11

The phytobenthic zone

Hans Kautsky, Georg Martin, and Pauline Snoeijs-Leijonmalm

Abstract

1. Phytobenthic communities consist of macrophytes (macroalgae, vascular plants and mosses) with their accompanying fauna and microorganisms.
2. The phytobenthic communities occur in the photic zone, which in the Baltic Sea extends from the water surface down to a ~20 m water depth, but in turbid coastal waters only down to ~5 m.
3. The type of vegetation is determined by the available substrate, which is a result of geography and geology in combination with currents. Most macroalgae grow attached to hard substrates whereas vascular plants and charophytes grow on sandy or soft (silt and mud) substrates.
4. Generally, the coastal areas of the Baltic Sea consist of mixed substrates with an intermingled vegetation of vascular plants and algae. In the northern Baltic Sea hard substrates dominate in the outer archipelagos, and in the southeastern Baltic Sea sandy and muddy substrates dominate.
5. Luxuriant stands of macrophytes provide food, shelter and spawning habitats for the associated sessile and mobile micro-, meio- and macrofauna, including fish.
6. On an ecosystem-wide scale, the phytobenthic communities vary along the large-scale Baltic Sea gradient. Biomass decreases with lower salinity and colder climate, while the proportion of freshwater species increases.
7. On a local scale, the phytobenthic communities are mainly, directly or indirectly, shaped by water movement (*e.g.* by the occurrence of sandy beaches and rocky shores) and winter ice cover. Light and substrate availability give rise to typical depth zonation patterns, ending with soft-substrate communities deepest down.
8. On a small scale (patches), phytobenthic community structure and composition is influenced by microhabitat structure and biotic interactions.
9. The phytobenthic communities in the brackish Baltic Sea are more sensitive to disturbance than their marine counterparts due to low diversity, physiological stress and the loss of sexual reproduction when species approach their salinity limit.

Keywords

Baltic Sea gradient • Community structure • Food-web interactions • Habitat-forming macrophytes • Human impacts • Phytobenthic communities • Productivity

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11.1 The substrate shapes the vegetation

11.1.1 Phytobenthic communities

The phytobenthic zone comprises the photic zone that contains vegetation growing on hard, sandy and soft substrates (Fig. 11.1). Usually, the coastal areas of the Baltic Sea show mixes of these substrates ("mixed substrates") on a local scale. Phytobenthic communities include all organisms (*e.g.* bacteria, protists and fauna) associated with the vegetation of macroalgae, mosses and vascular plants that forms the three-dimensional structure on the substrate.

Quantitative sampling of phytobenthic communities growing on hard or mixed substrates is impossible without SCUBA diving (Boxes 11.1 and 11.2). Phytobenthic investigations in the Baltic Sea Area include also the *Mytilus trossulus*-dominated belts at a ~20–30 m water depth, just below the photic zone, even if macrophytes are basically absent here. These belts are a continuation of the presence of *Mytilus trossulus* in the phytobenthic communities of the photic zone and are also preferably studied by SCUBA diving. Zoobenthic communities on soft substrates are, on the contrary, sampled usually from a ship using cores or other sampling devices (*cf.* Box 10.1).

Substrates in the photic zone that are highly unstable on a short time scale, such as constantly moving sand or gravel on exposed coasts, lack any macroscopic vegetation. This is especially the case along the southern and southeastern coasts of the Baltic Sea proper where immense amounts of sand originating from land are delivered from glacial deposits and by riverine runoff to the sea (*cf.* Fig. 2.6). However, whenever even a small patch of hard substrate occurs in a sand-dominated environment, macroalgae attach and the biodiversity of the area increases (Fig. 11.2c).

11.1.2 Algae and vascular plants grow on different substrates

The phytobenthic communities on hard substrates are dominated by attached macroalgae (Fig. 11.2a, c), but aquatic mosses, too, may attach to hard substrates. Rooted vascular plants increase proportionally with decreasing substrate grain size (*cf.* Table 2.3), and on sandy and soft substrates (silt and

