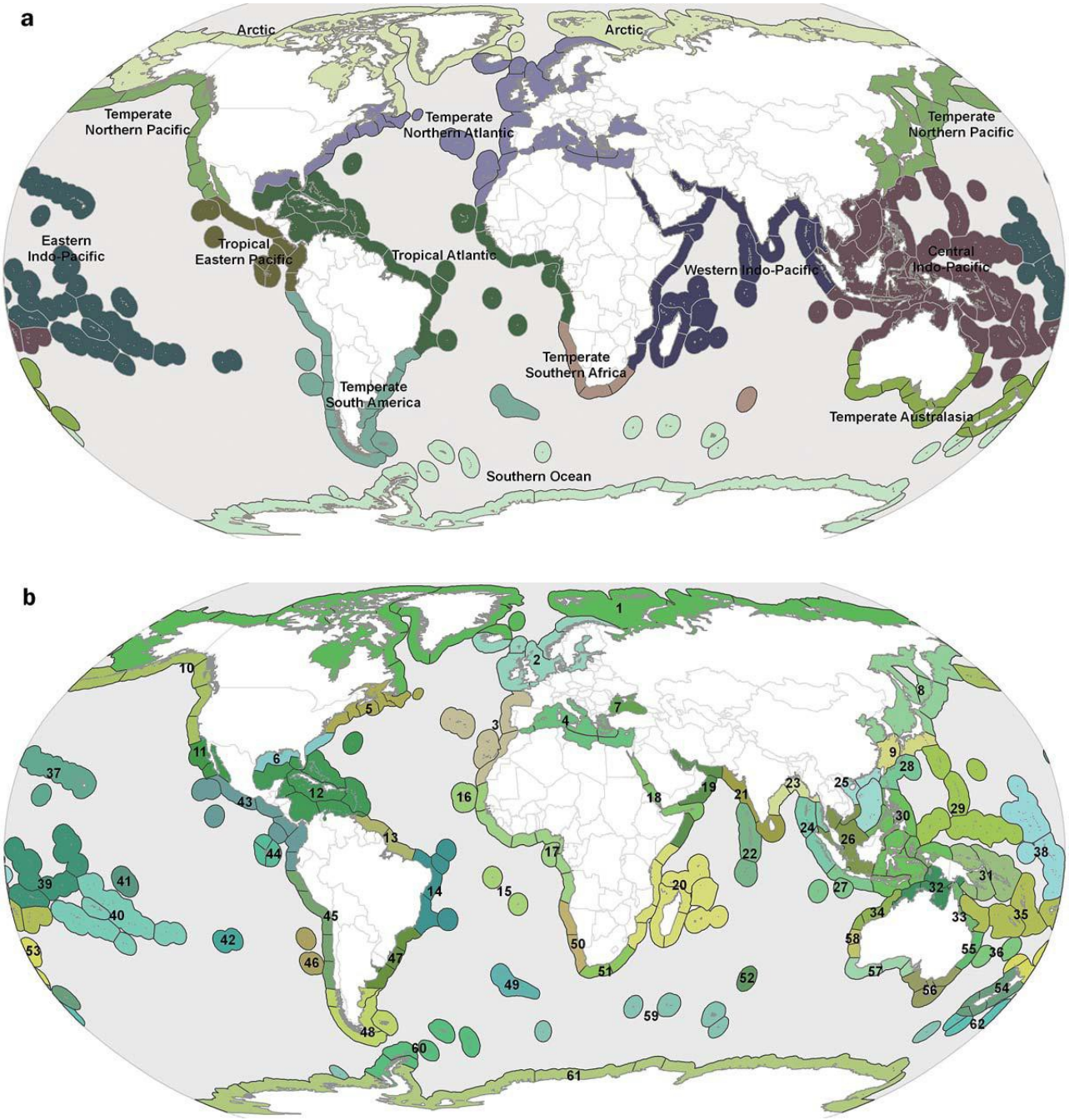
Cold temperate regions
of
the northern hemisphere



- European coasts – cold and warm temperate regions

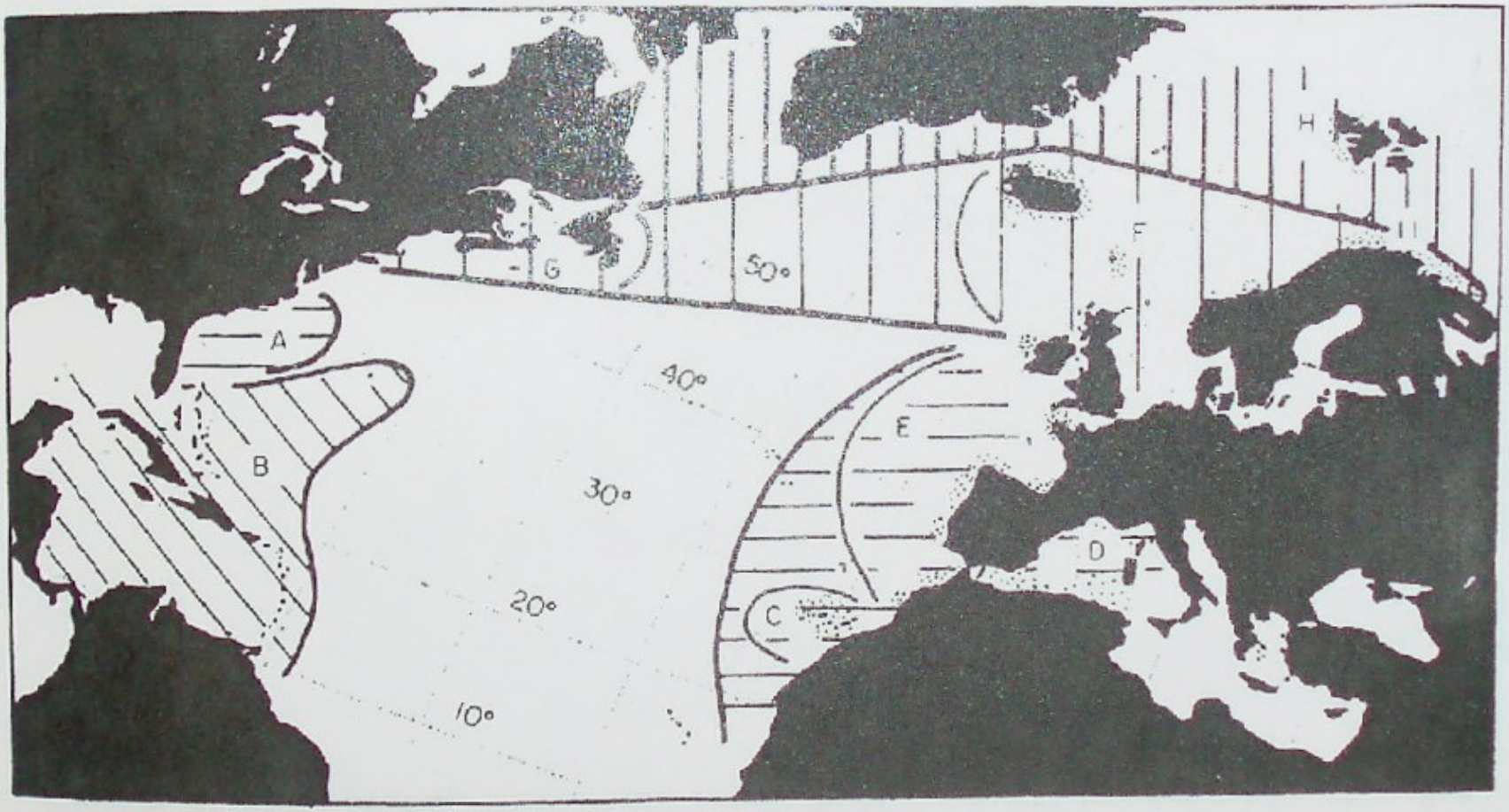
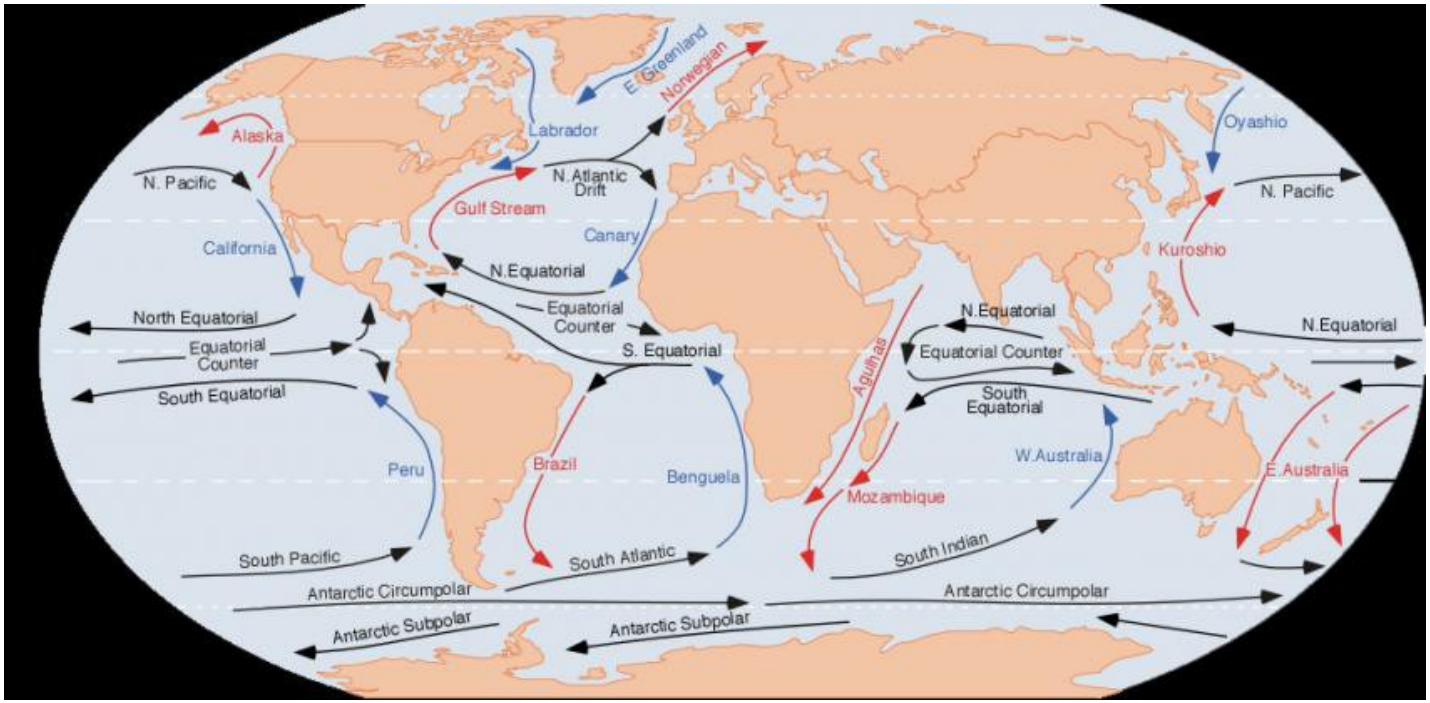
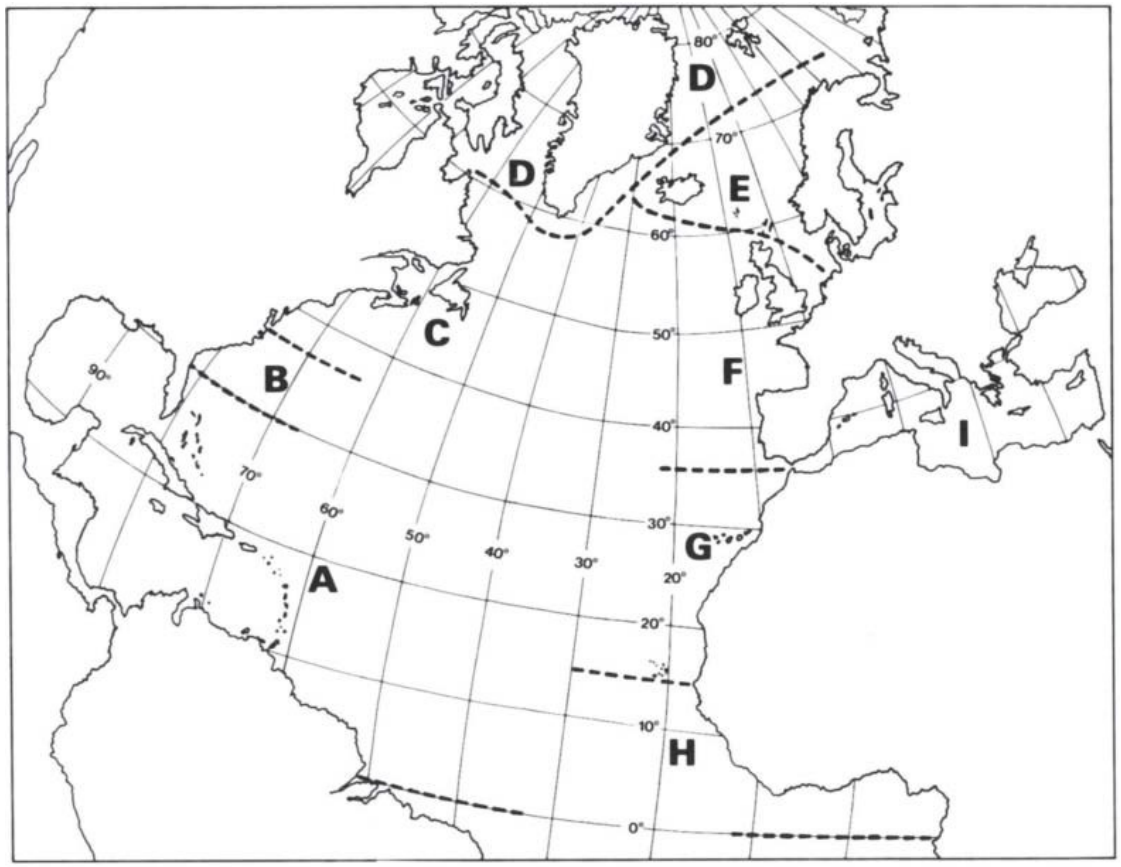


Fig. 2.45 Phytogeographical regions and provinces in the North Atlantic. A = warm temperate Carolina region; B = western Atlantic tropical region; C,D,E = warm temperate Mediterranean–Atlantic region (C = Canary province; D = Mediterranean province, E = Lusitania province); F,G = cold temperate North Atlantic region (F = eastern province; G = western province), H = Arctic region. (From van den Hoek 1975.)


E. Greenland
Norwegian
Labrador
Alaska
N. Pacific
N. Atlantic Drift
Gulf Stream
Canary
California
N.Equatorial
North Equatorial
Equatorial Counter
South Equatorial
S. Equatorial
Peru
Brazil
Benguela
South Pacific
South Atlantic
Antarctic Circumpolar
Antarctic Subpolar
Aguilhas
Mozambique
South Indian
Oyashio
N. Pacific
Kuroshio
N.Equatorial
Equatorial Counter
South Equatorial
W.Australia
E.Australia
Antarctic Circumpolar
Antarctic Subpolar

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



Alvarez et al., 1988, Phycologia

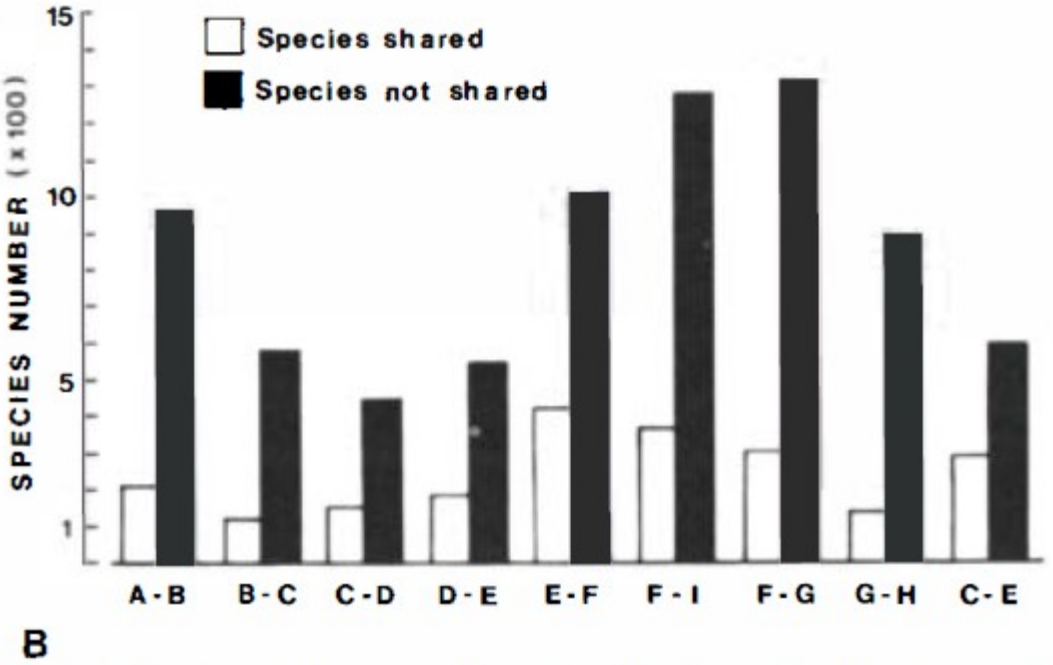


Fig. 6. A. Dendrogram showing floristic similarities of biogeographic regions along the North Atlantic Ocean and the Mediterranean Sea. B. Histograms depicting number of species shared and not shared by adjacent biogeographic regions along the North Atlantic Ocean and the Mediterranean Sea. The comparison between cold temperate Eastern and Western regions is also provided (C–E). Bold letters indicate regions shown in Table 3.

Alvarez et al., 1988, Phycologia

Table 2. Seaweed species numbers for each geographic area of the North Atlantic Ocean and major taxonomic groups

	Area	Chlorophyta	Phaeophyta	Rhodophyta	Whole flora
1	Tropical America	203	115	425	743
2	Warm USA	68	70	189	327
3	Temperate USA	83	114	124	321
4	Cold temperate Canada	82	115	119	316
5	Arctic Canada	55	65	57	177
6	Spitzbergen Is.	13	32	28	73
7	Greenland	45	73	63	181
8	Iceland	46	77	76	199
9	Färoes Is.	39	77	90	200
10	Shetland Is.	51	86	128	265
11	Arctic Norway	42	85	81	208
12	Southern Norway	68	135	161	364
13	Denmark	74	125	150	349
14	Ireland	80	142	243	465
15	United Kingdom	94	184	289	567
16	Atlantic France	137	191	335	663
17	Atlantic Iberia	104	139	328	571
18	Temperate Africa + Canary Is.	146	127	409	682
19	Tropical Africa	69	56	214	339
20	Mediterranean Spain + Balearic Is.	117	116	365	598
21	Mediterranean France	95	109	331	535
22	Corsica	69	89	277	436
23	South-western Italy	101	129	408	638
24	Adriatic Sea	98	119	306	523
25	Greece	96	89	296	481

