia from Indian ocean, in 1984 – aquarium in Monaco, the grazer-resistant population from Stuttgart ZOO; nowadays: most of the Mediterranean.
Invasion biology of *Caulerpa taxifolia* in the Mediterranean


additional recent invasion of *C. taxifolia* var. *distichophylla*

from SW Australia;

probable hybridization with the "original *C. taxifolia* invader"

Undaria pinnatifida

Laminaria (Saccharina) japonica

both from Japan, through oyster aquaculturists

Caulerpa racemosa var. cylindracea (= Caulerpa cylindracea)

Fig. 3. First sighting of *Caulerpa racemosa* in Libya in 1991 (● + arrowhead) and subsequently observed colonies (●) in the Mediterranean Sea and the Canary Islands (from Verlaque et al., 2004; Piauzzi et al., 2005a, amended).

Verlaque & Klein, 2008, 
Joint and differential dynamics of invasions in C. taxifolia and C. cylindracea

- C. taxifolia populations virtually died off at many places since 2008
- similar decline was observed also in Croatian C. taxifolia populations
- hypotheses: large annual variation in temperature, parasites, predators
- native C. prolifera also fluctuated greatly in abundance in 20th century

"A realistic perspective on the kinetics of the spreading of C. taxifolia indicates that the risk posed by this alga to major endemic species is much lower than was formerly predicted. Today this alga still persists in highly urbanized and disturbed areas, as for instance close to large touristic marinas or sewage systems, or in correspondence of Posidonia oceanica dead matte areas, which represent ideal substrata for its spread."

Montefalcone et al., 2015, Biol. Invas. 17
Halimeda incrassata invasion in W Mediterranean

2005 – first records from Madeira (Porto Santo Island), 30 m depth
2013 – first records from Mallorca

Wirtz & Kaufmann, 2005, Aquar. 431.
The Laminariales in the Mediterranean

e.g., strait of Messina – *S. polyschides* in the upper sublittoral
the lower sublittoral (isothermic submergence)

*Laminaria rodriguezii* – Mediterranean endemite, in 50-120 meters, Algeria to Adriatic
otherwise: *L. ochroleuca, Phyllariopsis brevipes, Saccorhiza polyschides*
The lower sublittoral algae in the Mediterranean

*Codium coralloides, Dasycladus vermicularis, Caulerpa prolifera, Zanardinia prototypus*

**coralligene** – blocs of biogennic material on soft bottom, bivalves, cnidarians, red algae
*Mesophyllum lichenoides, Pseudolithophyllum expansum, coral - Corallium rubrum*
Seaweeds on sand in the Mediterranean – *C. prolifera*, *C. racemosa*, *Cymodocea nodosa* (+ *Cl. prolifera*, *Penicillus capitatus*)
Black Sea – brackish appendix of the Mediterranean; it was freshwater before 18 000 years large temperature fluctuations (-1 ro 29°C).

*Phyllophora* meadows – *P. nervosa, P. truncata* (relict arctic cold-temperate species)
90% of algal biomass is formed by these two taxa, they primarily reproduce asexually loose lying or on shells, Sernow`s Phyllophora Sea – 5 mil. t, 15 tis. km sq., the single largest red-algal ecosystem in the world

**Zostera noltii, Z. marina, C. barbata**

**Aral Sea/Lake, Caspian Sea** – remnants of the Paratethys Sea

*Zostera noltii*, Mediterranean species endemites – *Monosiphon caspicum, Polysiphonia caspica, Laurencia caspica, Titanoderma caspicum*

brackish species