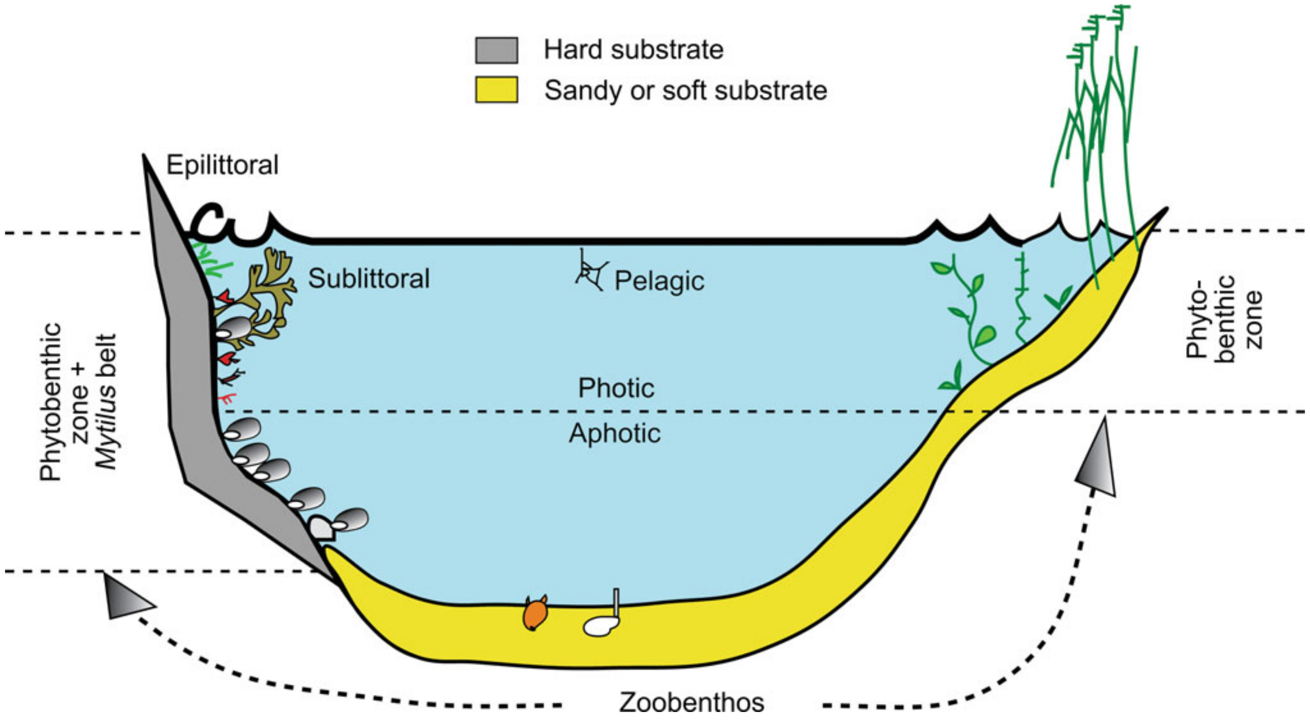


Fig. 11.1 Schematic summary of habitat variability in the phytobenthic zone, which comprises the photic zone that contains vegetation on hard, sandy and soft substrates. The *Mytilus trossulus* belt, which stretches down to a ~30 m water depth into the aphotic zone, is usually included in phytobenthic studies in the Baltic Sea Area. Figure: © Hans Kautsky

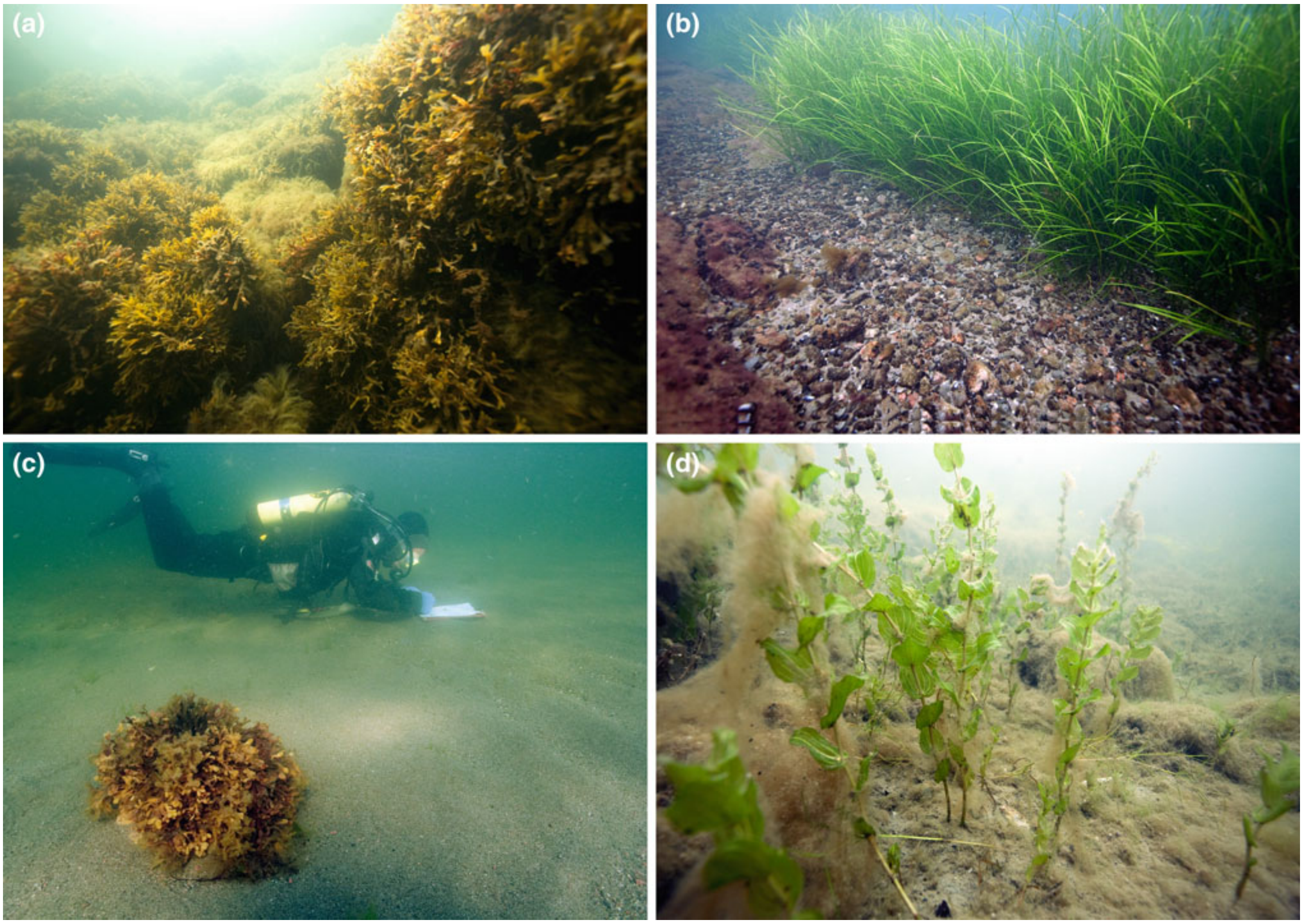


Fig. 11.2 Phytobenthic communities on different substrates in the Baltic Sea. (**a**) A *Fucus*-dominated vegetation on hard substrates. (**b**) A *Zostera marina*-dominated vegetation on sand and gravel to the right, red algae on stones to the left. (**c**) A *Fucus*-dominated vegetation on a boulder, surrounded by sand on which a macroscopic vegetation is lacking because of substrate instability. (**d**) A *Potamogeton perfoliatus*-dominated vegetation with the brown filamentous alga *Pylaiella littoralis* as epiphyte on soft substrate. (**a**, **c**, **d**) Höga Kusten, Bothnian Sea, (**b**) Askö, Baltic Sea proper. Photo: © Hans Kautsky

mud) they dominate the vegetation (Fig. 11.2b, d). One group of algae, the charophytes, grow on sandy and soft substrates as well. They are anchored with root-like filaments (rhizoids) that can be used for nutrient uptake (Vermeer et al. 2003). The vegetation on sandy and soft substrates stabilises the substrate: vascular plants achieve this by their rhizomes and roots and the charophytes by their rhizoids.