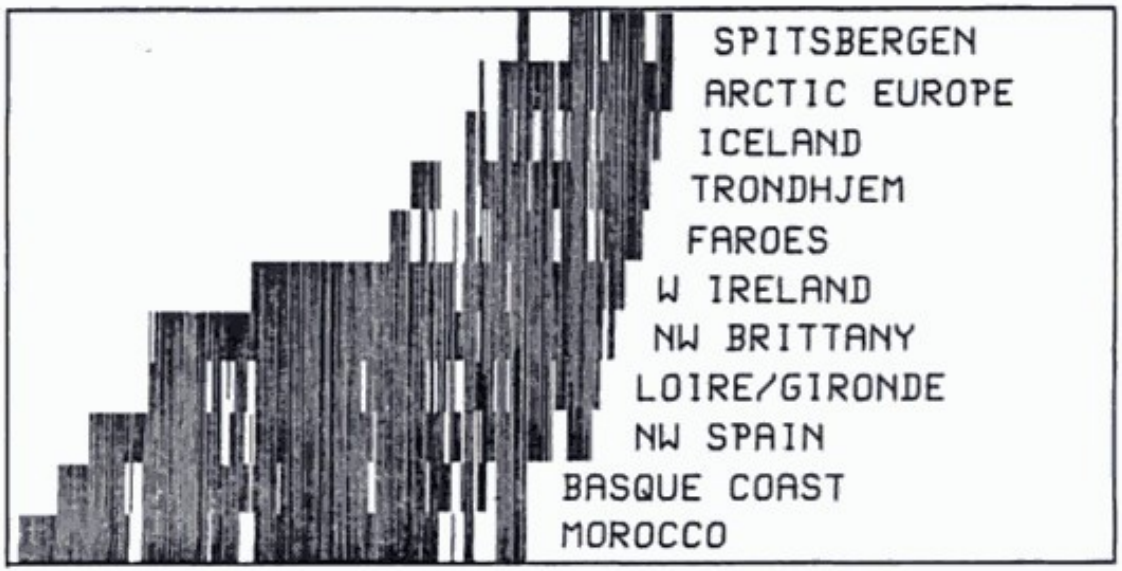
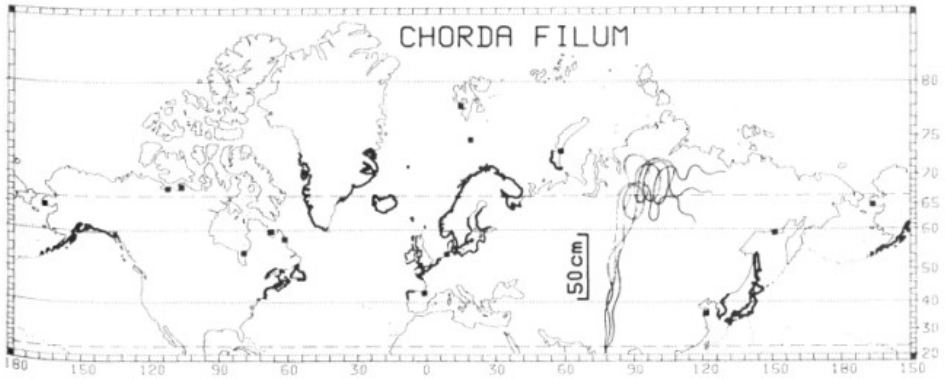
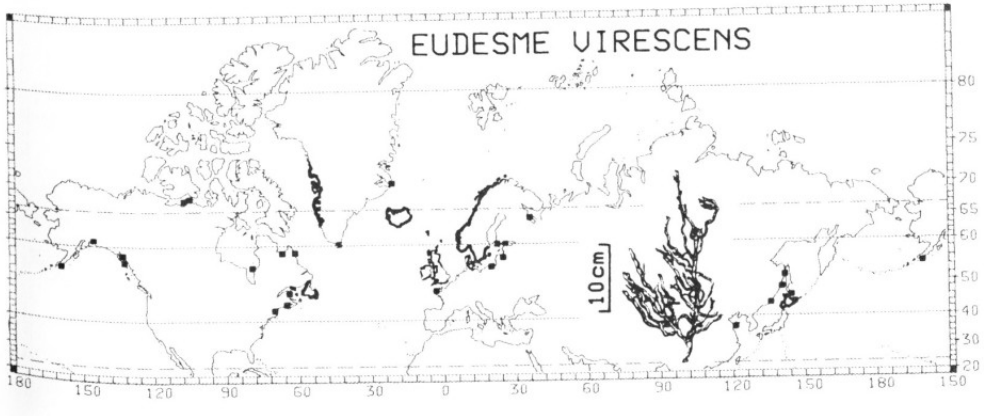
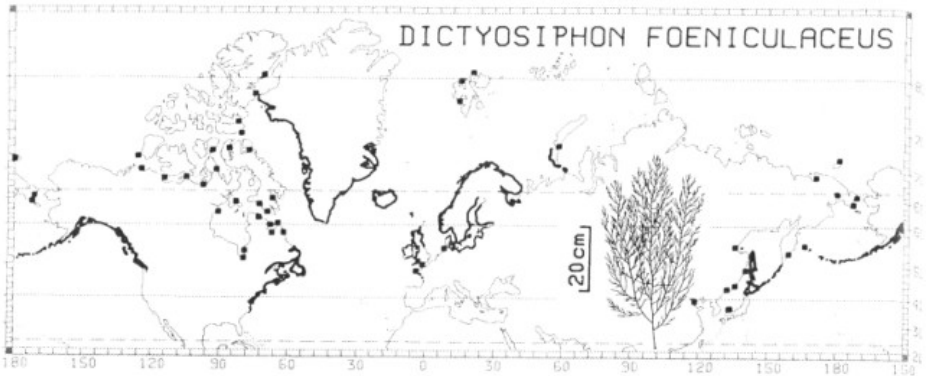
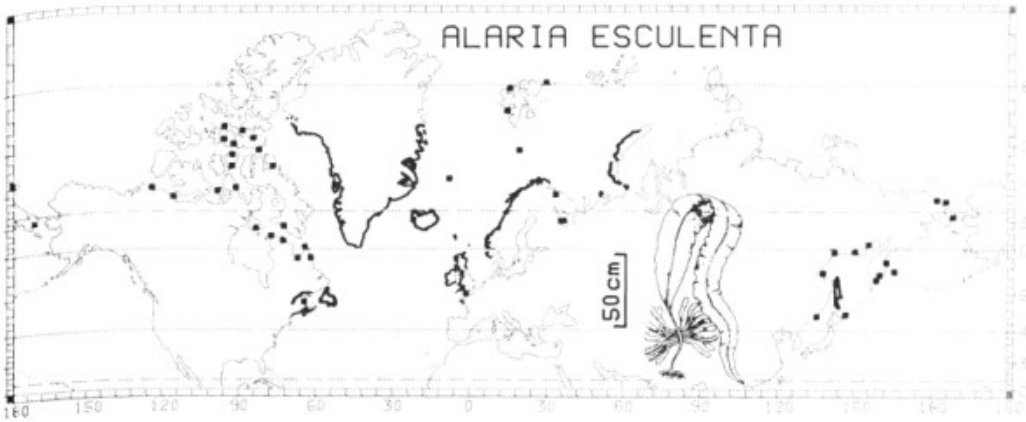


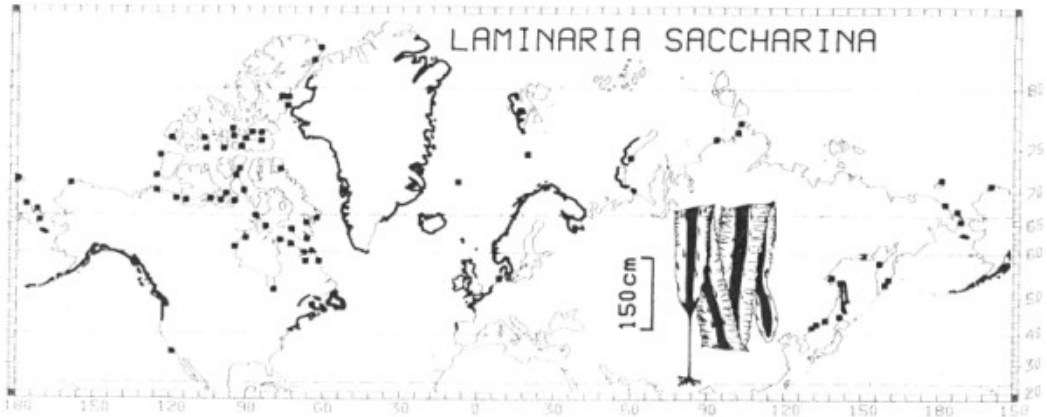
Fig. 2.44 Latitudinal distribution of seaweed species along the coasts from Morocco to Spitsbergen. Each vertical line represents the distribution span of one species. (After van den Hoek 1975.)

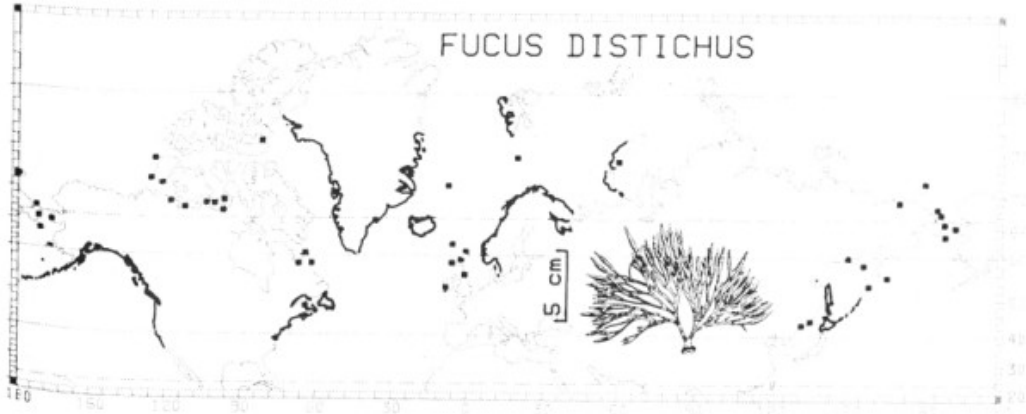

CHORDA FILUM
50cm

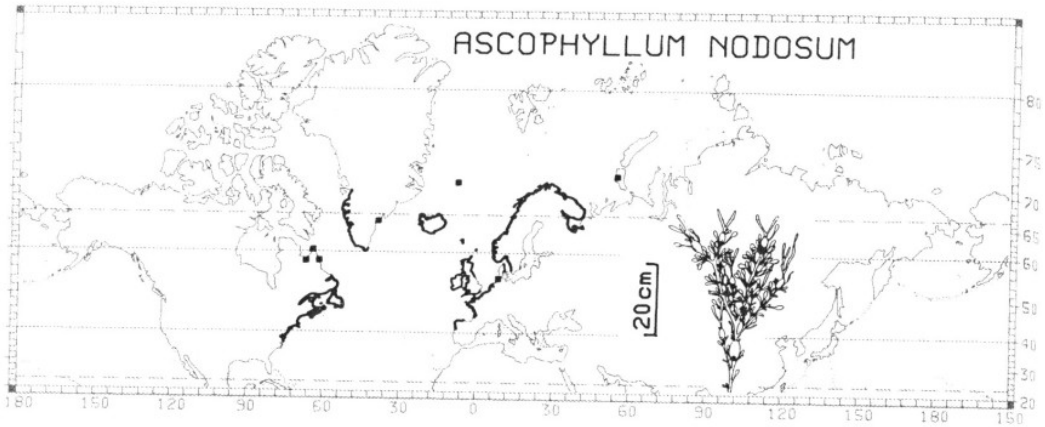

EUDESME VIRESCENS
10cm

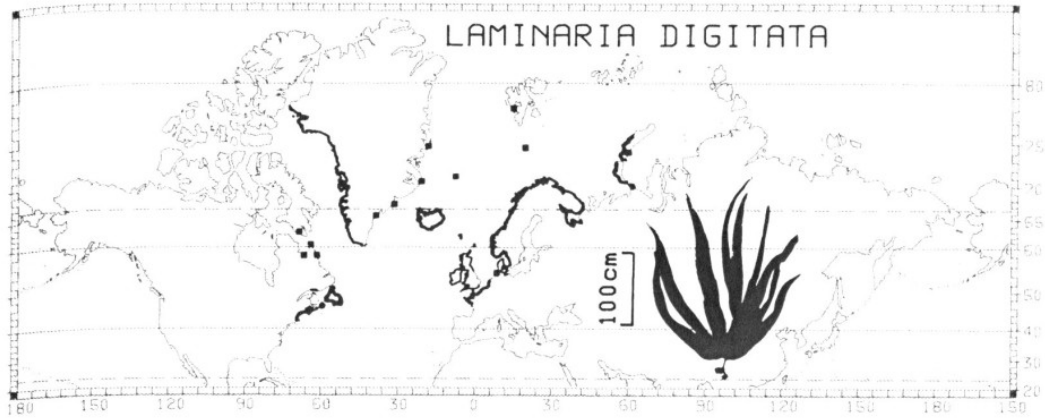

DICTYOSIPHON FOENICULACEUS
20cm

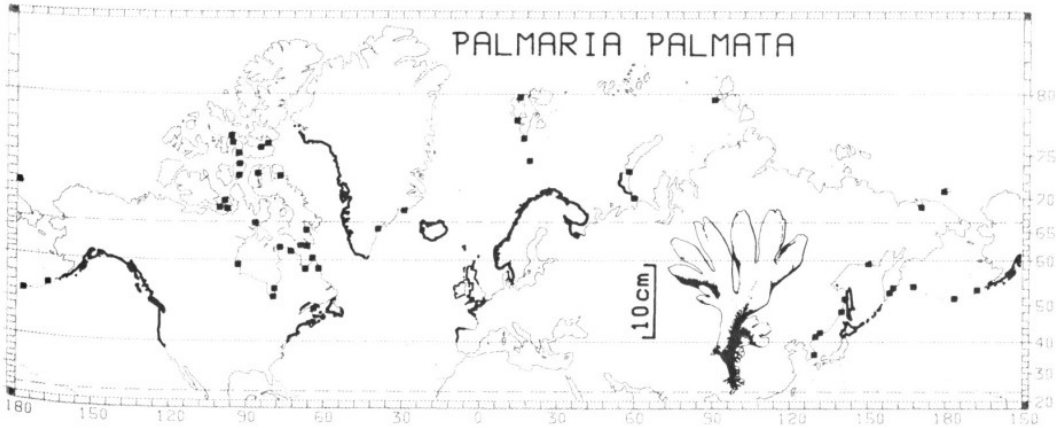

ALARIA ESCULENTA
50cm

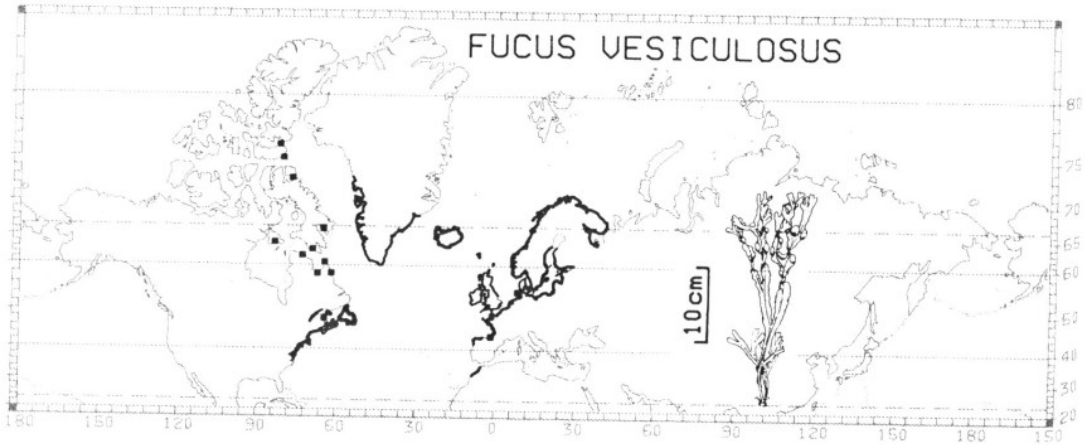

LAMINARIA SACCHARINA
150cm

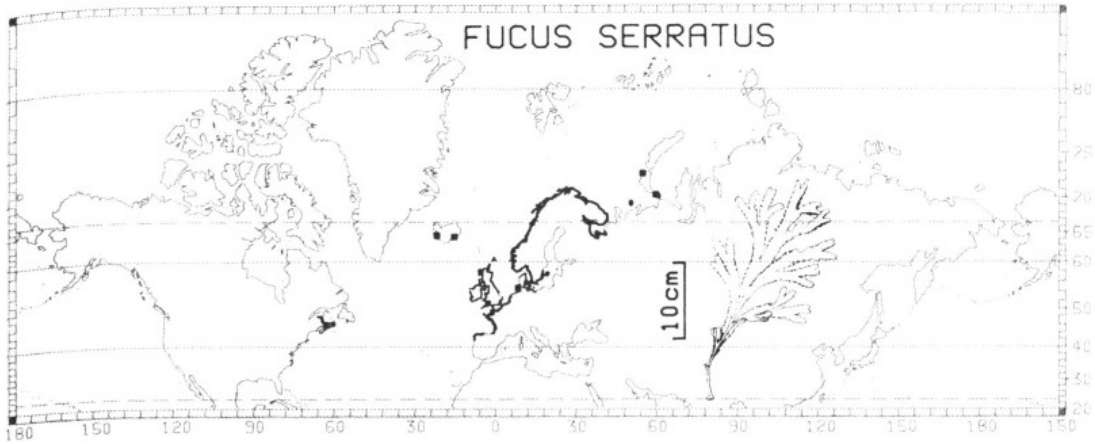

FUCUS DISTICHUS
5 cm

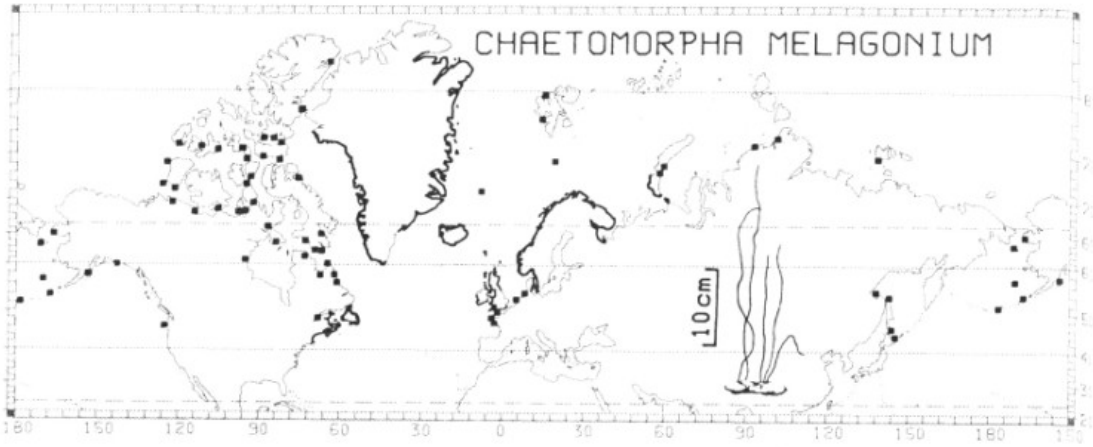

ASCOPHYLLUM NODOSUM
20cm

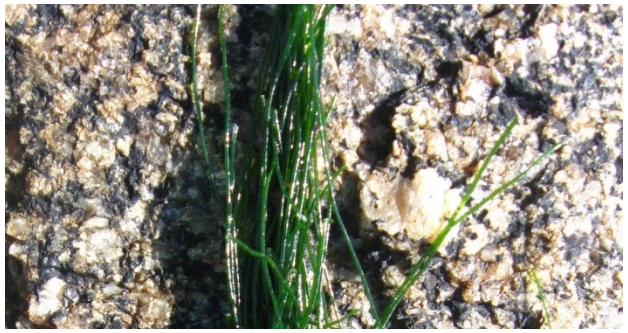

LAMINARIA DIGITATA
100cm

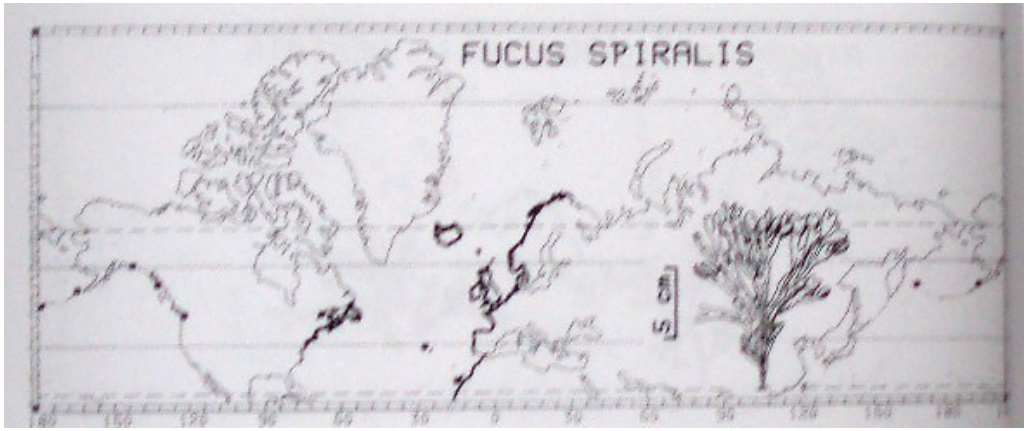

PALMARIA PALMATA
10cm

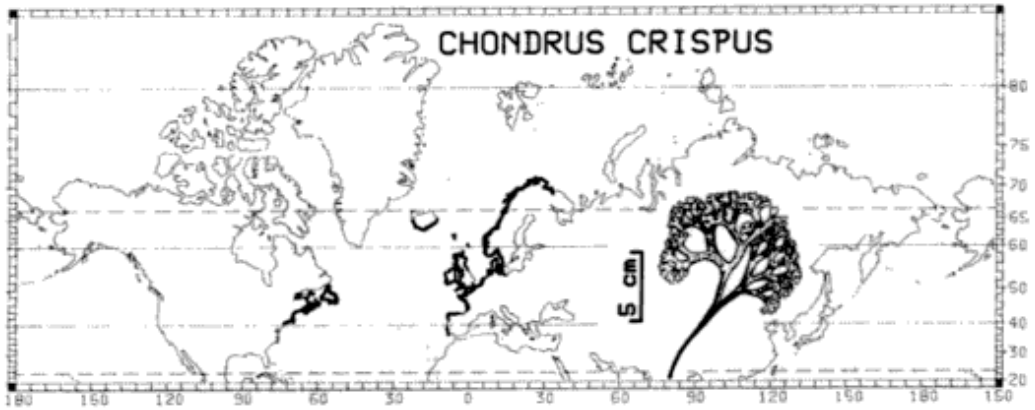

FUCUS VESICULOSUS
10cm

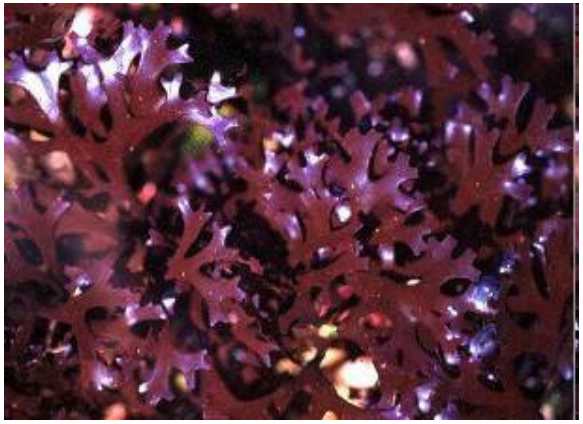

FUCUS SERRATUS
10cm


CHAETOMORPHA MELAGONIUM
10cm




FUCUS SPIRALIS
5 cm


CHONDRUS CRISPUS
5 cm



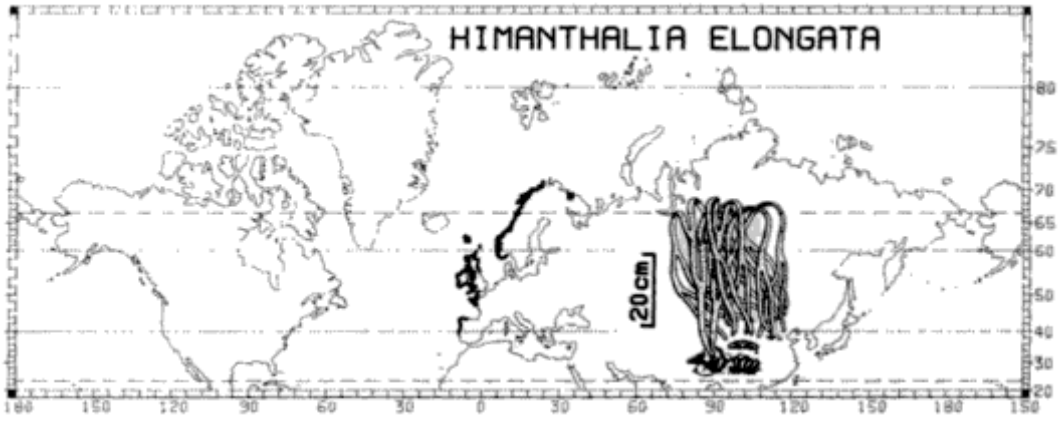

HIMANTHALIA ELONGATA
20cm

Fig. 3. Typical understorey algae at different depths in the sublittoral zone off Helgoland (from Lüning, 1970; 1990).