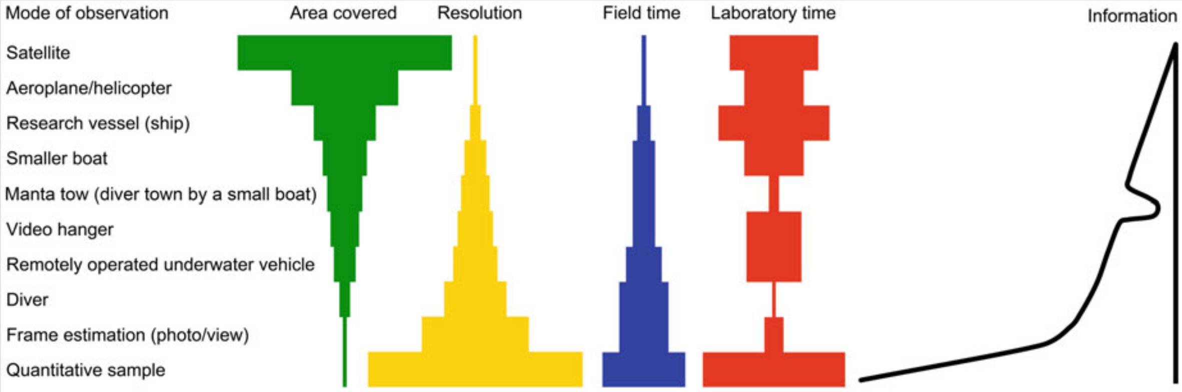
A mosaic of different substrates ("mixed substrates") yields the highest biodiversity of macrophytes and associated fauna since algae, mosses, vascular plants, epifauna and infauna occur side by side (Fig. 11.3). At some highly exposed sites, wind-induced wave action may affect the whole photic zone. However, there usually is a depth gradient with boulders and stones at the water line, because the influence of wind-induced wave action is strongest at the sea surface, and finer material deeper down, with silt and mud in the deepest parts. In most parts of the Baltic Sea, the seafloor in the lower part of the photic zone is covered by soft substrates.

The grain size of the substrate that occurs at a given site is to a large extent determined by sorting through water movement (Box 11.3). At sites continuously exposed to strong wave action (except for areas with sand deposition), only bedrock and large boulders are left as the finer grain sizes are continuously washed away, and the rock is covered by macroalgae. The substrate gets finer in concert with a decrease in wave exposure or current velocity: from boulders to stones (cobbles and pebbles), gravel, sand, silt, and finally to mud (*cf.* Table 2.3). Thereby, the proportion of rooted vascular plants and charophytes in the phytobenthic community increases.

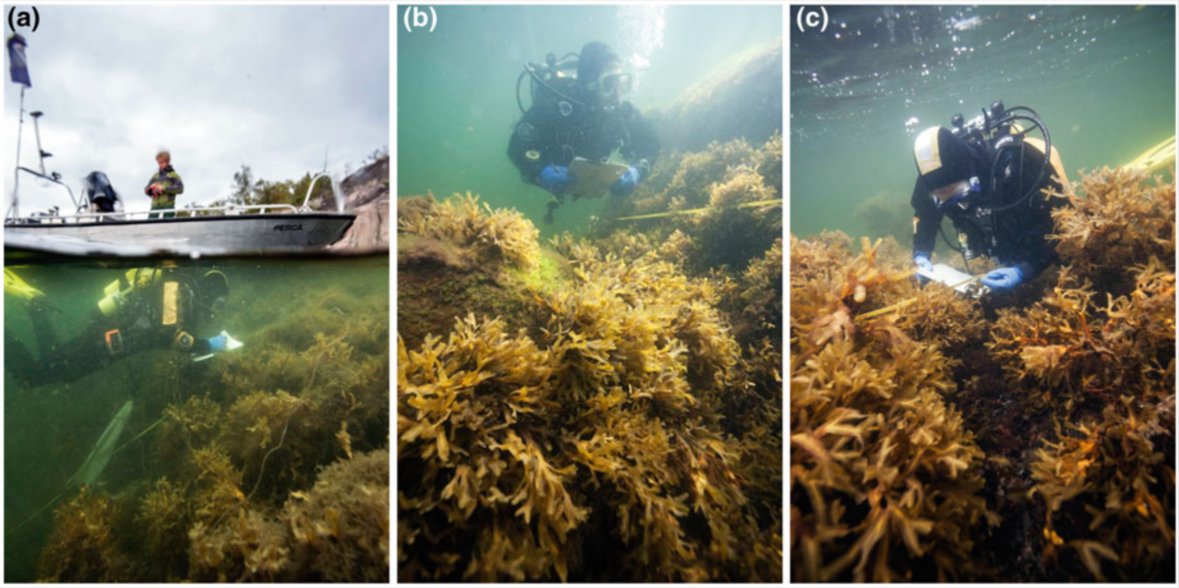
Box 11.1: Methods for studying phytobenthic communities

Different methods

Depending on the scope of the study, indirect or direct methods are used to investigate phytobenthic communities (Box Fig. 11.1). The indirect methods include satellite imagery, aerial photography, laser scanning, multibeam and echosounding detection, which can cover large geographical areas, but the resolution of the community descriptors is poor. These indirect methods yield signals that need to be interpreted and verified through sea-truthing. The observations from space and air also depend on weather conditions (*e.g.* cloudiness) and water turbidity, and biological parameters can usually only be mapped down to a few metres water depth in the dark coastal waters of the Baltic Sea. At the other end of the scale we find direct observation by divers. In many cases, scientific diving is the most reliable method to study the phytobenthic zone because divers can easily take a closer look or remove obscuring objects. Quantitative sampling during diving is the most elaborate method, but achieves the highest resolution of biomass and community composition. In between, there are various other methods, some of which also include diving or more complicated equipment such as underwater vehicles and video equipment hanging from boats. Each method is a trade-off between the area covered, data resolution, time spent to collect the data and information achieved (Box Fig. 11.1).



Box Fig. 11.1 Comparison of the different methods used to study the phytobenthic zone. Figure modified from Kautsky (2013)



Box Fig. 11.2 SCUBA diving to a maximum water depth of 30 m is used for quantitative biological studies in the phytobenthic zone. (**a**) Boat with diving flag and diver making notes. (**b**, **c**) Diver working along a transect in the *Fucus* belt of the Baltic Sea. Photo: © Hans Kautsky

Box Fig. 11.3 A diver using a "Kautsky frame" (recommended by the HELCOM COMBINE Guidelines, http://www.helcom.fi), which is a square with three metal sides and a sampling bag attached to the fourth side of the square (Kautsky 2013). A scraper is used to scrape the phytobenthic communities from the rock into the sampling bag. Photo: © Hans Kautsky

Diving

Marine biologists use diving as a tool to perform observations or experiments below the water surface (Box Fig. 11.2). The diving procedure should be kept as simple as possible so that the diver can focus primarily on the work to be carried out. There should never be any violation of safety rules. These rules are established in national safety regulations for scientific diving and must be followed in the respective countries when diving. Diving may be performed with SCUBA (self-contained underwater breathing apparatus) or with air from the surface (using a hose). The latter method gives the diver unlimited time under water, but the diver is spatially limited by the length of the hose. It is recommended to wear a dry suit with clothes under while SCUBA diving in the cold waters of the Baltic Sea. Since the Baltic Sea underwater environment is also relatively dark, it is also recommended to wear a bright-coloured diving suit or at least bright-coloured flasks, fins and gloves. Divers completely dressed in black are difficult to observe under water, which may be fatal in case of an accident. When using SCUBA diving, field work is limited by depth and time spent under water. For security reasons the maximum depth should not exceed 30 m unless the diver is especially trained for deep-water diving. The work under water should be carried out as easily as possible by not carrying more air and equipment than necessary and by good ahead-planning of the dive, *e.g.* planning to not stay too long in deep water in order to reduce the decompression time on the way back to the surface. The recommended equipment is 2·4·300 atm air tanks (2400 L). Technical diving increases exposure time, but at the cost of heavier equipment and a more complicated handling of the equipment, *e.g.* gas controls. This means that one has more details to keep in mind, which is less secure. Never dive alone unless you have contact to the surface by two-way communication and a security diver at the surface.

Quantitative sampling and depth distributions

The recording of phytobenthic community parameters can be performed along transect lines, with or without frames placed on the seafloor (Kautsky 2013). Estimations of the substrate type and species composition, and their cover on the substrate, requires a botanically skilled diver. A new diver has to practice under surveillance before good work can be performed. Free estimates of overall vegetation coverage in an area are made faster than cover estimates of species within a number of replicate frames (Box Fig. 11.3). However, cover estimates always have a degree of subjectiveness and destructive quantitative sampling is the best method to obtain accurate data on species composition and biomass. Drawbacks are the limited area sampled and the need for many replicate samples to reflect an entire area because the phytobenthic vegetation is usually patchy. Such samples take time (*i.e.* are expensive) to process. The lower limits of occurrence of many species, including the key species *Fucus vesiculosus* and *Zostera marina*, were in earlier years recorded by dredging, *i.e.* without knowing if the species was actually growing at the dredged depth or had drifted there. It was not until SCUBA diving was introduced that reliable data of depth distributions could be collected.

Box 11.2: The early days of scientific diving in the Baltic Sea

Marianne Hielm Pedersén

A pioneer diving ecologist in the Baltic Sea

In 1938, Mats Wærn, a PhD student at Uppsala University (Sweden) became a pioneer in the systematic use of diving and underwater photography for collecting scientific data in the phytobenthic zone of the Baltic Sea (Wallentinus et al. 1992). Until then, dredging had been the only way to study submarine organisms. However, sampling with a dredge mixes organisms from different substrates and depths, so that their exact habitats cannot be determined, and biomass cannot be measured in a reliable way. Mats Wærn was interested in how the macroalgal vegetation on rocky shores changes along environmental gradients, *e.g.* salinity, exposure to wave action and water depth. He was also in this respect a pioneer because at that time ecology was a young science and most phycologists were taxonomists. Mats

Box Fig. 11.4 Mats Wærn and his team in the 1940s. During his diving expeditions he was assisted by six persons, one diving chief, two persons pumping down air, one person to keep records of the underwater observations transmitted by the diver using a telephone, and two others in a small rowing boat to assist with the camera and other equipment. The copper helmet was put on after the pumping had started and the diver was lowered to the seafloor, and taken up after the dive, with the help of a rope. Anecdotically: before young Mats was allowed to dive, his mother tested walking on the seafloor in a heavy diving suit and found it safe enough for her son to practice. (**a**) Mats in the thick clothing he wore under his diving suit. (**b**) Mats in his heavy diving suit with the rope around his chest. (**c**) Nils Quennerstedt (also a PhD student at Uppsala University at that time) preparing for a dive. (**d**) Mats going down, note the rope, air hose and telephone line. Photo: © Uppsala University

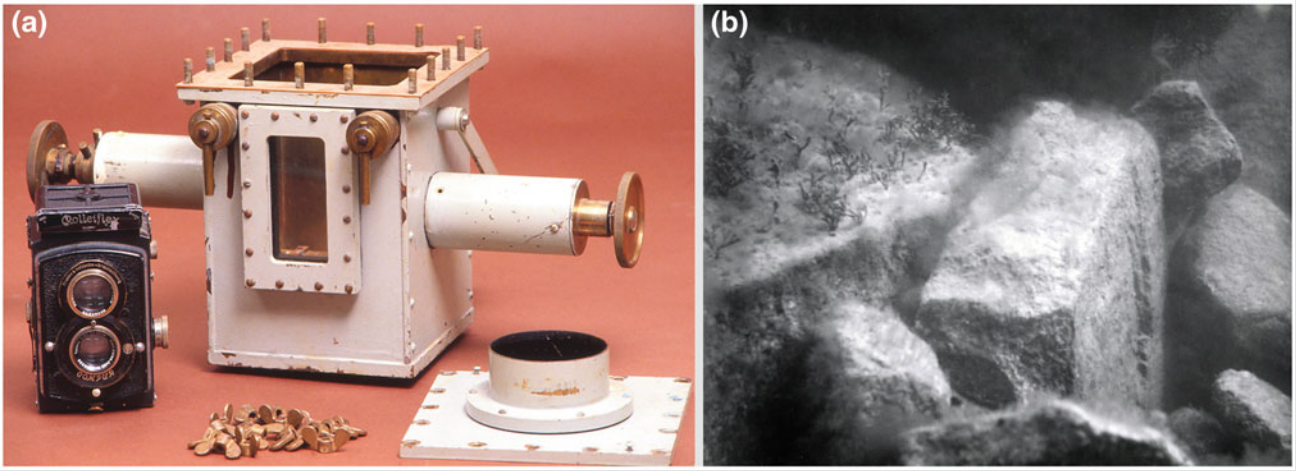
Wærn's herbarium, kept at Uppsala University (Sweden), is an "ecological herbarium", *i.e.* he mounted whole communities on the herbarium sheets (*cf.* Fig. 11.28a), including animals. His doctoral thesis "Rocky-shore algae in the Öregrund archipelago" (Wærn 1952) is a rich source of both ecological and taxonomic information on the macroalgae of the Baltic Sea.