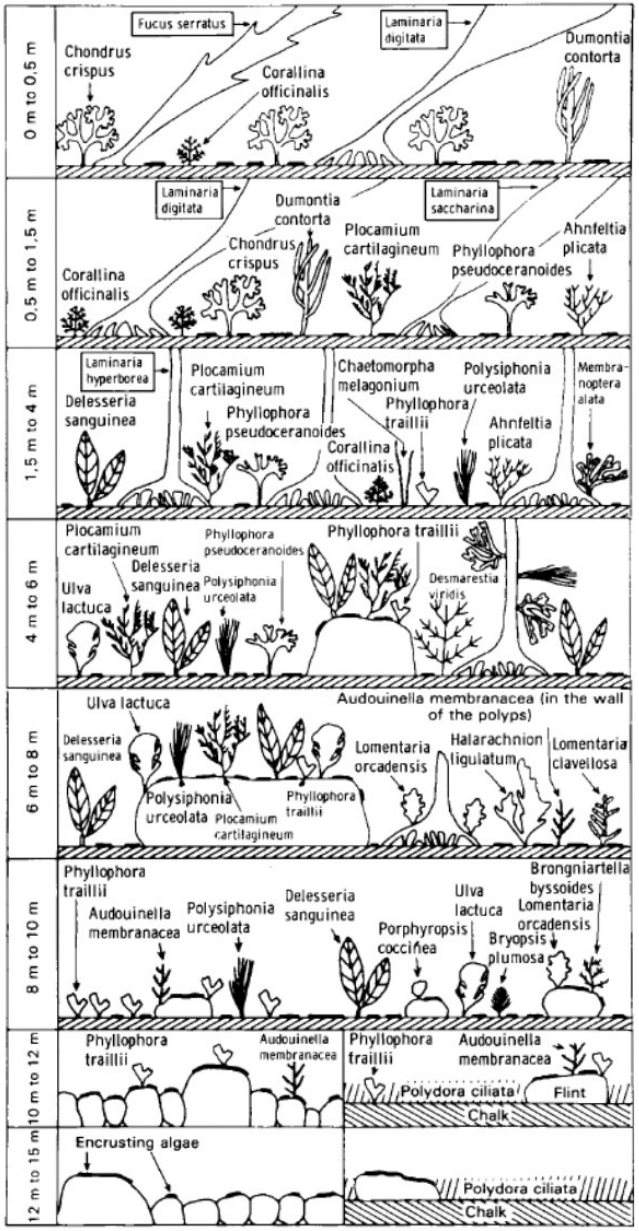
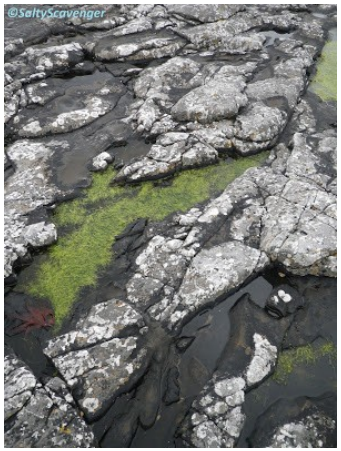
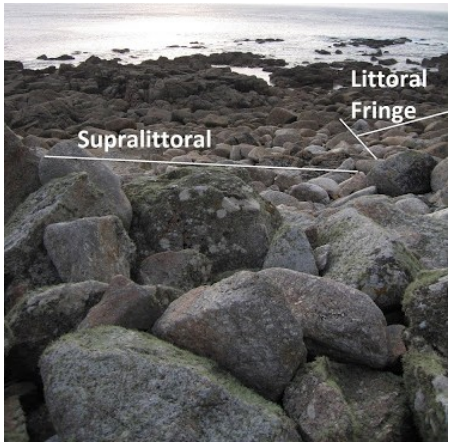


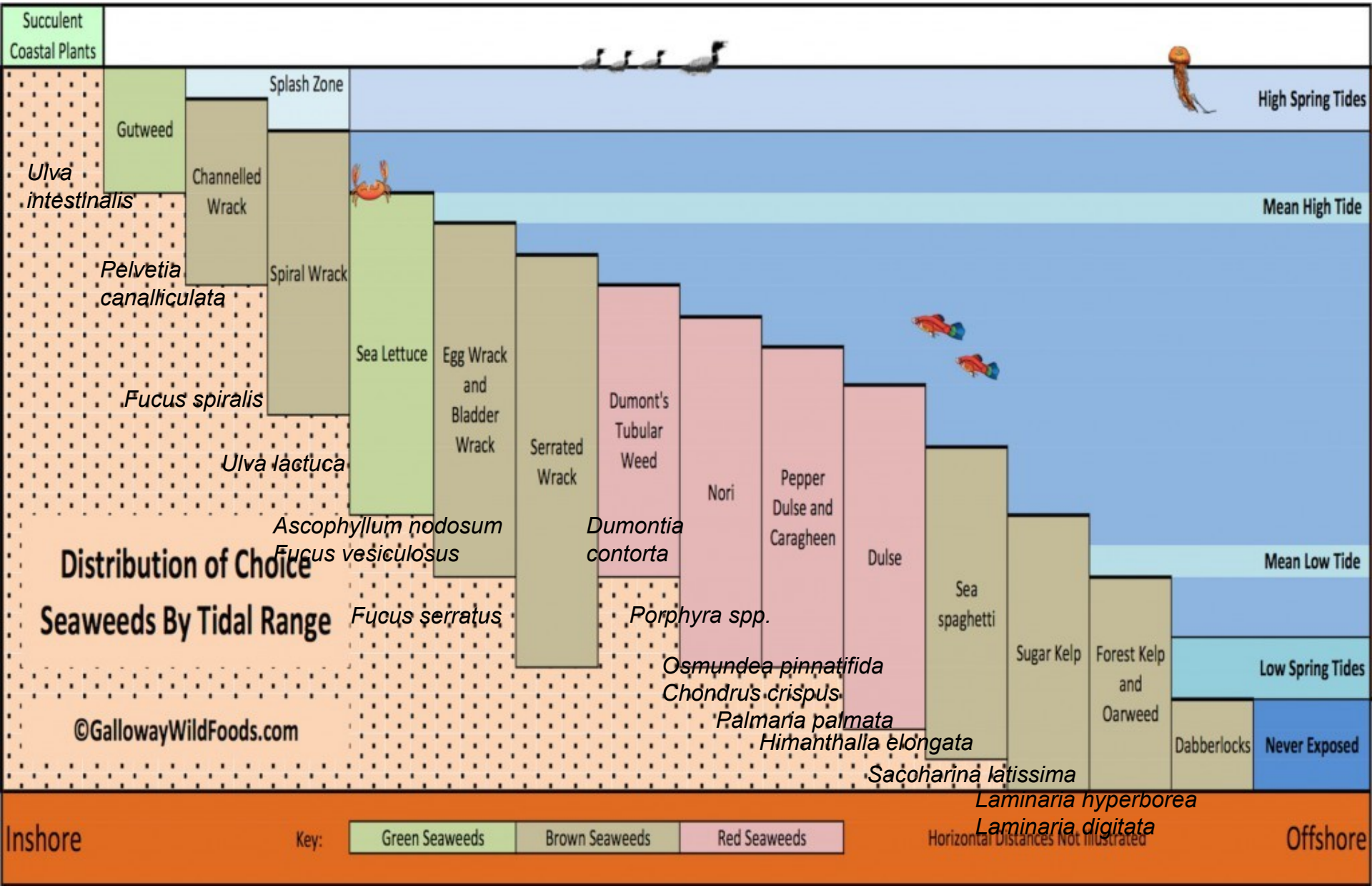
Fig. 2.49 Zonation off Helgoland. Typical understory algae at different depths in the sublittoral zone. (From Lüning 1970.)



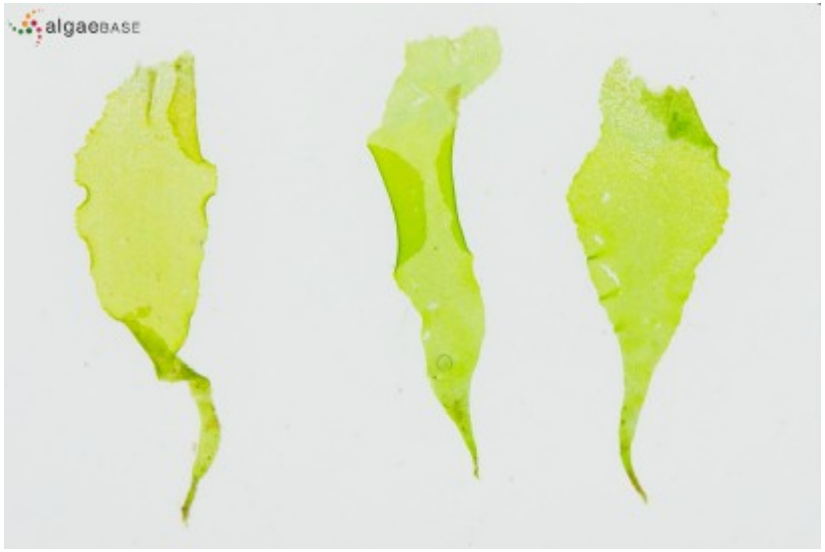


Birkett et al., 1998, Infralit Reef Biot Kelp Sc, 7

Intertidal of NW Europe



- North Atlantic supralittoral (spray zone) – characteristic genera *Prasiola* + *Rosenvingiella*



- *Prasiola stipitata*

- vertical zonation - Galicia

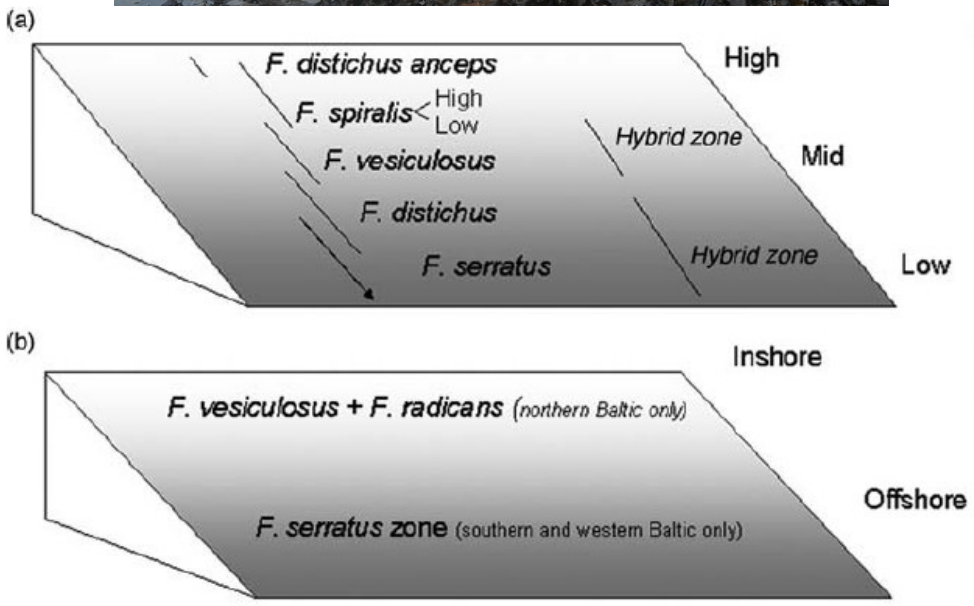
other genera – Ulva (tubular), Blidingia

Pelvetia
canaliculata
(channelled wrack)

Dumontia contorta

Osmundea pinnatifida

Fucus belt in the NW Atlantic lies in the intertidal



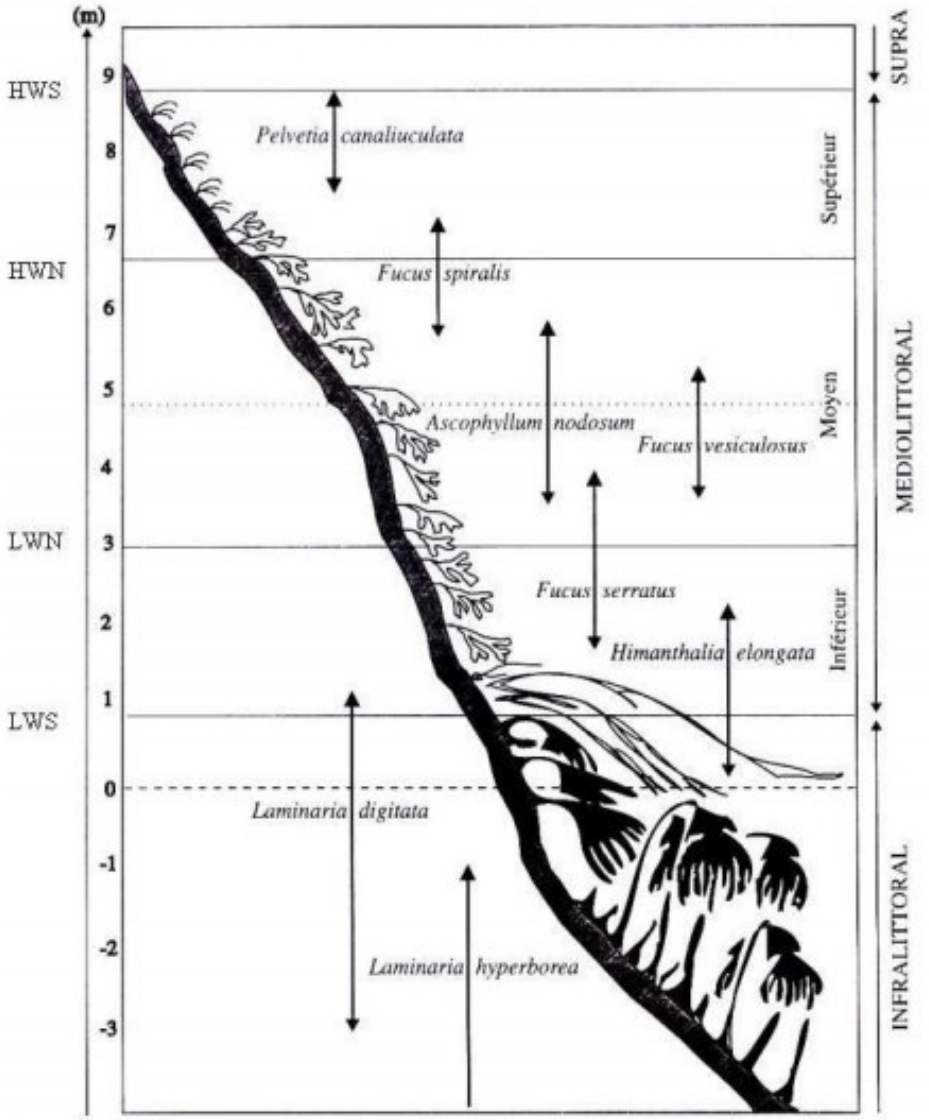
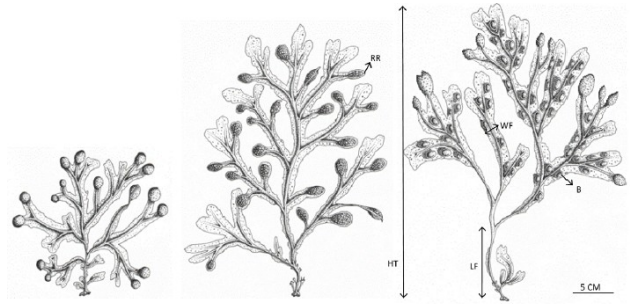


Figure 2.1 Zonation patterns characteristic of *Fucus* species along (a) intertidal and (b) atidal shores of the Baltic Sea.

De Oliveira et al., 2006, EARSeL eProceedings



F. spiralis *F. spiralis* var. *platycarpus* *F. vesiculosus*

Figure 2. Drawings of morphotypes and illustration of morphological traits. Drawings of the three morphotypes. Added in the last drawing, illustration of measurements used to characterize morphotypes. Illustration of measurements used for the receptacles in the insert at the top. All traits are listed by abbreviation (see text for full explanation).
doi:10.1371/journal.pone.0019402.g002

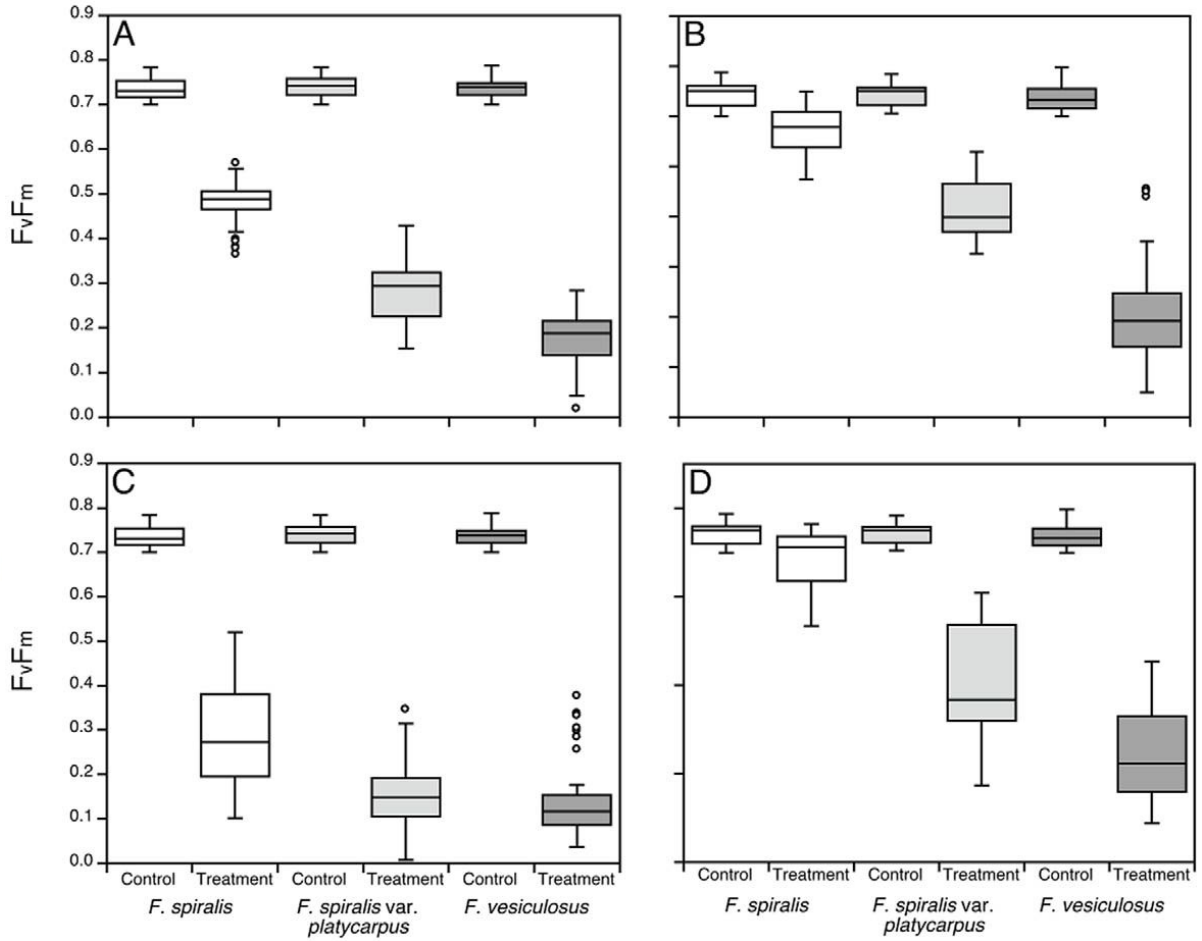


Figure 5. Physiological resilience to air exposure. Measurements of photoinhibition of PSII maximum quantum yield of *F. spiralis*, *F. spiralis* var. *platycarpus* and *F. vesiculosus* (zones pooled) after recovery from the following treatments: (A) and (B) morphotypes air exposed at 33°C (±0.5°C) at a PPFD of 250–300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (HL) after 1 and 6 hours of recovery respectively; (C) and (D) morphotypes air exposed at 37°C (±0.5°C) in HL after 1 and 6 hours of recovery respectively.
doi:10.1371/journal.pone.0019402.g005