A heavy diving suit

Mats Wærn still used a heavy diving suit (Box Fig. 11.4) because the aqua-lung, the first open-circuit, self-contained underwater breathing apparatus ("SCUBA") had not been invented until 1943, by the engineer Émile Gagnan and the naval lieutenant, explorer and filmmaker Jacques-Yves Cousteau. While a SCUBA diver floats in the water, a diver with a heavy diving suit walks around on the seafloor. This has both advantages and disadvantages: walking on the seafloor may be more stable, like walking on land, and diving time is much longer (Mats Wærn's dives usually lasted for 4–5 hours); however, it is easy to stir up sediments and destroy one's view. The diving suit Mats Wærn used was the so-called "German double suit" with the lead weights around the waist, which was safer for a marine biologist compared to the alternative in the 1940s, an "English heavy suit" with the lead weights hanging on the chest. Since the diver had to crawl on his knees when sampling the algal vegetation there was a more significant risk with the English suit that the diver would come up with his legs first if he should lose his balance and allow air into the lower part of the diving suit.

Underwater photography

Mats Wærn designed a water-proof camera housing for photographing the *in situ* phytobenthic communities (Box Fig. 11.5). This enabled him to use the camera under water and even to adjust the distance and wind the film, the lock on the camera housing having been tightened with 16 winged nuts. However, he could not set the aperture and exposure time under water. Therefore, Mats first measured the aperture and exposure time with a Sixtus light meter in a glass jar and reported the data to his assistants in the boat by telephone. Then the assistants prepared the camera, tightened the 16 winged nuts, and lowered the camera down into the water with a rope. When Mats received the camera he waited until the light meter gave the same values as before and then took the photograph. The phytobenthic communities were recorded following a standard procedure. When Mats found a suitable place he ordered "weight down" and the water depth was determined with a rope and a weight at its lower end. Then he made a general survey of the type of seafloor and all vegetation in sight, usually within a distance of 2–8 m, and estimated the degree of coverage for the different algal species on a 1–5 ordinal scale. All observations were directly reported by telephone to the record-keeper in the boat. A frame was placed on the rock and the cover in the frame was estimated, after which all algae within the frame were scraped off from the rock surface, collected in a bag, and sent up for later detailed analyses in the laboratory, including microscopy and herbarium mounting.



Box Fig. 11.5 Early underwater photography in the Baltic Sea. (**a**) Mats Wærn's Rolliflex camera with the water-proof housing. (**b**) A photograph taken with this camera, showing the lower limit of the *Fucus* vegetation (in the upper left part of the photograph) and *Battersia arctica* on the vertical surface (in the right part of the photograph) at a water depth of 10 m at an exposed site at Halsaren in the Södra Kvarken area (Sweden). The photograph was taken on 17 July 1944 at 4 p.m. with aperture 3.5 and exposure time 1/2 seconds. Photo: © Uppsala University

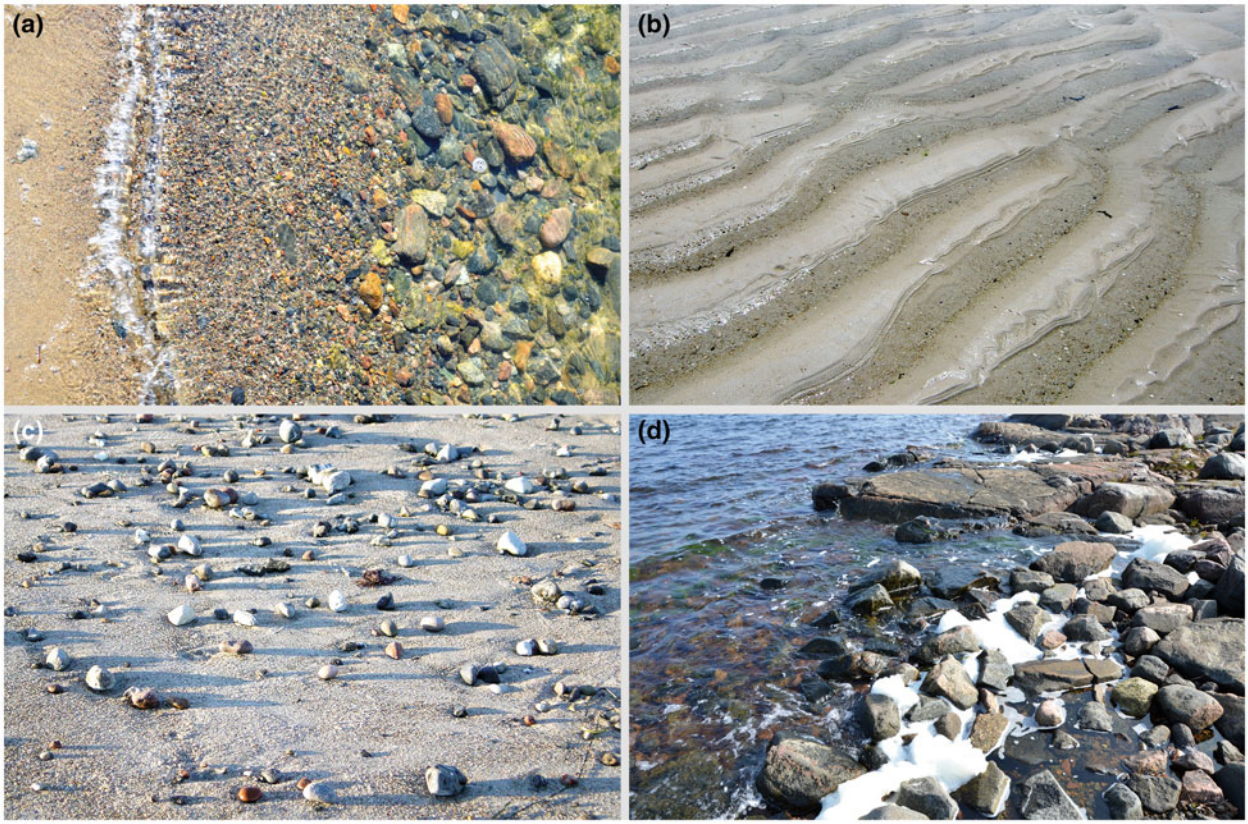
Box 11.3: Water movement determines the type of substrate

Water movement determines the type of substrate along the coasts because sediment grains are sorted by grain size in water movement. For example, when the waves lose energy by friction, first stones, then gravel and finally sand are deposited on a beach (Box Fig. 11.6a).