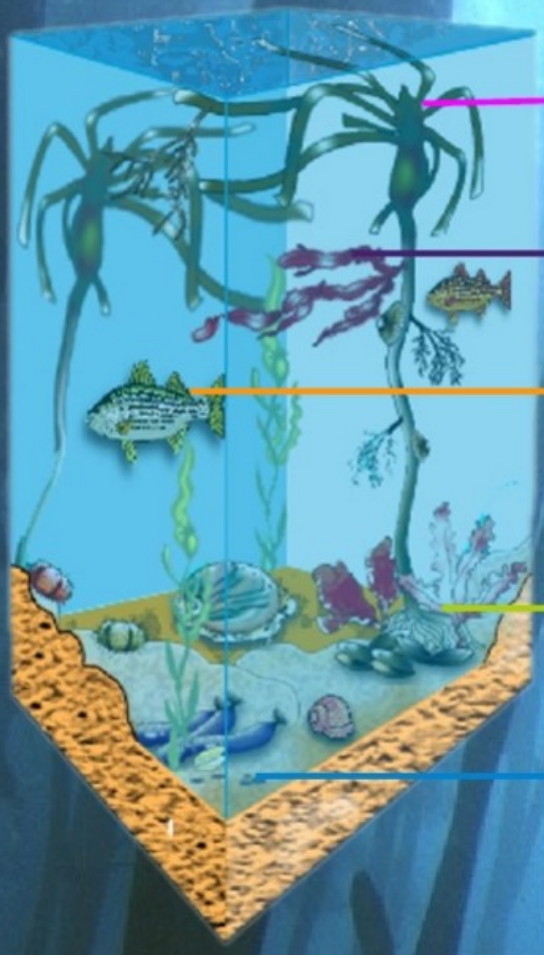
underlying physiological data at the level of individual species illustrate the vertical structure of the intertidal *Fucus* belt

Zardi et al., 2011, Plos One

Kelp vegetation ("kelp forests")
i.e. cold temperate sublittoral vegetation

Kelp forest

Structure



Canopy

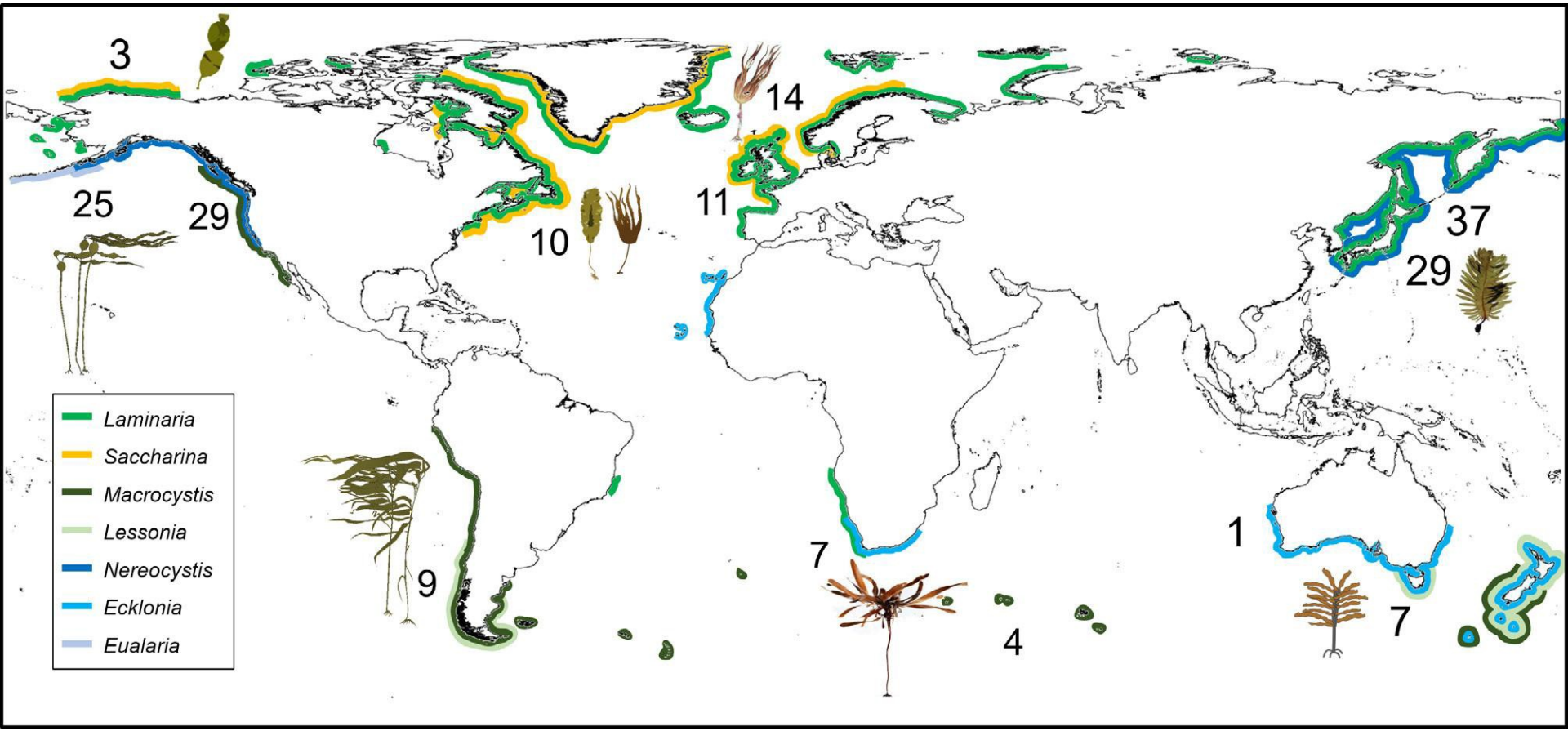
Epiphytes

Water column

Understory

Encrusting

Layers



Wernberg et al., 2019, World Seas

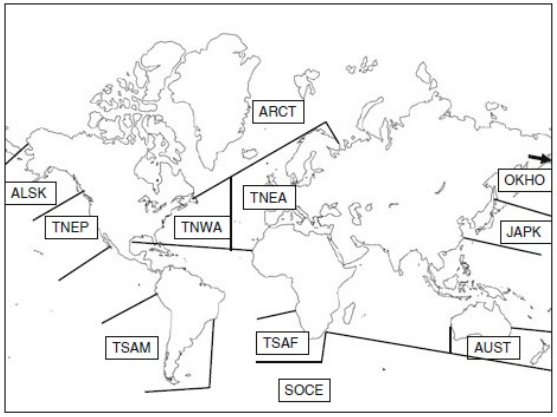


Fig. 1 The 11 world regions used for the biogeographical analysis (adapted from the system of Spalding et al. 2007, see text) (*TNEP* temperate Northeast Pacific, *ALSK* Alaska, *ARCT* Arctic, *TNWA* temperate Northwest Atlantic, *TNEA* temperate Northeast Atlantic, *OKHO* Okhotsk Sea, *JAPK* Japan, Korea, *TSAM* temperate South America, *SOCE* Southern Oceans, *TSAF* temperate South Africa, *AUST* Australasia)

major differences between N and S hemispheres in kelp community structure

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

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

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)

	OKHO	JAPK	ALSK	TNEP	ARCT	TNWA	TNEA	TSAM	SOCE	TSAF	AUST
Alaria (15)	6	5	3	1	5	1	1	0	0	0	0
Laminaria (22)	6	2	4	6	4	4	6	1	1	1	0
Saccharina (20)	6	10	5	5	3	3	2	0	0	0	0
Ecklonia (7)	0	3	0	0	0	0	1	0	0	2	3
Eisenia (6)	0	1	0	2	0	0	0	3	0	0	0
Lessonia (9)	0	0	0	0	0	0	0	4	5	0	3

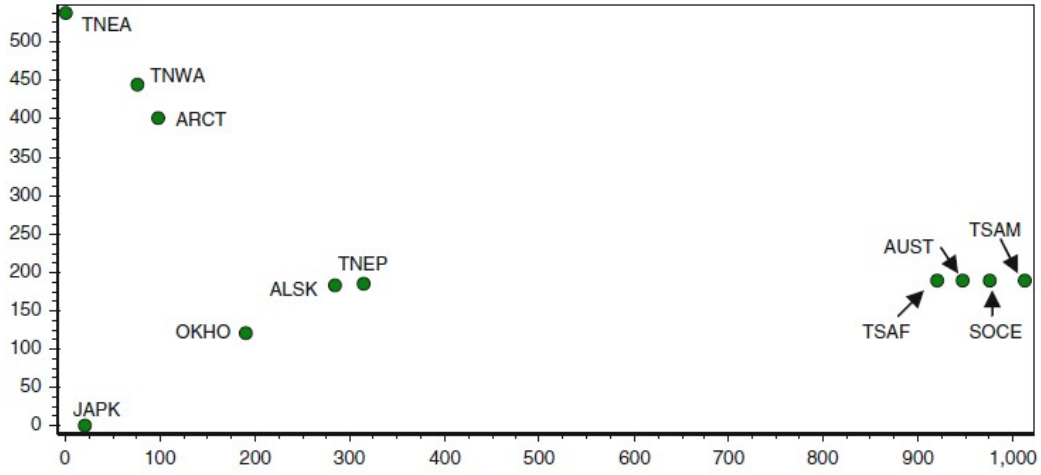
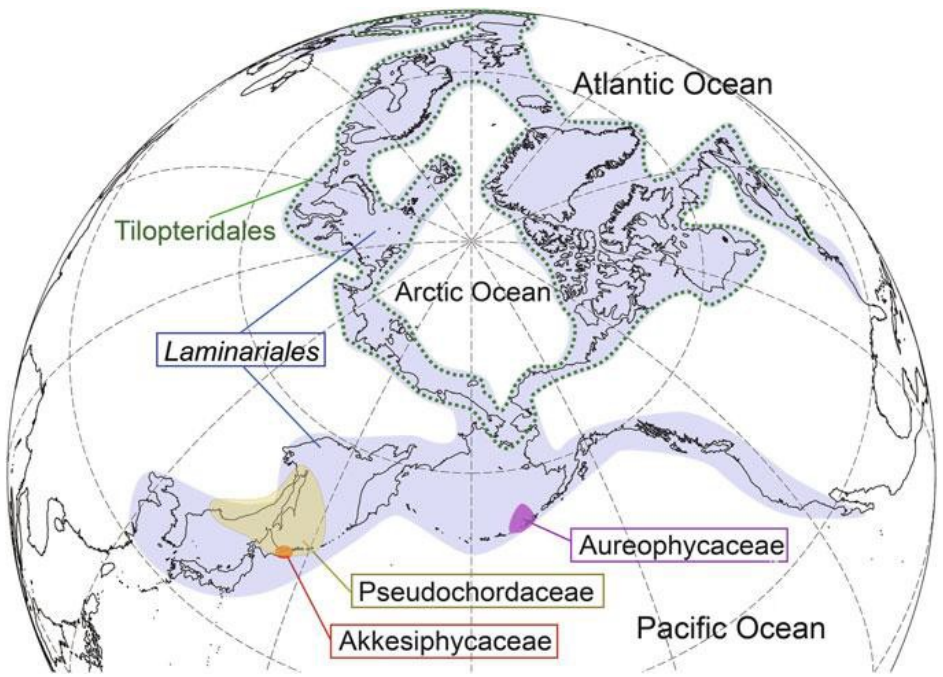
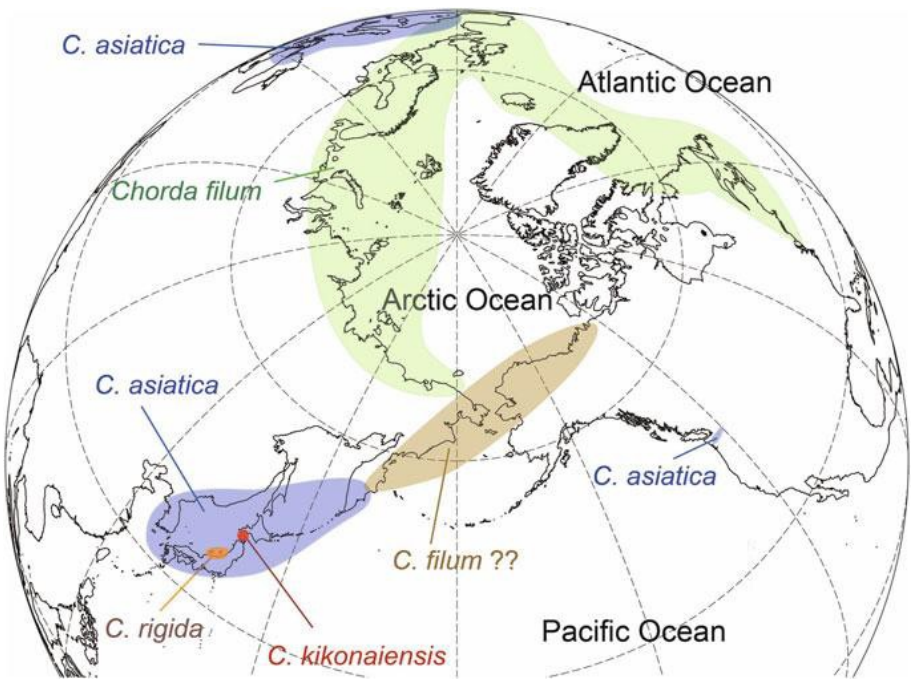
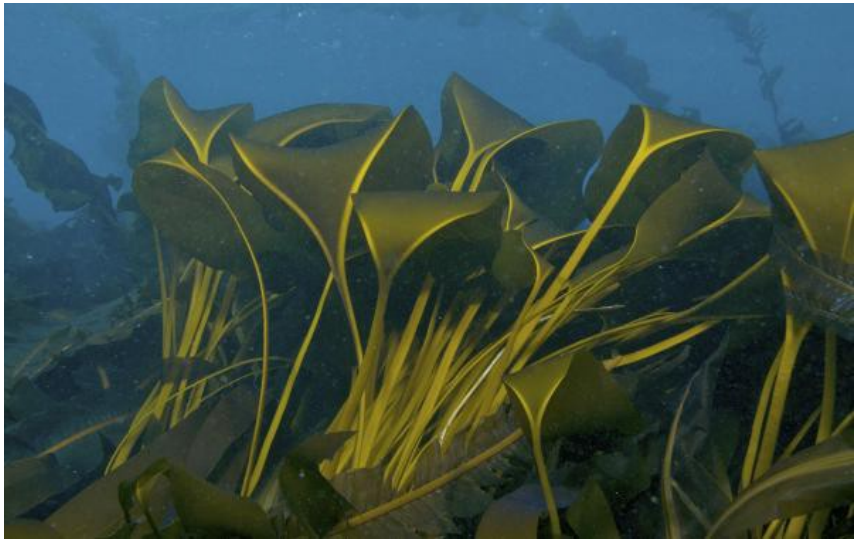


Fig. 4 DECORANA analysis of 11 world temperate marine regions, based on the kelp species that occur in them (Eigenvalues: Axis 1, 0.9414; Axis 2, 0.6482). Region codes as in Fig. 1

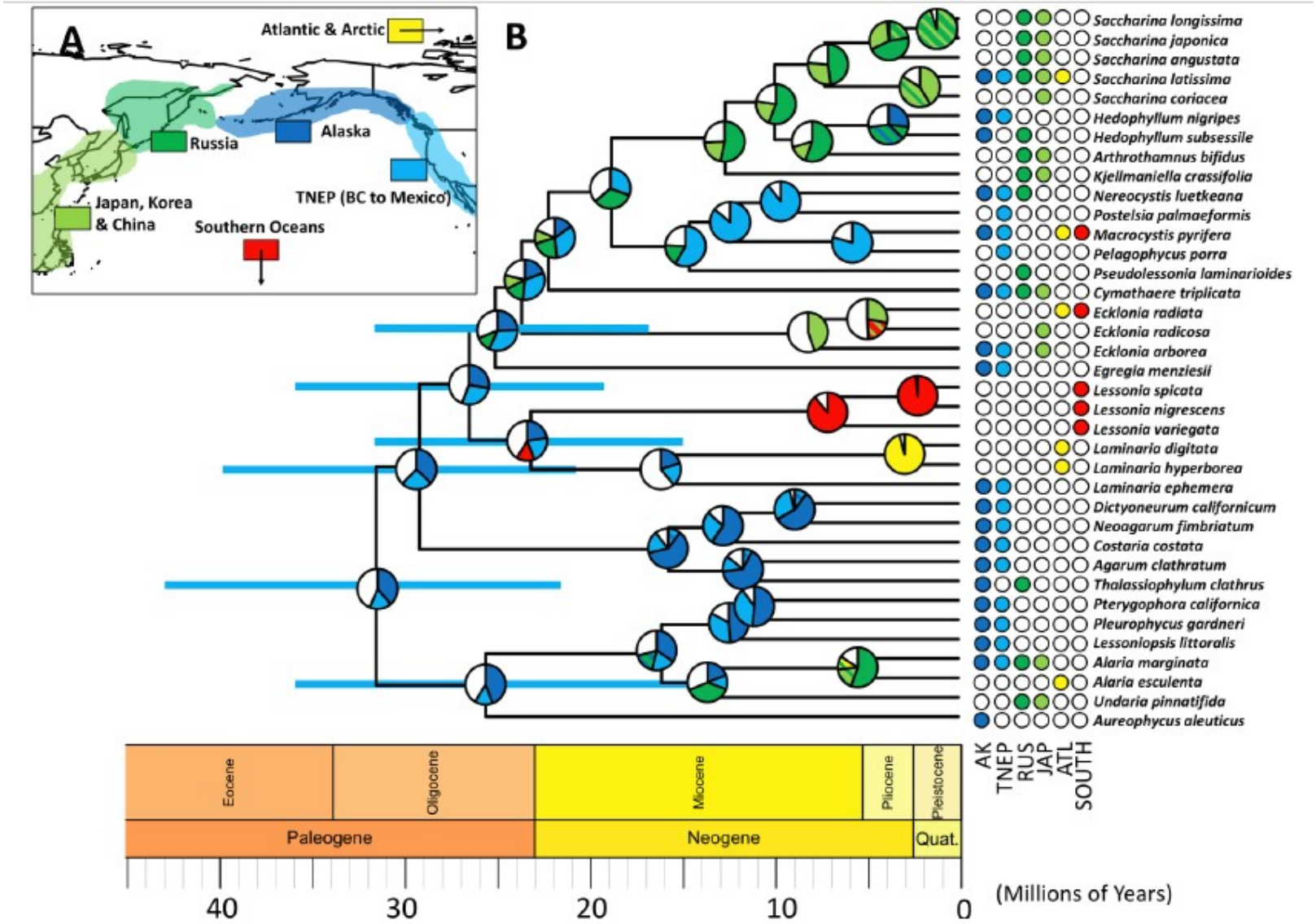
Bolton, 2010, Helgol. Mar. Res. 64: 263-279.







Kawai et al., 2016, In: Seaweed Phylogeography



evolutionary origin of kelps in N Pacific
secondary colonization of Arctic and N Atlantic
probably three independent transitions to S hemisphere

Starko et al., 2019, Mol Phyl Evol

European kelp species

The dominant seaweed species along the European coastline are brown algae mainly belonging to the Laminariales (kelp) and Tilopteridales (kelp-like) which are distributed from the lower intertidal down to, approximately 30 m in the subtidal zone, depending on the clarity of the water.

In Europe, these orders include the native species:

Alaria esculenta (Linnaeus) Greville
Chorda filum (Linnaeus) Stackhouse
Laminaria digitata (Hudson) J.V. Lamouroux
L. hyperborea (Gunnerus) Foslie
L. ochroleuca Bachelot de la Pylaie
L. rodriguezii Bornet
L. solidungula J. Agardh
Saccharina latissima (Linnaeus) C.E. Lane, C. Mayes, Druehl and G.W. Saunders
non-native species: *Undaria pinnatifida* (Harvey) Suringar.

"pseudokelps" (Tilopteridales)
Phyllariopsis brevipes (C. Agardh) E.C. Henry and G.R. South
P. purpurascens (C. Agardh) E.C. Henry et G.R. South
Saccorhiza polyschides (Lightfoot) Batters
S. dermatodea (Bachelot de la Pylaie)

Araújo et al., 2016, Biodiv Conserv

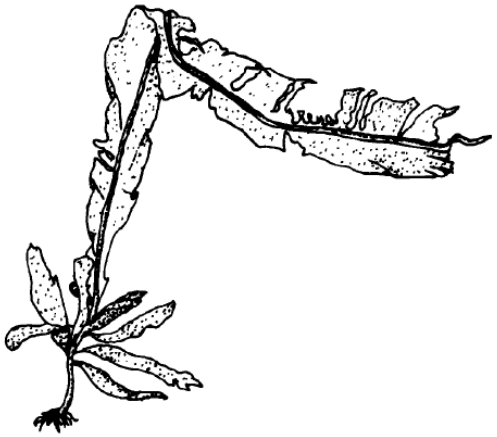
Table 9. Temperature tolerance ranges for kelp species in UK waters

(upper and lower lethal limits can be estimated as 1-2°C beyond the growth limits)
* indicates that the temperature restrictions are not known.