Along sandy coasts, a constant transport of sand takes place. Depending on the local water movement, sand is either deposited along the shoreline or an aberration of the shore occurs. On sandy bottoms, ripple marks are shaped by the sorting of grain size (Box Fig. 11.6b), and can be observed from the water surface down to a water depth of >30 m at offshore sites.

On unstable sandy beaches the sand is constantly moved by wave action. When the sand is washed away by a storm, larger stones and boulders are left and are subsequently covered by a new sand layer. This is particularly visible after storms when the shoreline can look entirely different than before the storm, *e.g.* a beach can suddenly be covered by stones when storm waves wash away the sand that completely covered the stones before the storm (Box Fig. 11.6c). This also occurs below the water surface and, especially in areas where the waves break, temporary stone ridges can appear.

A steady stream of large waves leaves only bedrock and boulders on an exposed beach. Often foam is created in this process (Box Fig. 11.6d), which is a natural phenomenon; decaying organic matter allows the seawater to mix with air and foam can accumulate where waves break on the coast.



Box Fig. 11.6 Water movement determines the type of substrate along the coasts. (**a**) The waves are sorting sediment by grain size. (**b**) Ripple marks shaped by sorting according to grain size. (**c**) An unstable sandy beach covered by stones and boulders after a storm. (**d**) A steady stream of large waves leaves only bedrock and boulders on an exposed beach. Photo: (**a**, **d**) © Pauline Snoeijs-Leijonmalm, (**b**, **c**) © Hendrik Schubert

Fig. 11.3 The highest diversity in the phytobenthic communities of the Baltic Sea is found on mixed substrates. Here, patches of *Fucus vesiculosus*-dominated vegetation on hard substrate grow mixed with patches of *Stuckenia pectinata*-dominated vegetation on soft substrate at Askö, Baltic Sea proper. Photo: © Hans Kautsky

Coasts with bedrock and boulder fields dominate in the western and northeastern Baltic Sea proper, as well as in parts of the Gulf of Finland and the Gulf of Bothnia (*cf.* Fig. 2.8). On coasts directly exposed to the open sea, a macroalgal vegetation can be found on the bedrock and large boulders throughout the whole photic zone (Fig. 11.4). In boulder fields, which are more common in the Baltic Sea than exposed bedrock, the boulders often occur mixed with patches of smaller-grained and soft substrate. Therefore, boulder fields usually support a "mixed vegetation" (consisting of both macoalgae and vascular plants) that is dominated, depending on the relative amounts of the different substrate types, by attached algae or rooted vascular plants and/or charophytes (Fig. 11.5).

11.1.3 The vegetation along a substrate gradient

The typical archipelago coasts of the Baltic Sea are characterised by gradients in exposure to wave action. Water circulation strengthens towards the outer archipelago (Fig. 11.6). This increases the transport of particles and decreases sedimentation so that bedrock is mainly found at the outer edges of the archipelago while boulders tend to dominate the outer and middle parts, and soft substrates the inner parts. At the outer skerries, soft substrates start at a ~25 m water depth or deeper, but in the innermost archipelago area soft substrates with submerged vascular plants may start already at an 0.1 m water depth – if not replaced by a reed belt.

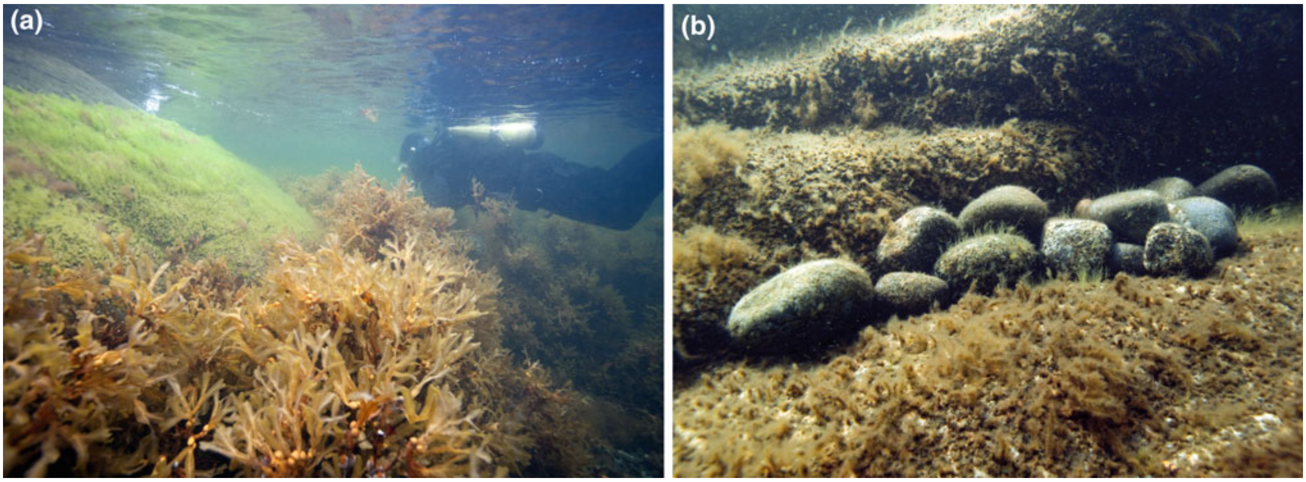


Fig. 11.4 Bedrock is dominated by algal communities. (**a**) The *Cladophora* belt and the *Fucus* belt on bedrock at Askö in the Baltic Sea proper. (**b**) A *Pylaiella littoralis*-dominated vegetation on bedrock and boulders at Höga Kusten in the Bothnian Sea. Photo: © Hans Kautsky

From the inner archipelago to the outer archipelago, the phytobenthic vegetation shifts in concert with the available substrate (Fig. 11.6), from a vegetation dominated by rooted plants (Fig. 11.7a) via a mixture of algae and vascular plants (Fig. 11.3) to algae-dominated communities (Fig. 11.4). Common on soft substrates are also communities that consist of entangled loose-lying vascular plants and/or algae (Fig. 11.7b).