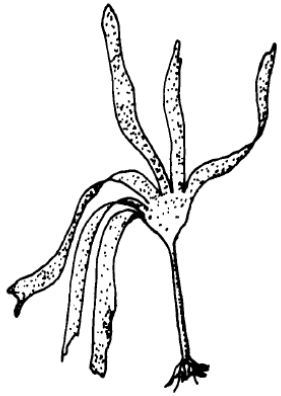
kelp species & data source	temperature ranges	
	Sporophyte growth & reproduction	gametophyte growth & reproduction
Alaria esculenta Sundene, 1962	upper: 16°C / * lower: * / *	upper: * / * lower: * / *
Laminaria digitata Gayral & Cosson, 1973	upper: 18°C / 18°C lower: 0°C / *	upper: 17°C / below 13-15°C lower: 0°C / 2-6°C
Laminaria hyperborea Kain, 1964	upper: 15°C / 20°C lower: 0°C / 19°C	upper: 21°C / below 18°C lower: * / *
Laminaria ochroleuca Lüning, 1990	upper: 22-23°C / * lower: * / *	upper: * / 21°C lower: * / 5°C
Laminaria saccharina Lüning, 1990	upper: 18°C / 20°C lower: 0°C / *	upper: 22-23°C / below 18°C lower: * / *
Saccorhiza polyschides Norton, 1977	upper: 24°C / * lower: 3°C / *	upper: 25°C / below 17°C lower: * / 5°C
Undaria pinnatifida Akiyama, 1965	upper: 28-30°C / * lower: * / *	upper: 27°C / below 25°C lower: * / *
	where two figures are shown these indicate seasonal tolerances	

Alaria esculenta

Alaria esculenta



Laminaria digitata



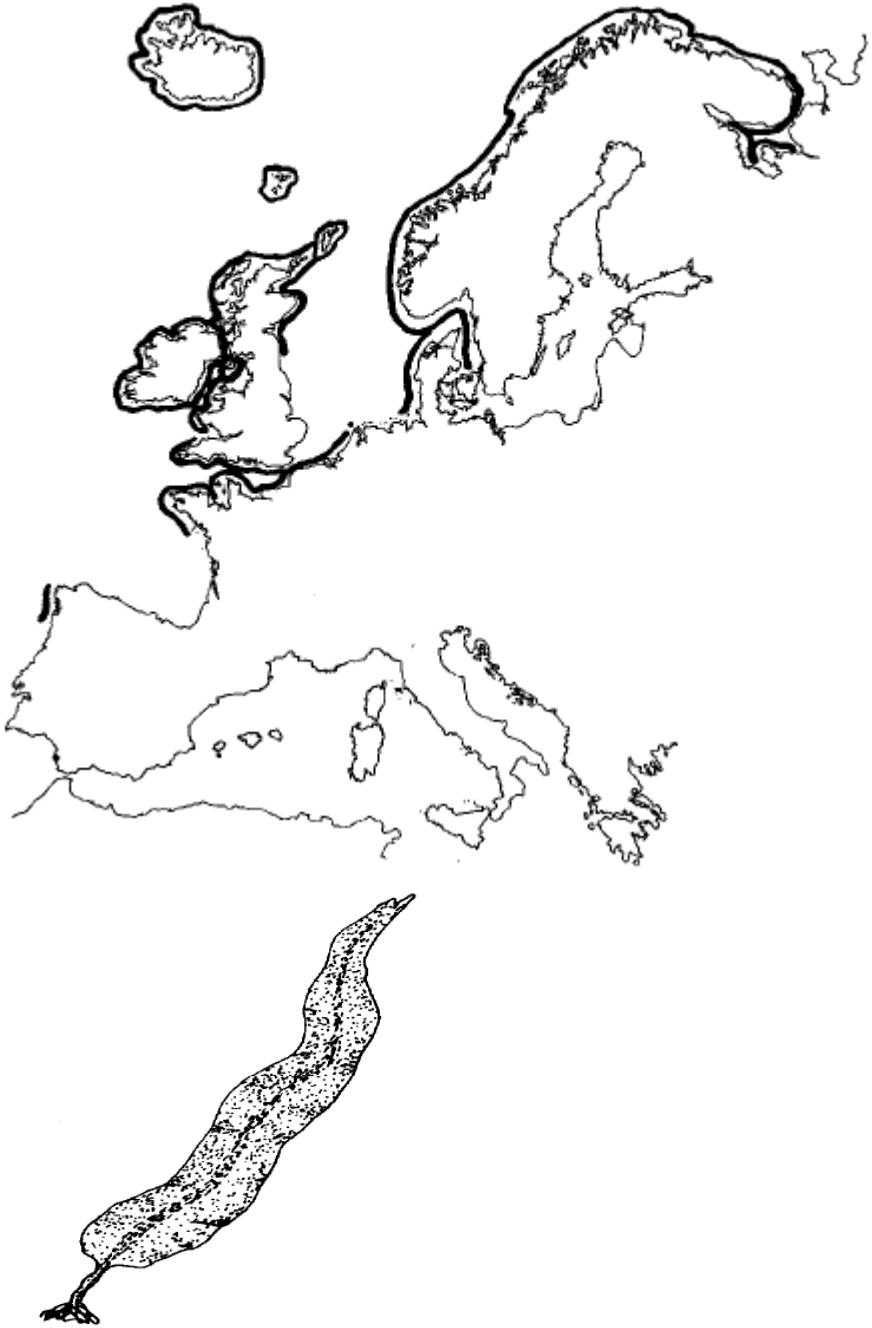
Laminaria hyperborea

Laminaria ochroleuca

Laminaria ochroleuca

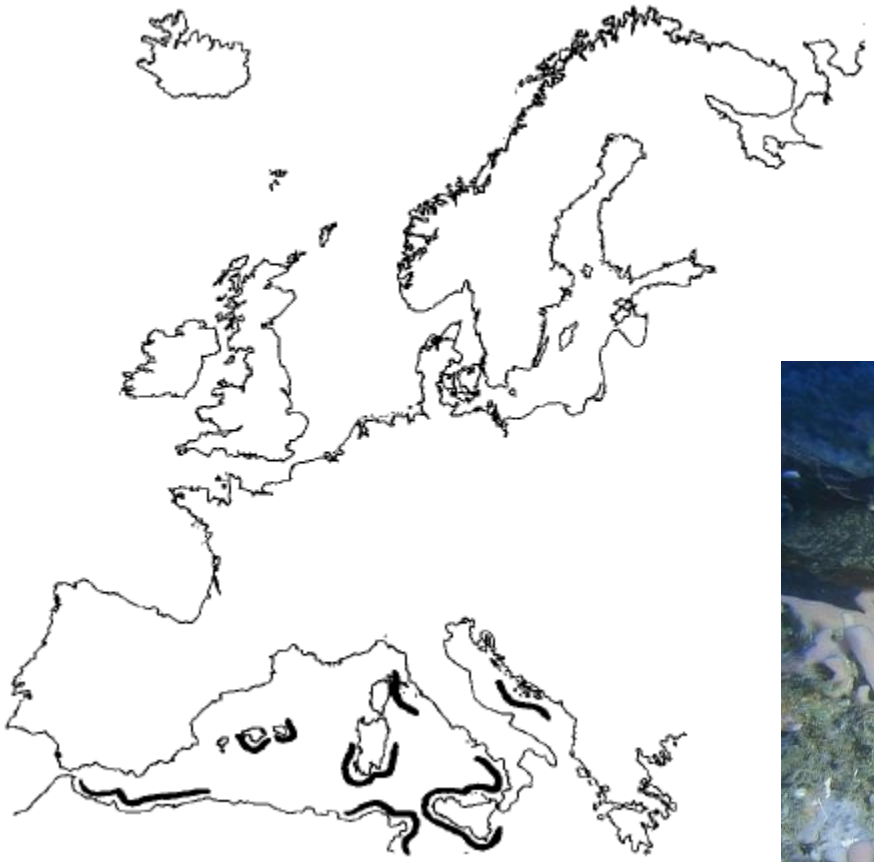
In appearance this plant is very similar to *L. hyperborea*, but the stipe and the frond are a much lighter colour with a yellowish cast. The stipes are smooth and generally lack epiphytes and epifauna.

Laminaria saccharina

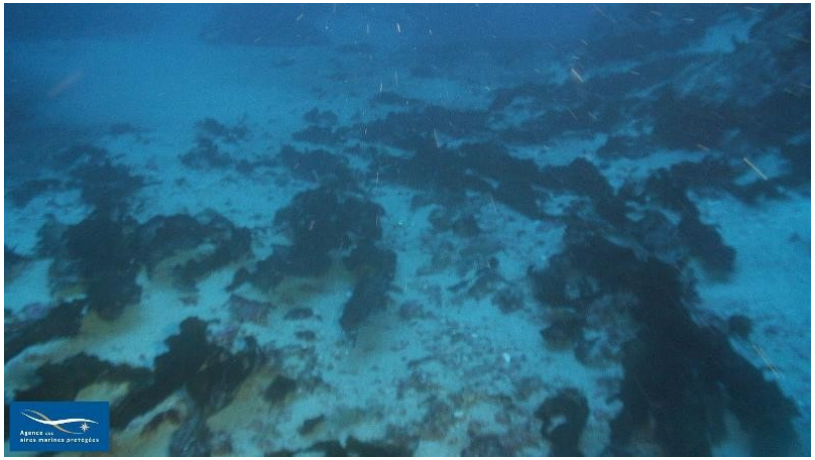


S. latissima

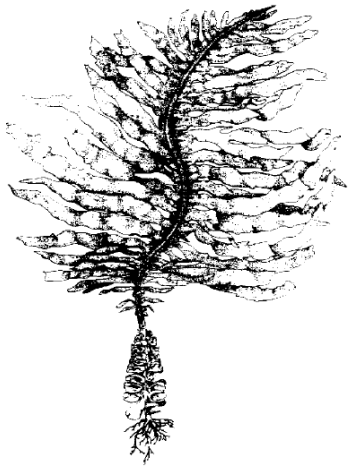
Laminaria rodriguezii



This species is endemic to the Mediterranean and is found on the coasts of Algeria, Tunisia, Majorca, Corsica, Sicily and the shores of the Adriatic Sea. However, it is restricted to depths of 50 - 120 m where the water temperatures do not exceed 15 °C.

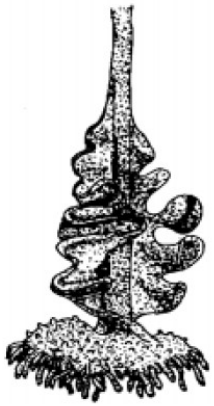


Undaria pinnatifida



Saccorhiza polyschides

Saccorhiza polyschides



Phyllariopsis breviceps

A warm-temperate species found in deep water. The southern range ends at the Western Sahara border with Morocco, extending northward on the eastern Atlantic coast to Biarritz. This species is also found in the western basin of the Mediterranean.

Phyllariopsis purpurascens

A warm-temperate species found in deep water. The southern range ends at the Western Saharan border with Morocco, extending northward on the eastern Atlantic coast to the Spanish-Galician coast. This species is found in the southern part of the western basin of the Mediterranean.

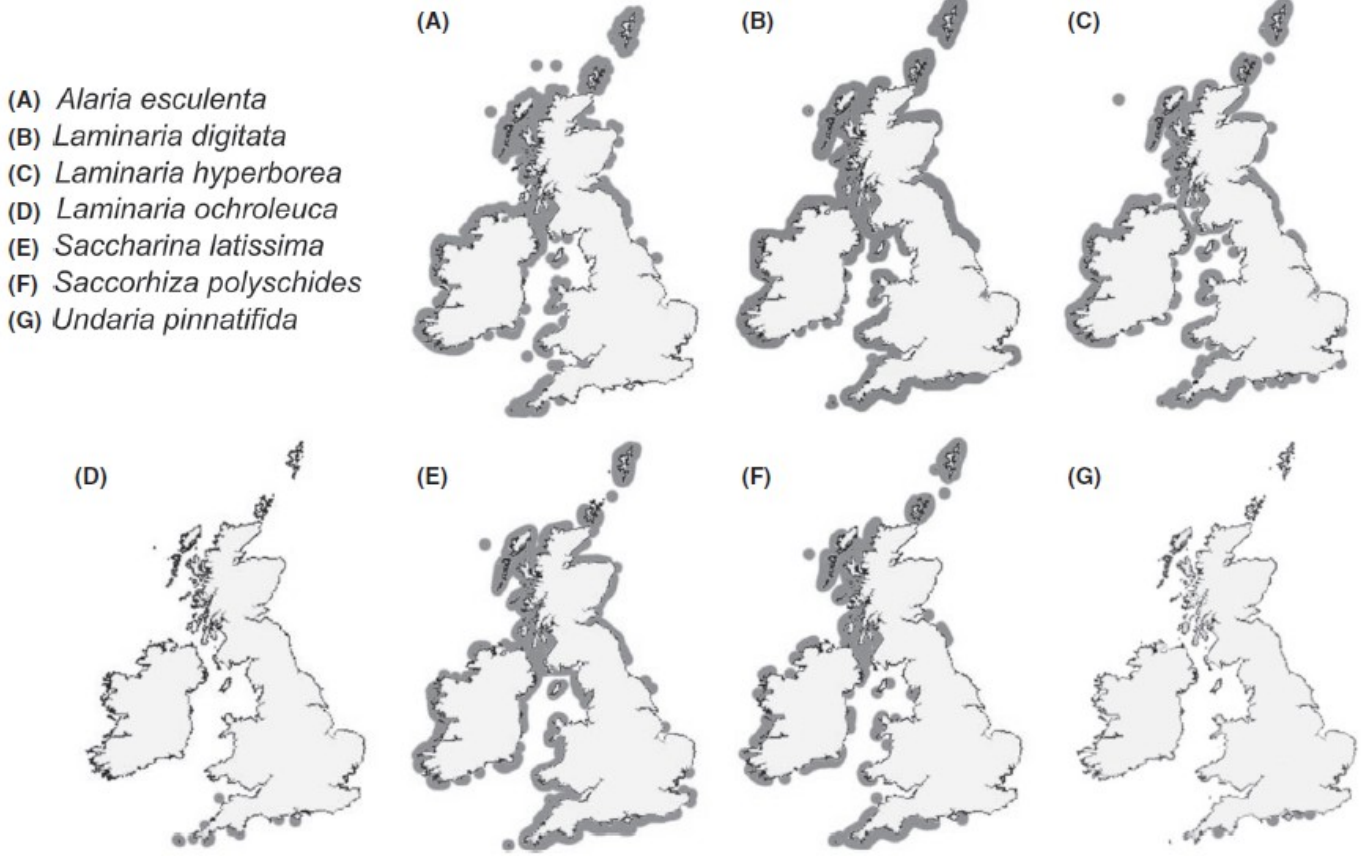
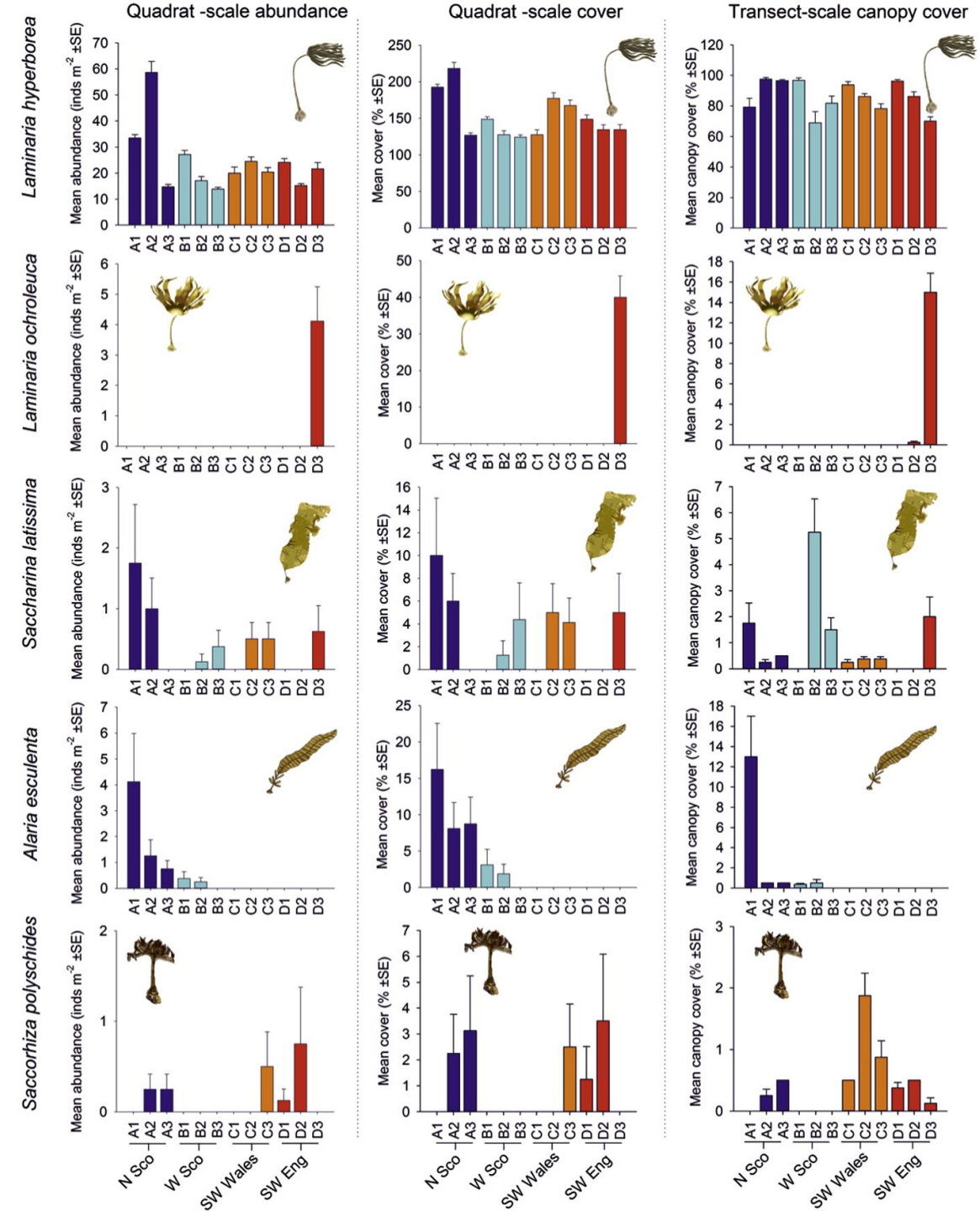


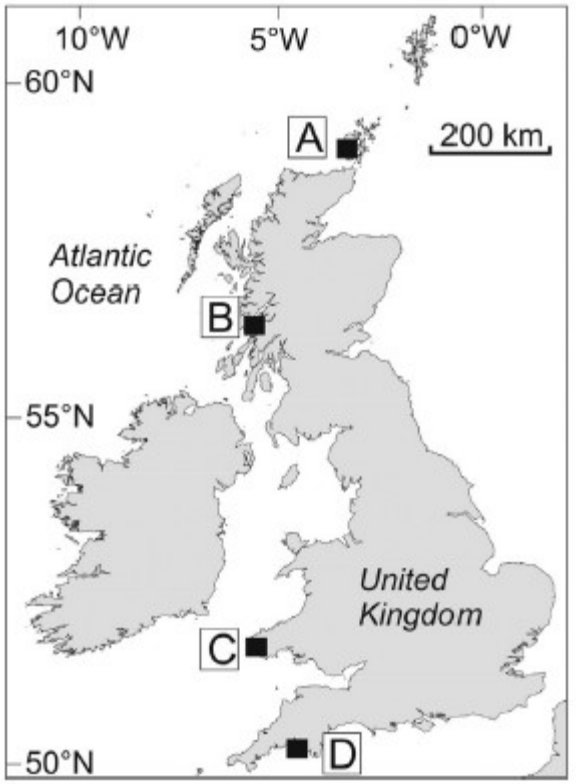
Figure 2. Dark gray hatching indicates the recorded distributions of kelp species in the UK and Ireland (data reproduced from MarLIN, with permission).

Table 1. Kelp species in UK and Irish waters. The geographic range and approximate depth range, typical mature sporophyte length, and lifespan of kelps in UK/Irish waters are shown. Also shown is the predicted change in abundance and/or range of each species in response to continued environmental change.

Species	Distribution	Depth range (m)	Length (m)	Lifespan (years)	Change (?)
Laminaria hyperborea	Arctic–Portugal	0–30	1–3	5–18	Decrease
Laminaria digitata	Arctic–France	0–15	1–2	4–6	Decrease
Laminaria ochroleuca	UK–Morocco	0–30	1–3	5–18[1]	Increase
Saccharina latissima	Arctic–France	0–30	1–3	2–4	Decrease
Alaria esculenta	Arctic–France	0–35	1–2	4–7	Decrease
Saccorhiza polyschides[2]	Norway–Morocco	0–35	2–3	1	Increase
Undaria pinnatifida	Global NIS[3]	0–15	1–3	1	Increase

Smale et al., 2013, Ecol Evol





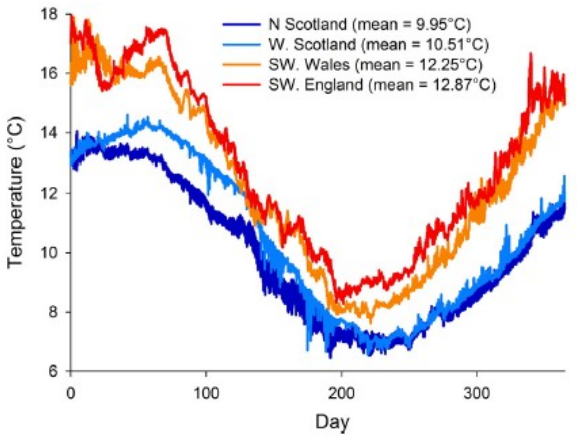
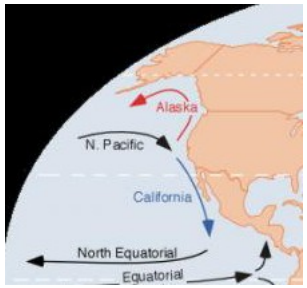


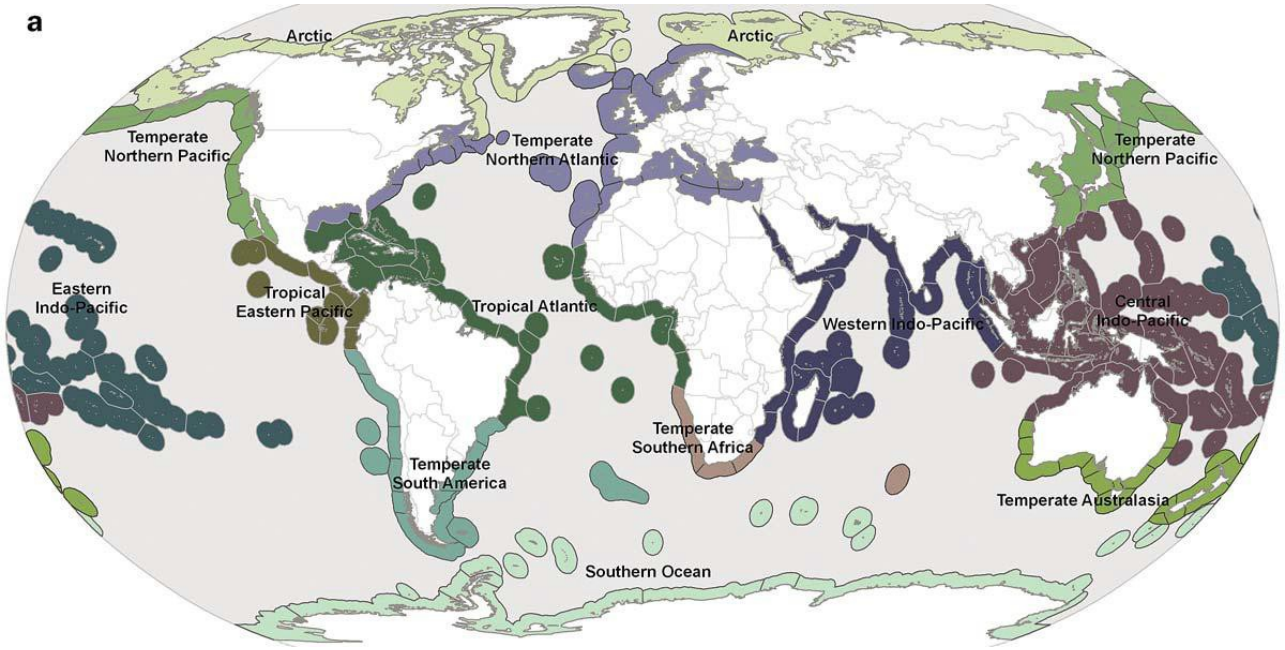
Fig. 2. Annual temperature variability at a subtidal study site (~2 m depth b.c.d.) within each study region. Temperature record spans July 2014–July 2015, with measurements obtained every 30 min.

Smale & Moore, 2017, J Exp Mar Biol Ecol

Kelp ecosystems of NW American coast

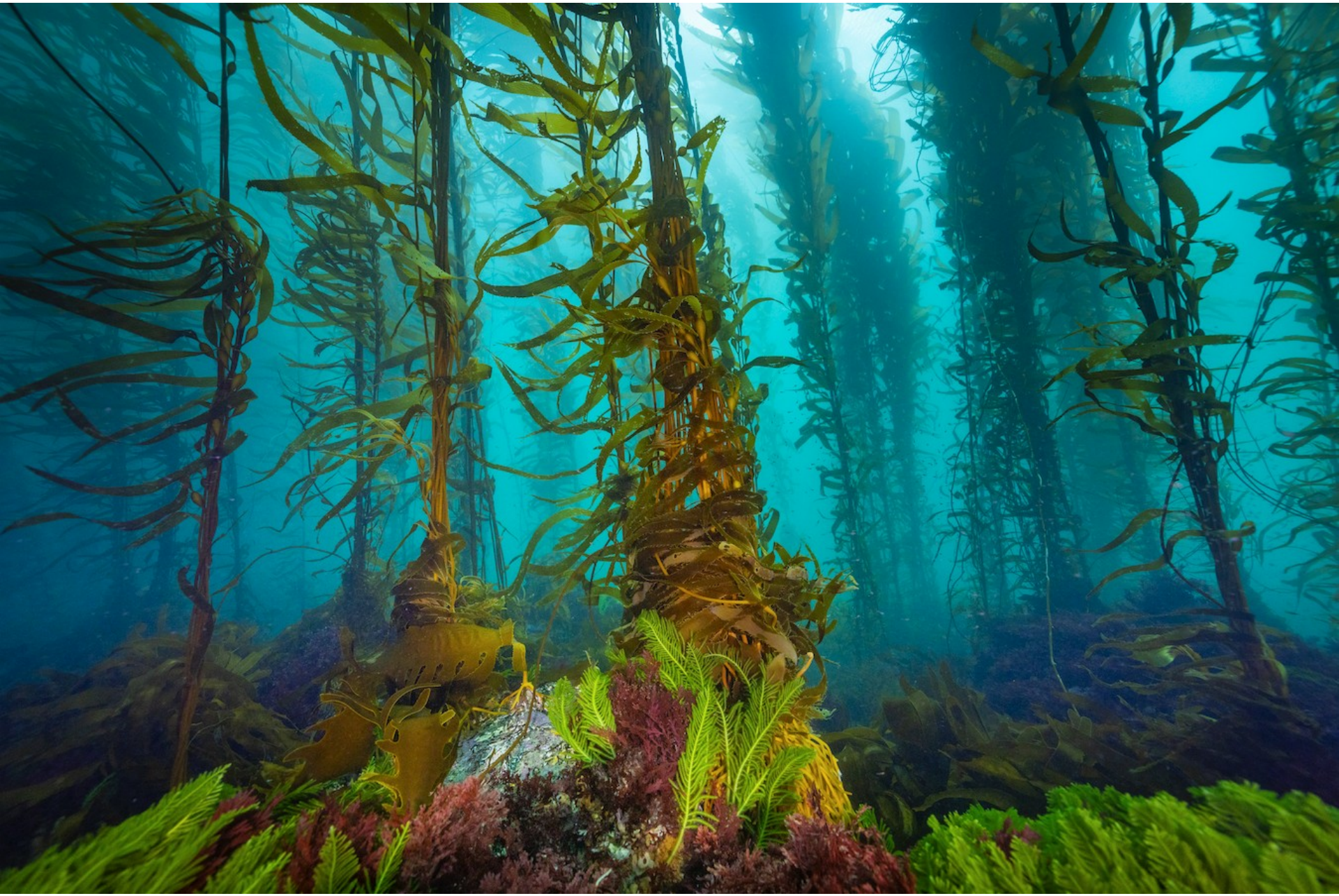
N parts of this region - primary radiation centre of Laminariales





Nereocystis, Macrocystis

Kelp:
Baja, CA



Upper eulittoral of Pacific cold temperate habitats

Postelsia palmaeformis (palm kelp) - only up to Vancouver Island

vertical differentiation in the Pacific cold temperate sublittoral

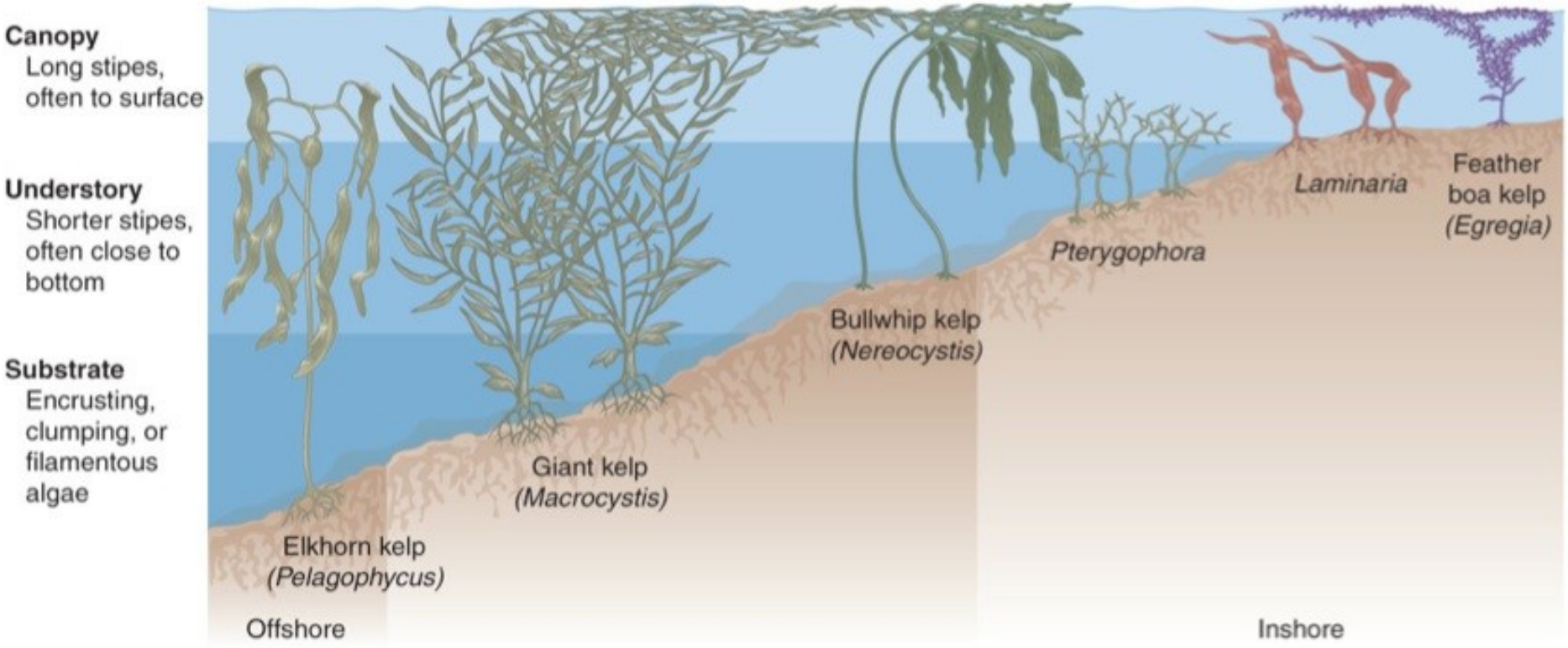
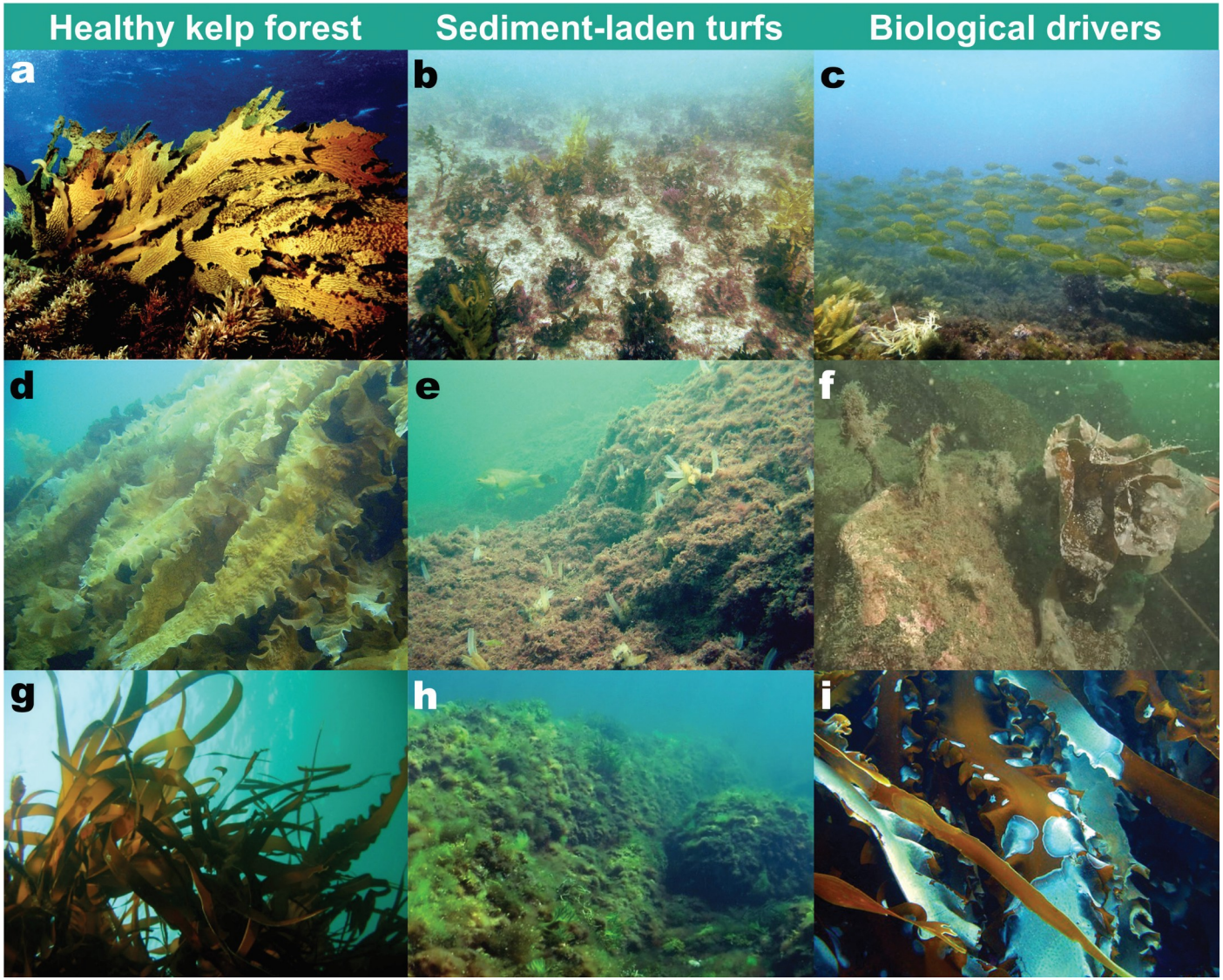


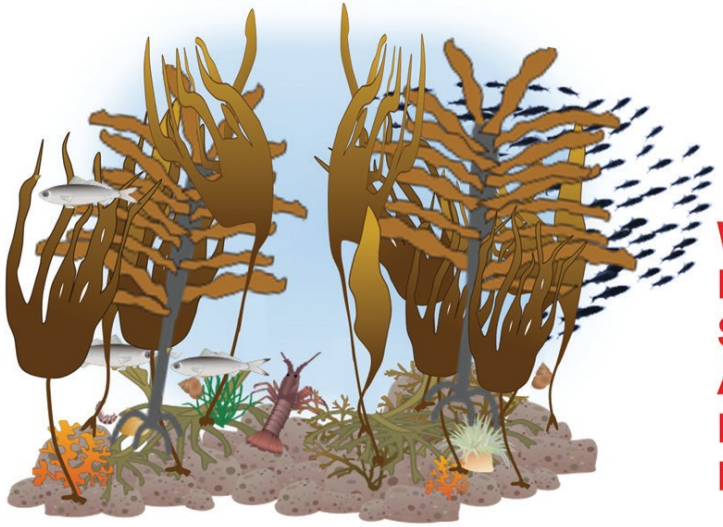
Fig. 4.20 General structure of a West Coast kelp forest, with a complex understory of plants beneath the dominant *Macrocystis* or *Nereocystis*.



Transition from kelp forests to turf-dominated vegetation

Filbee-Dexter & Wernberg, 2018, BioScience

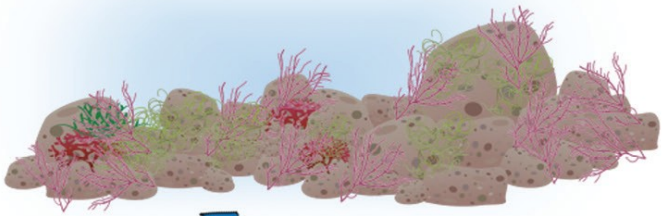
Figure 2. Kelp forests have undergone regime shifts from lush, structurally complex forests to highly simplified, sediment-laden turf reefs. Examples include the disappearance of forests of Ecklonia radiata *from Western Australia (top panel),* Saccharina latissima *from southwestern Norway (middle panel), and* Laminaria digitata *and* S. latissima *from Atlantic Canada (bottom panel). The photographs show healthy kelp forests (a, d, g), sediment-laden turf reefs (b, e, h) and biological drivers: (c) tropical herbivores (*Siganus fuscescens*) cropping kelp recruits, (f) epiphytes smothering kelps, and (i) the invasive bryozoan (*Membranipora membranacea*) encrusting and weakening kelp fronds. Photographs: Thomas Wernberg (a, b, c), Hartvig Christie (d, e, f), Karen Filbee-Dexter (g), and Robert Scheibling (i, h).*



Kelp forest

Warming
Heat waves
Storms
Acidification
Eutrophication
Harvesting

Epiphytism
Competition
Herbivory
Species invasion



Turf reef

High sediment load
Limited space
Low spore supply
High grazing intensity

Low kelp
recruitment

Low light
Physical abrasion
High spore supply

High kelp
recruitment

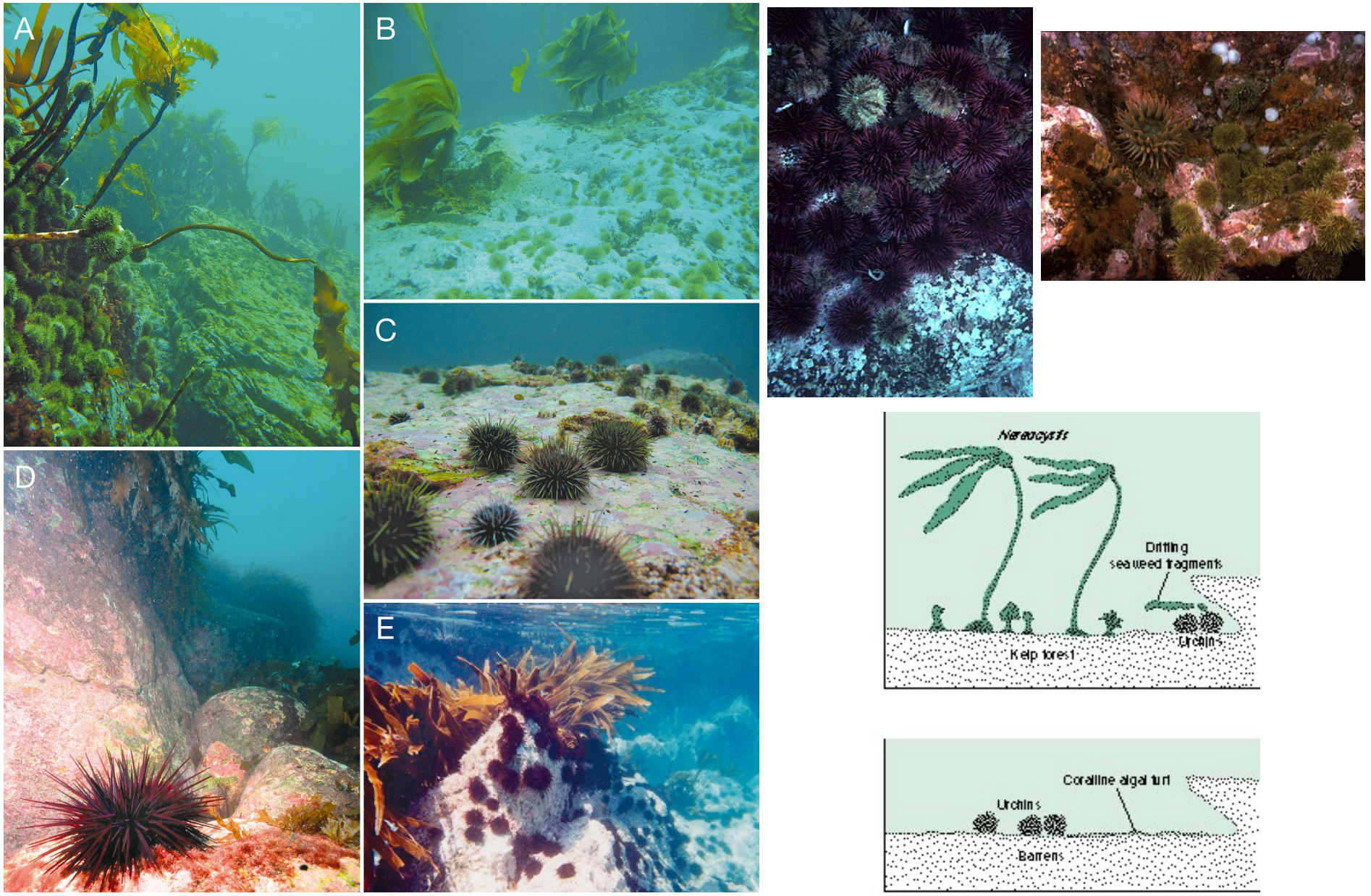
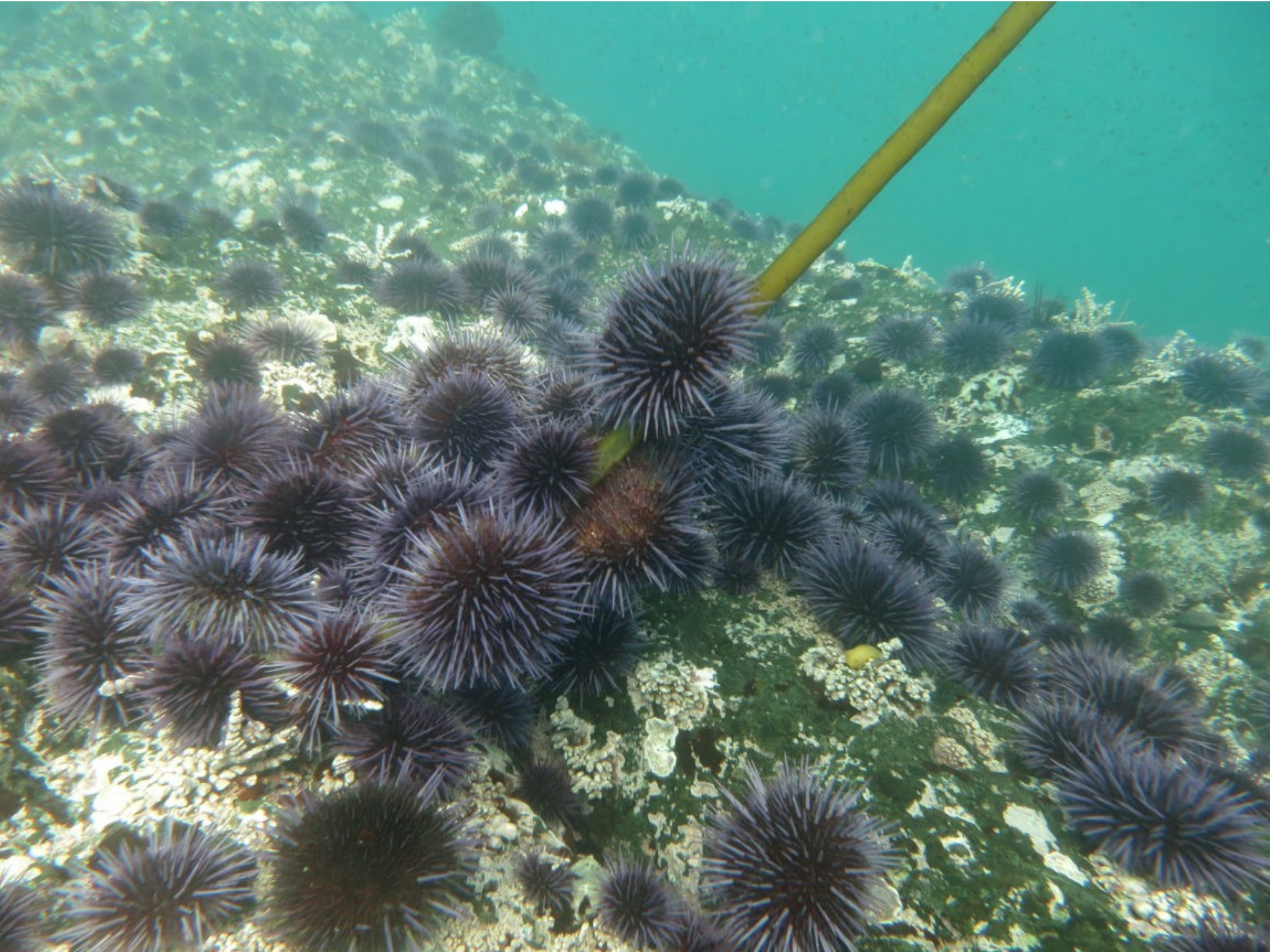