Along an archipelago gradient, salinity-dependent community changes may occur in the case of freshwater runoff causing a horizontal salinity gradient. Furthermore, archipelago gradients are often accompanied by nutrient gradients because the influence of land-derived nitrogen and phosphorus is usually larger in the inner parts than in the outer parts of an archipelago.

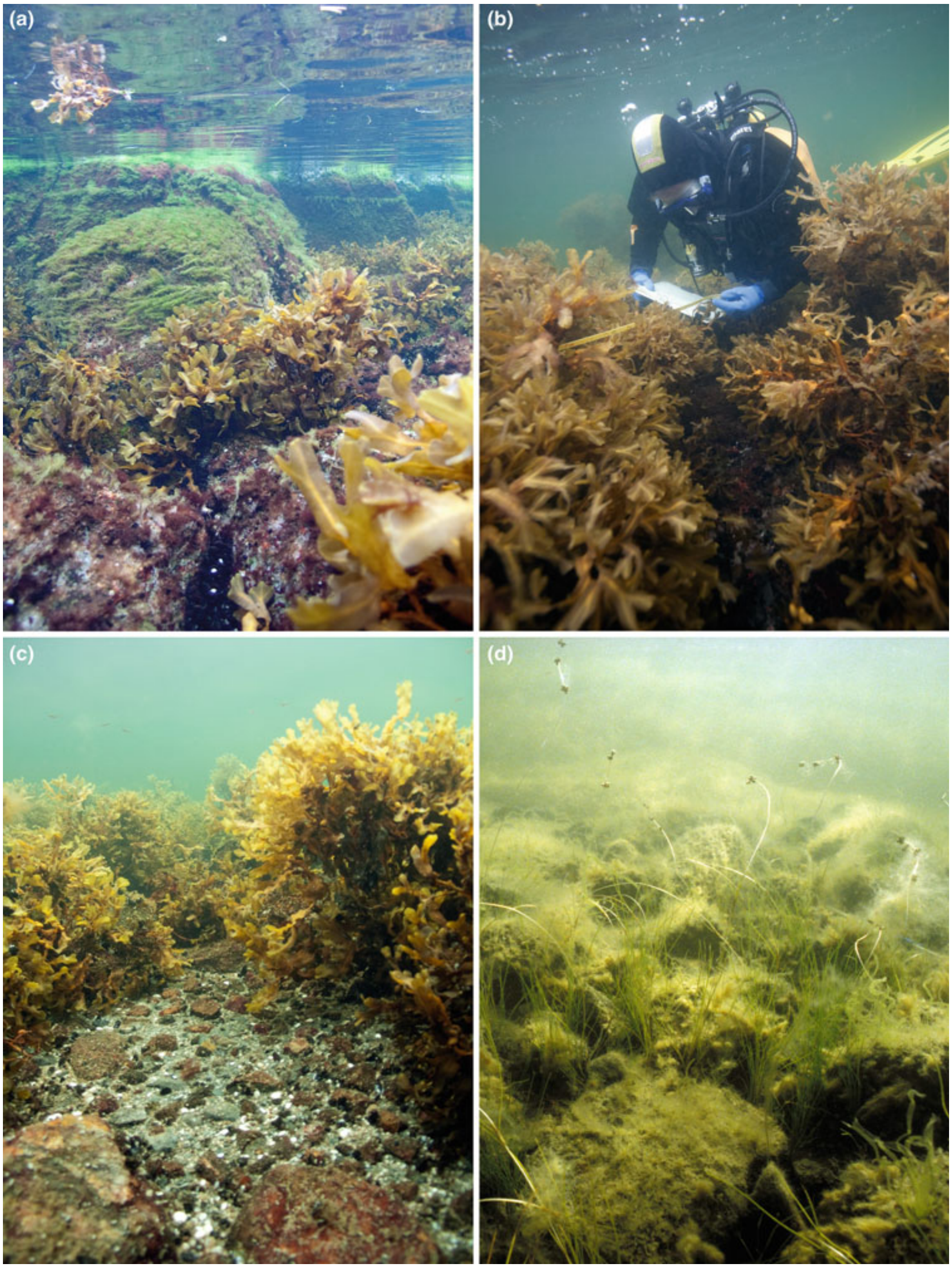


Fig. 11.5 Boulder fields with algal and mixed vegetation. (**a**) Boulders at a 1–2 m water depth with a zonation of *Cladophora glomerata*, *Fucus vesiculosus*, *Ceramium tenuicorne* and *Mytilus trossulus*. (**b**) A biologist recording the vegetation on boulders covered by *Fucus vesiculosus* at a ~2 m water depth. (**c**) Boulders at a ~2 m water depth with *Fucus vesiculosus* surrounded by patches of smaller-grained stones (unstable substrate) without vegetation. (**d**) Boulders at a ~0.5 m water depth with filamentous algae surrounded by patches of soft bottom with *Stuckenia filiformis* (syn. *Potamogeton filiformis*). (**a**, **b**, **c**) Askö, Baltic Sea proper, middle archipelago, (**d**) Höga Kusten, Bothnian Sea, inner archipelago. Photo: © Hans Kautsky