Fig. 1. (A) Destructive grazing front of sea urchins *Strongylocentrotus droebachiensis* advancing into a kelp bed near Halifax, Nova Scotia, Canada. Photo credit: R. E. Scheibling. (B) Extensive urchin (*S. polyacanthus*) barrens in the Aleutian Islands, USA. Photo credit: B. Konar. (C) Urchins *S. droebachiensis* on scoured coralline algae in barrens in Norway. Photo credit: C. W. Fagerli. (D) Range-expanding urchin *Centrostephanus rodgersii* forming patchy barrens in a kelp bed in southeast Tasmania. Photo credit: S. D. Ling. (E) *S. nudus* grazing a kelp bed in Japan. Photo credit: D. Fujita



urchin barrens – alternative stable-state systems; discontinuous phase shifts between

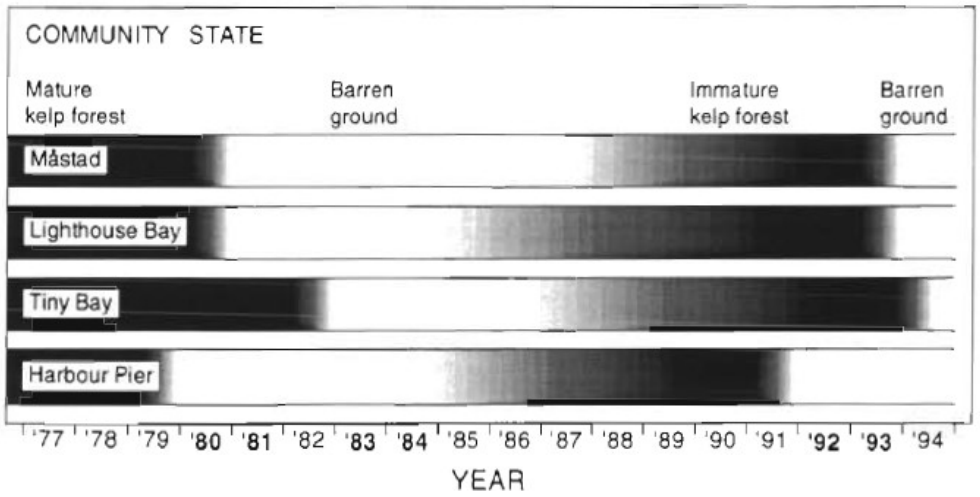
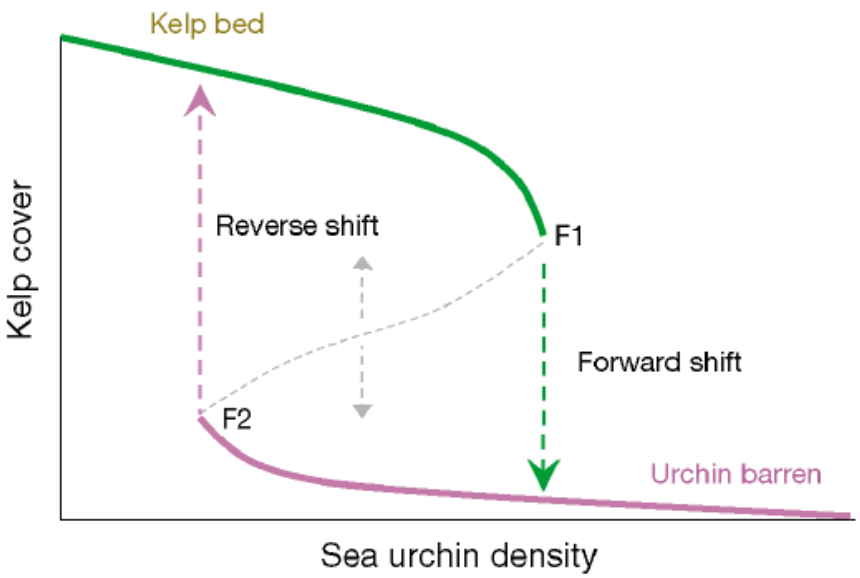


Fig. 2. *Laminaria hyperborea and Strongylocentrotus droebachiensis*. Community dynamics at 4 field sites on Værøy Island, Northern Norway. During the early 1980s, the mature *L. hyperborea* kelp forest was replaced by barren grounds dominated by the sea urchin *S. droebachiensis*. Kelp regrowth occurred in the mid 1980s, but this re-established kelp forest was destroyed and replaced by barren grounds again in the early 1990s when it was still successionally immature. Years when observations were made indicated with bold typeface. The time of kelp regrowth at Måstad and in Tiny Bay was estimated by ageing of kelp plants collected in 1992



Filbee-Dexter & Scheibling, 2014, Mar Ecol Progr Ser

Strongylocentrotus droebachiensis – Norway, *L. hyperborea*
parasitic nematode – *Echinomermella matsi* – may control sea urchin populations

however, the succession towards an ecologically mature kelp forest community has been interrupted by the unexpected recurrence of destructive grazing, and the macroparasite hypothesis must therefore be rejected in its present form

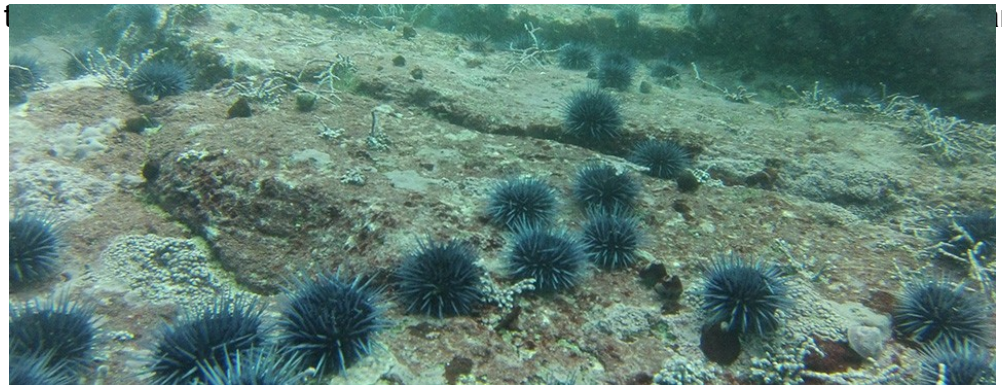
crabs and common eiders are also the common predators on urchins

the euphotic hard bottom component of the coastal ecosystem in Northern Norway has entered a cyclical domain

Hagen, 1995, Mar Ecol Progr Ser

N Europe – sea urchin barrens since 1970s (N Norway, Russia)

at t…nge…



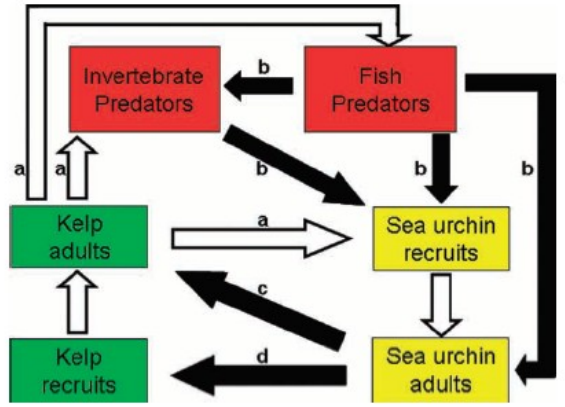


Figure 5. Conceptual figure describing possibly important interactions (arrows) between kelp (*Laminaria hyperborea*), sea urchins (*Strongylocentrotus droebachiensis*) and potentially important predators. Black arrows indicate a negative effect and white arrows a positive effect. (a) Adult kelp provides a habitat for sea urchin recruits, invertebrate predators and a nursery area and habitat for fish. (b) Invertebrate and fish predators prey on sea urchin recruitment. (c) If sea urchins become abundant they aggregate and graze down the kelp forest. Then the kelp and associated predators are lost and only sea urchins survive. (d) When the kelp forest is lost, sea urchin populations prevent kelp from re-establishing by grazing.

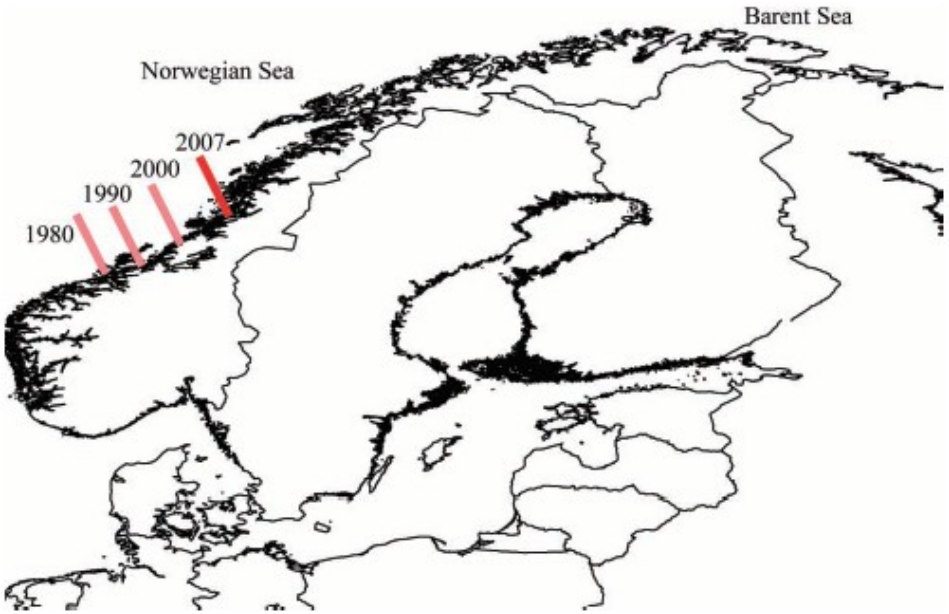
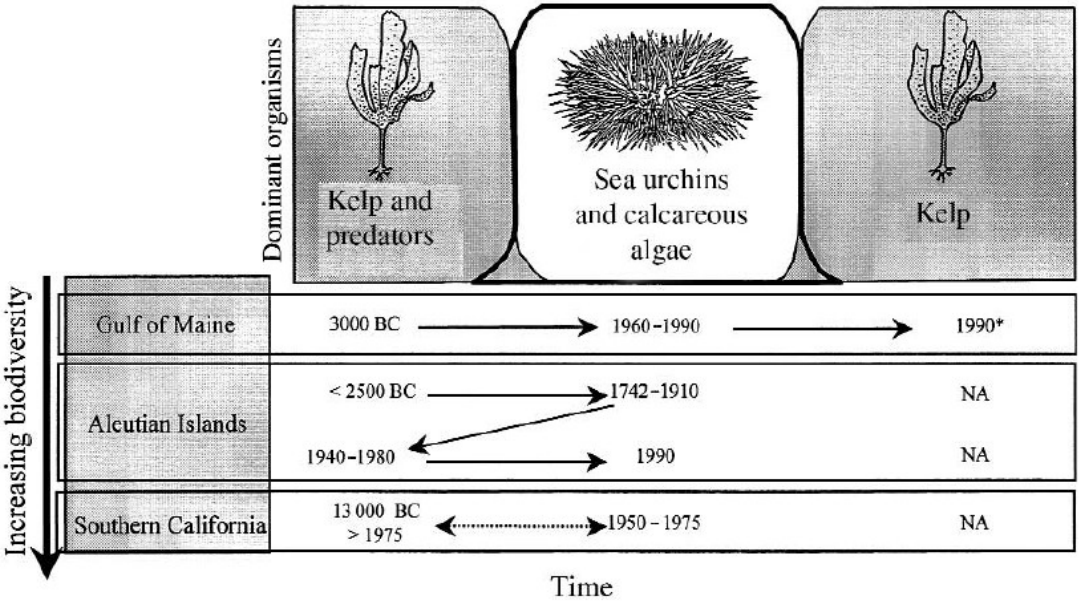


Figure 1. Retreating sea urchins. Movement of the border between kelp-dominated areas and barren ground from 1980 until 2007. The barren ground area had its largest extent in 1980 where the border extended south to 63°30′ N (Sivertsen 1982). Røv et al. (1990) showed that the border had moved to 63°40′ N by 1990 and in 2000 the border had at least moved to 64°10′ N (Sjøtun et al. 2001). In 2007 the border was situated at 65°30′ N (Norderhaug & Christie 2007).

Nordehaug & Christie, 2009, Mar Biol Res

(a-)cyclic dynamics of kelp forests in 20th (21th) century

Figure 2 Timing of phase changes in community state of kelp forests of North America. Kelp with vertebrate predators, sea urchins without kelp and kelp without predators have been identified for some or all of the case study locations. Kelp forests are listed from the greatest number of trophic levels on the left to fewest trophic levels on the right. Case studies are listed from lowest species diversity in Maine to highest diversity in southern California. See text or Table 4 for references.



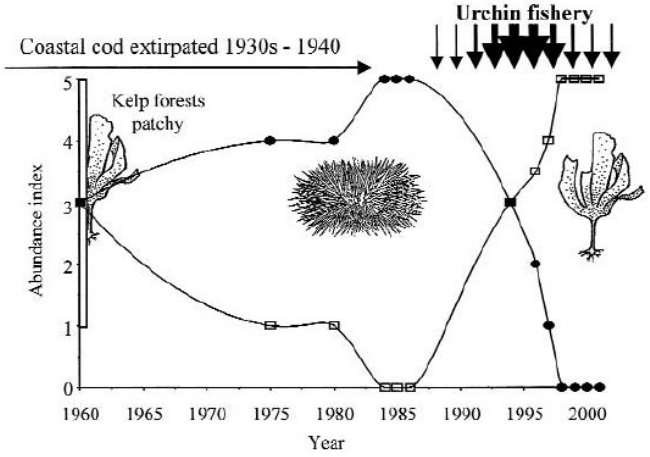


Figure 4 Temporal trends in kelp forests and sea urchins in the Gulf of Maine in the western North Atlantic. Width of arrowheads indicates the magnitude of the forcing function's impact.

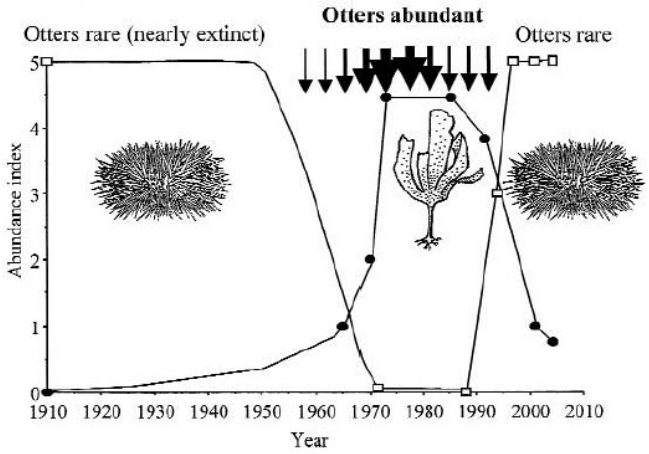


Figure 3 Temporal trends in kelp forests, predators and sea urchins of Amchitka, Alaska. Abundances estimated from several studies (see text) and Estes and Duggins (1995). Arrows indicate the timing of change in major community-changing forcing functions. Width of arrowheads indicates magnitude of the forcing function's impact.

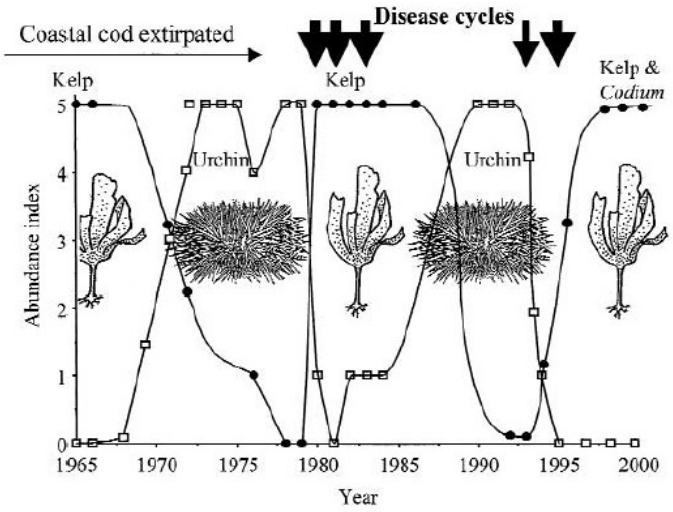


Figure 5 Temporal trends in kelp forests and sea urchins of Nova Scotia. Abundances estimated from Edelstein *et al.* (1969), Breen and Mann (1976), Warton and Mann (1981), Scheibling and Stephenson (1984), Scheibling (1986) and Johnson and Mann (1988). Width of arrowheads indicates the magnitude of the forcing function's impact.

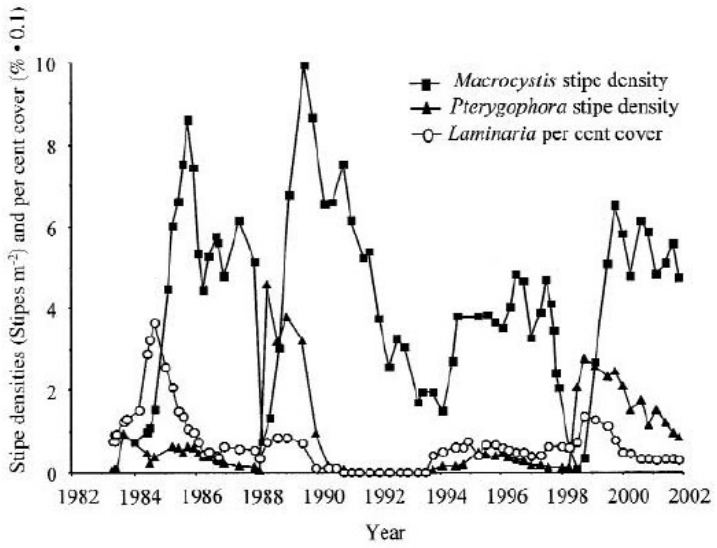


Figure 7 Temporal trends in the kelp forest of Point Loma, California, USA, 1983–1996 at 12 m depth (from Tegner *et al.* 1996*a*). Population density data are shown for canopy (*Macrocystis*) and stipitate (*Pterygophora*) kelps. Percentage cover data are shown for the prostrate kelp *Laminaria*.

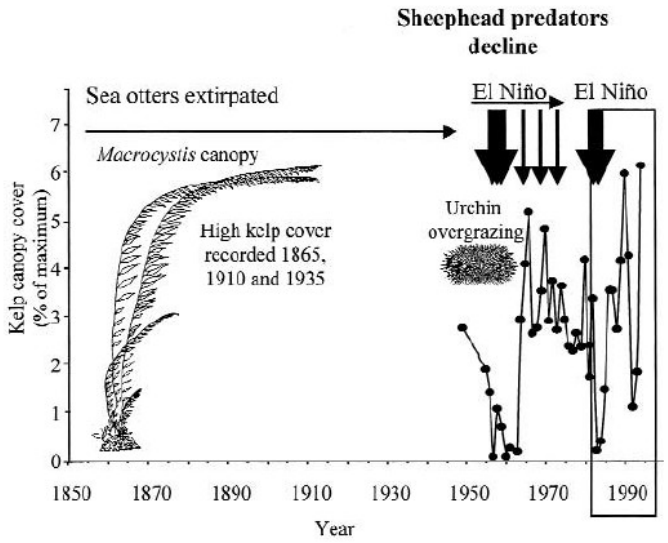


Figure 6 Temporal trends in kelp forests of Point Loma California. Abundance estimates summarized in Leighton *et al.* (1966), Tegner *et al.* (1996*a*), McGowan *et al.* (1998) and Tegner and Dayton (2000). Width of arrowheads indicates the magnitude of the forcing function's impact. The boxed area on the right of the figure indicates a period of high resolution subtidal data (see Fig. 3).

Steneck et al., 2002, Env Conserv

Zostera (marina) [eelgrass] meadows

(Alismatales, Zosteraceae)

commons.wikimedia.org/wiki/User:Fabelfroh

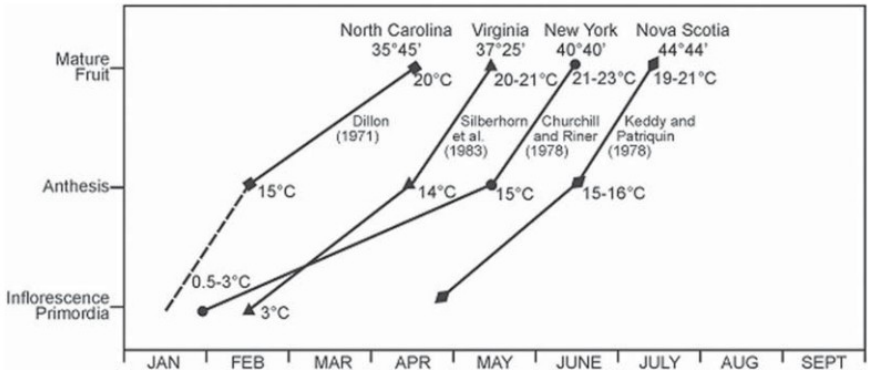


Fig. 5. Reproductive phenology of *Zostera marina* at different locations (with latitudes) along the east coast of the United States. The approximate temperature that was recorded for each event is also given (modified from Silberhorn et al., 1983).

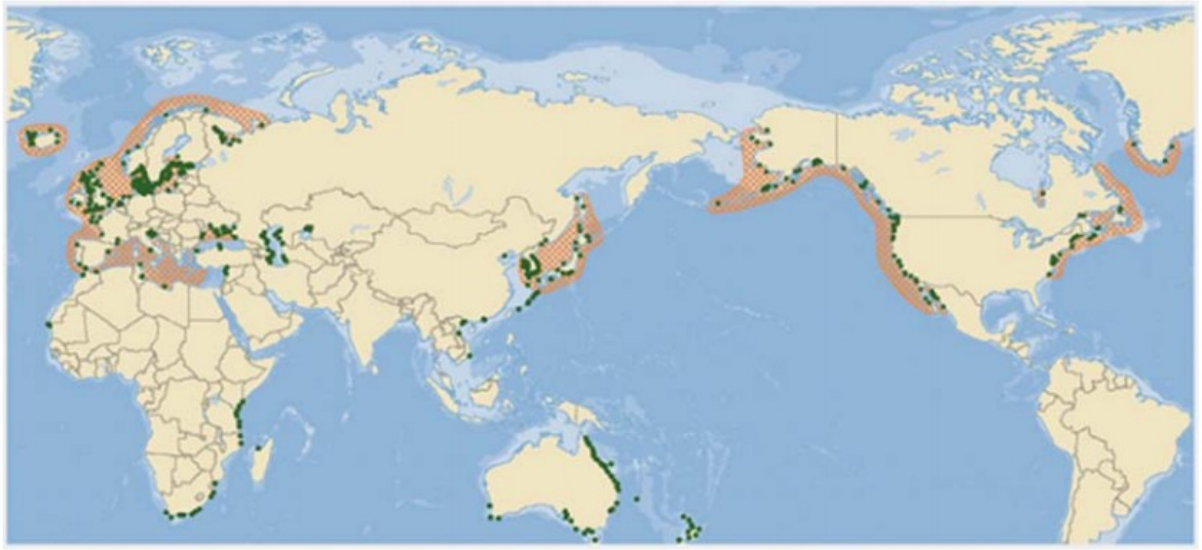
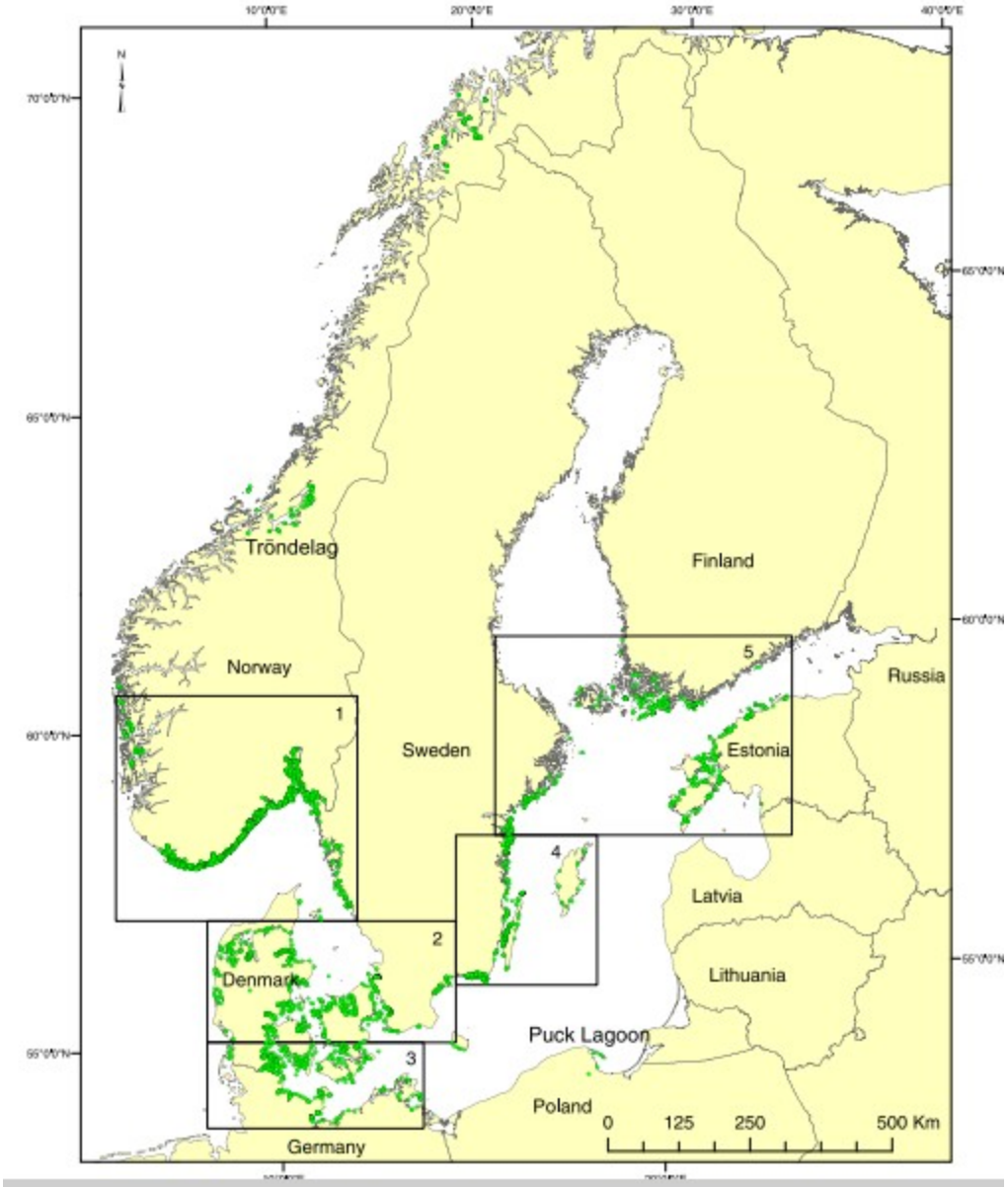


Fig. 2. Worldwide distribution of all *Zostera* species (dots indicate literature reports); shaded area indicates the range of *Zostera marina* (Green and Short, 2003).

Europe – *Z. marina* meadows cover ca 1800 km^2

Moore & Short, 2006, Biology of Zostera



Boström et al., 2014, Aquat Conserv

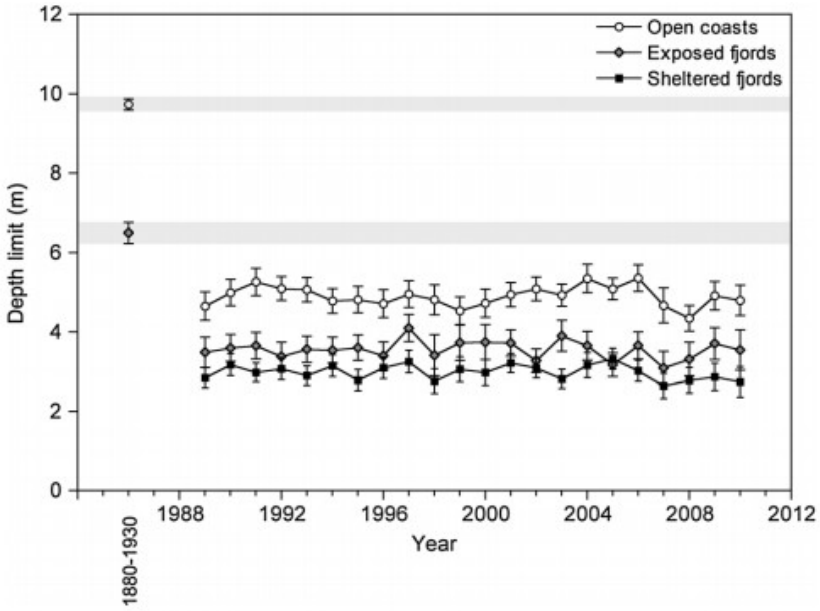
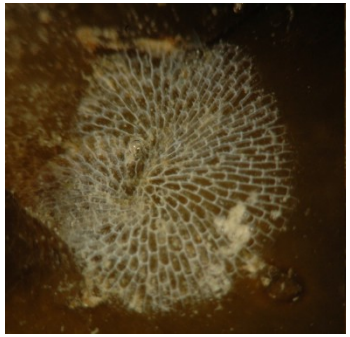


Figure 6. Temporal development in eelgrass depth limits in Danish coastal waters. Historical data represent means (± s.e.) of all observations along open coasts (n = 232) and fjords (inner, outer and Limfjorden all together, n = 75) for the period 1880–1930 (Krause-Jensen and Rasmussen, 2009). Data from 1989 to 2009 are nationwide means of deepest observations of 10% eelgrass cover in fjords and open coasts as compiled under the Danish national monitoring and assessment programme and modelled by generalized linear models (Hansen and Petersen, 2011).

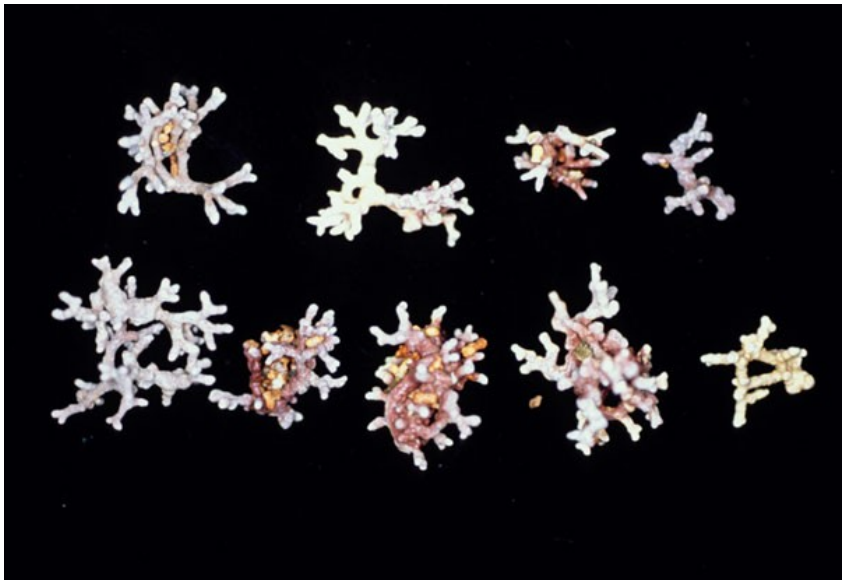
The lower sublittoral zone (<5% penetrating light)

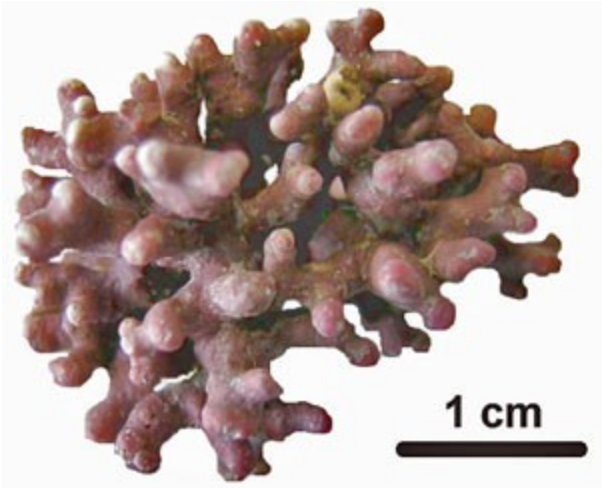
- Scattered *L. hyperborea*, but no more canopy-forming.
- Laminarias grow extremely slowly and, consequently, often have a lot of epiphytes (such as
- *Membranipora membranacea)*
- typical taxa: *Delesseria sanguinea, Phycodrys rubens, Desmarestia ligulata, Polysiphonia urceolata*



- morphological adaptations to low light intensities and absence of major wave action

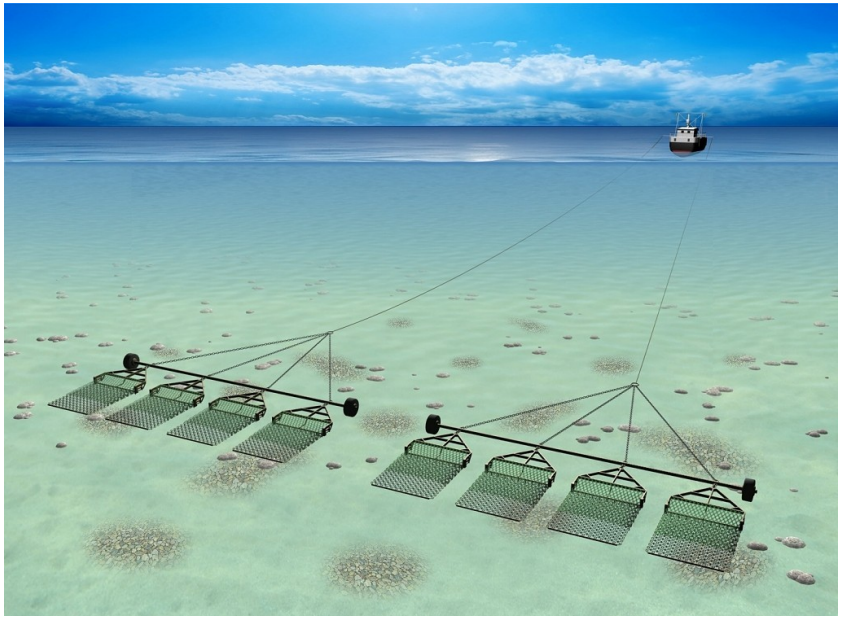
Maerl vegetation – (3-) to 25 m(-40) meters, sandy bottoms
dominated by *Phymatolithon calcareum, Lithothamnion corallioides*

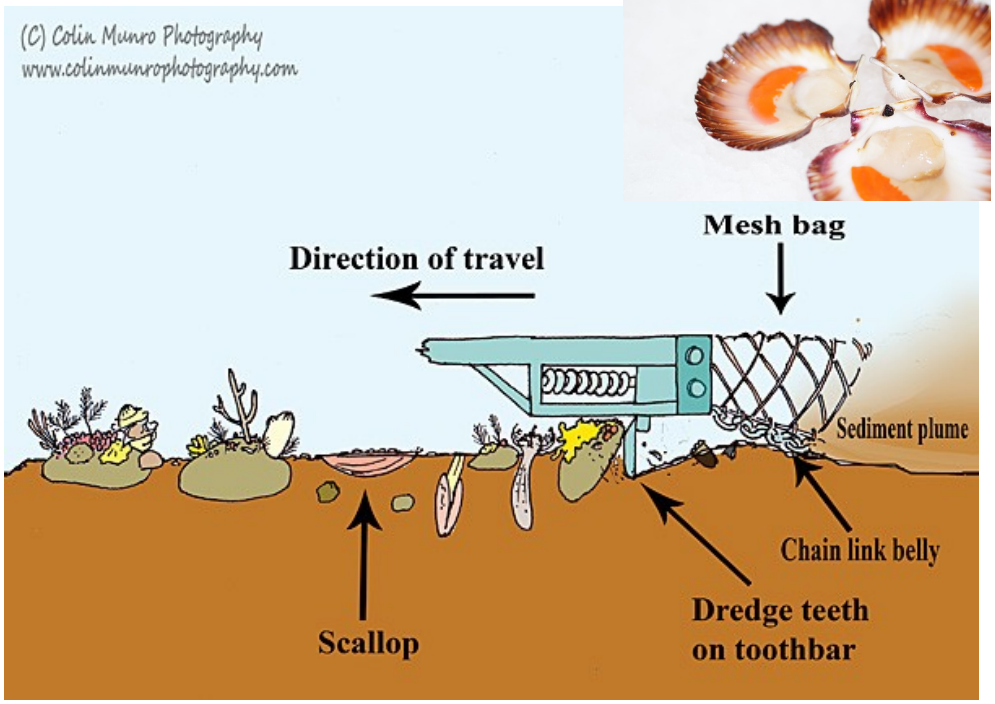




loose lying, encrusted…

maerl beds and disturbance by scallop dredging





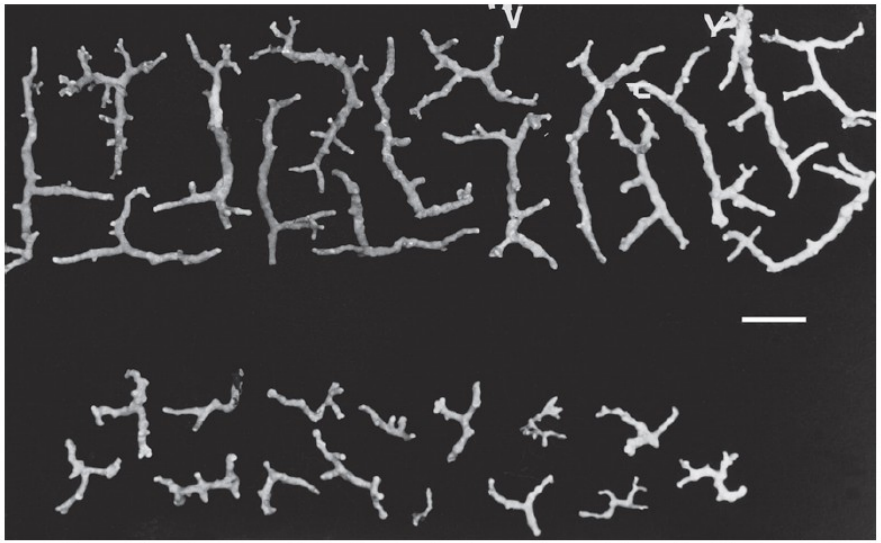
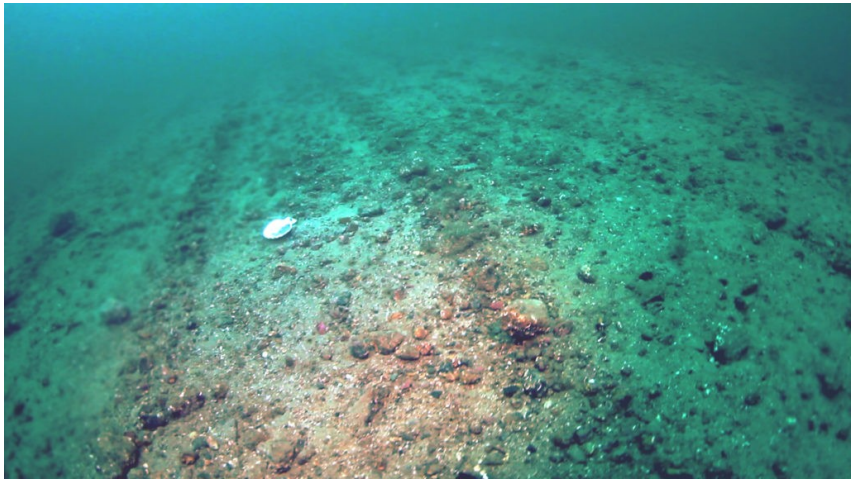


Figure 4. *Phytomatolithon calcareum* maerl thalli collected at Site 3 by Batters in 1891, before scallop fishing began in the Clyde Sea area (upper set), compared with specimens collected from the same site in 1995 (lower set). Scale bar represents 1 cm.

Hall-Spencer & Moore, 2000, ICES J Mar Sci



Main anthropogenic hazard for live maerl beds is smothering by fine sediment, such as that produced by trawling or maerl extraction, from sewage discharges or shellfish and fish farm waste, and sedimentation resulting from disruption to tidal flow.

Wilson et al., 2004