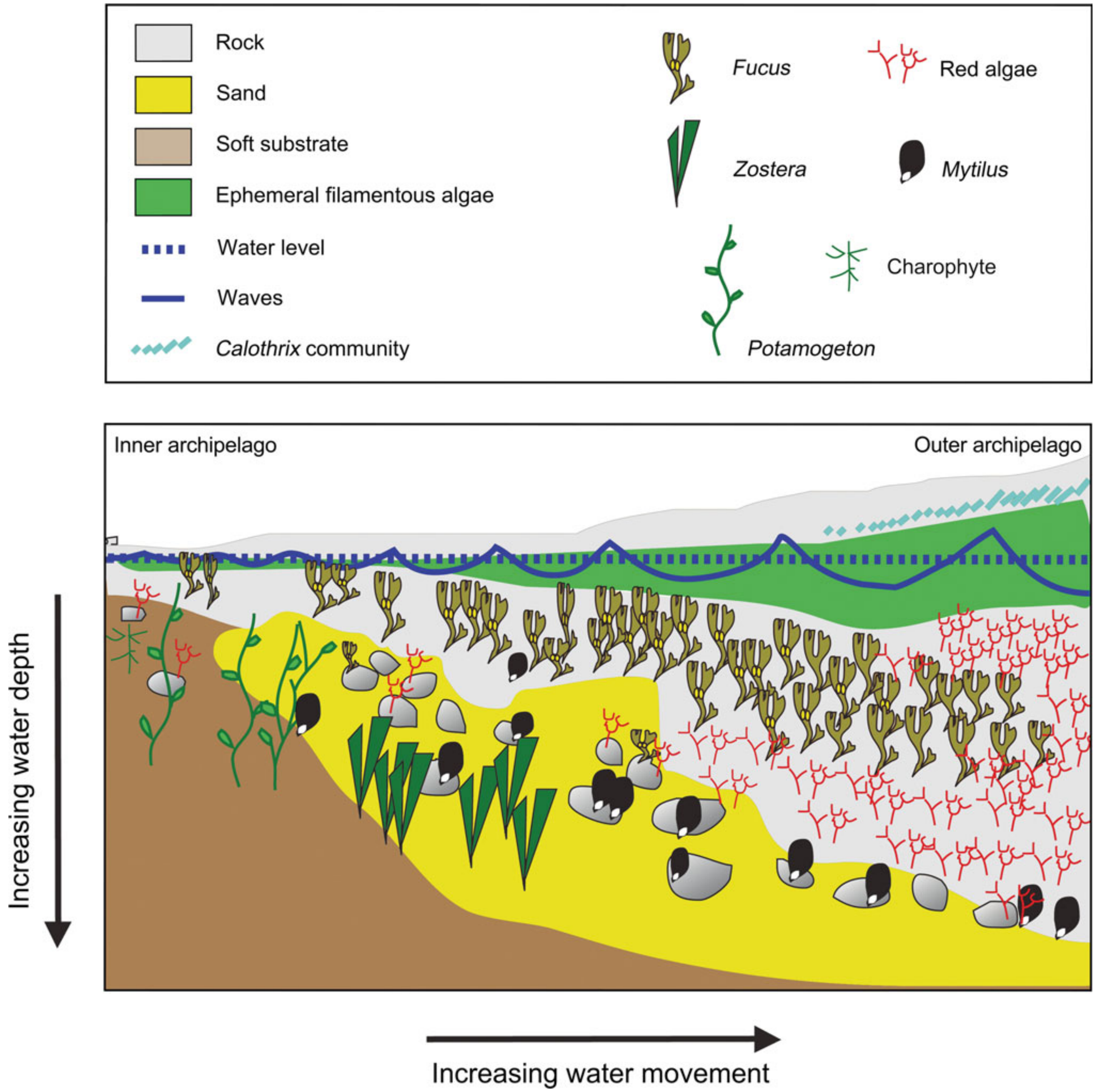


Fig. 11.6 Schematic summary of the relationship between exposure to waves, water depth, substrate and the type of phytobenthic vegetation along an archipelago gradient. Figure: © Hans Kautsky

11.1.4 Different rock types

Most of the rock on which phytobenthic communities grow in the Baltic Sea Area is hard, acidic igneous rock (granite) or metamorphic rock (gneiss). However, porous sedimentary calcareous rock (limestone) occurs in a belt from the southwestern Gulf of Finland, the Estonian islands of Saaremaa and Hiiumaa and Swedish islands of Gotland and Öland to the Danish island of Bornholm. Parts of these limestone coasts consist of klints (*cf.* Fig. 2.8), which are stepwise deeper terraces that follow the geological stratification. The uppermost klint terrace is often sheltered as waves break at its edge some distance from the shore, and it usually has a luxuriant growth of attached vegetation due to high insolation and good water exchange (Fig. 11.8). The klint coasts on the eastern sides of the islands of Saaremaa and Gotland often do not reach a water depth of 10 m until several km away from the coast. This allows phytobenthic vegetation to grow far off from the coastline, forming extensive areas with high primary production.

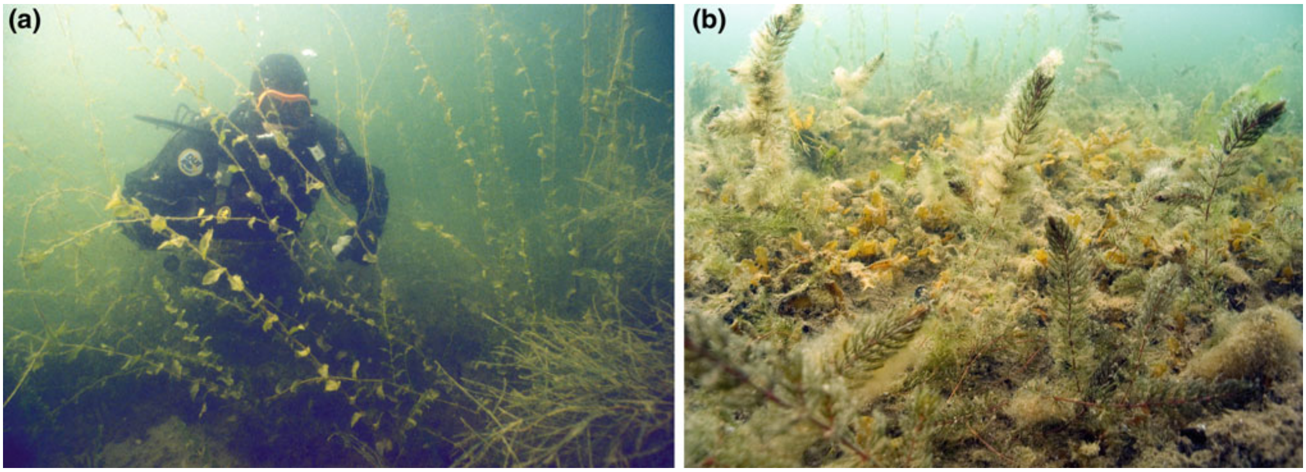


Fig. 11.7 Soft substrates (silt and mud) are dominated by rooted vascular plant communities or more or less loose-lying communities of vascular plants and/or algae. (**a**) A biologist studying a phytobenthic community dominated by *Potamogeton perfoliatus* and *Stuckenia pectinata* in Norafjärden, Bothnian Sea. (**b**) A phytobenthic community of loose-lying *Ceratophyllum demersum* entangled with loose-lying *Fucus vesiculosus* on soft substrate at Askö, Baltic Sea proper. Photo: © Hans Kautsky

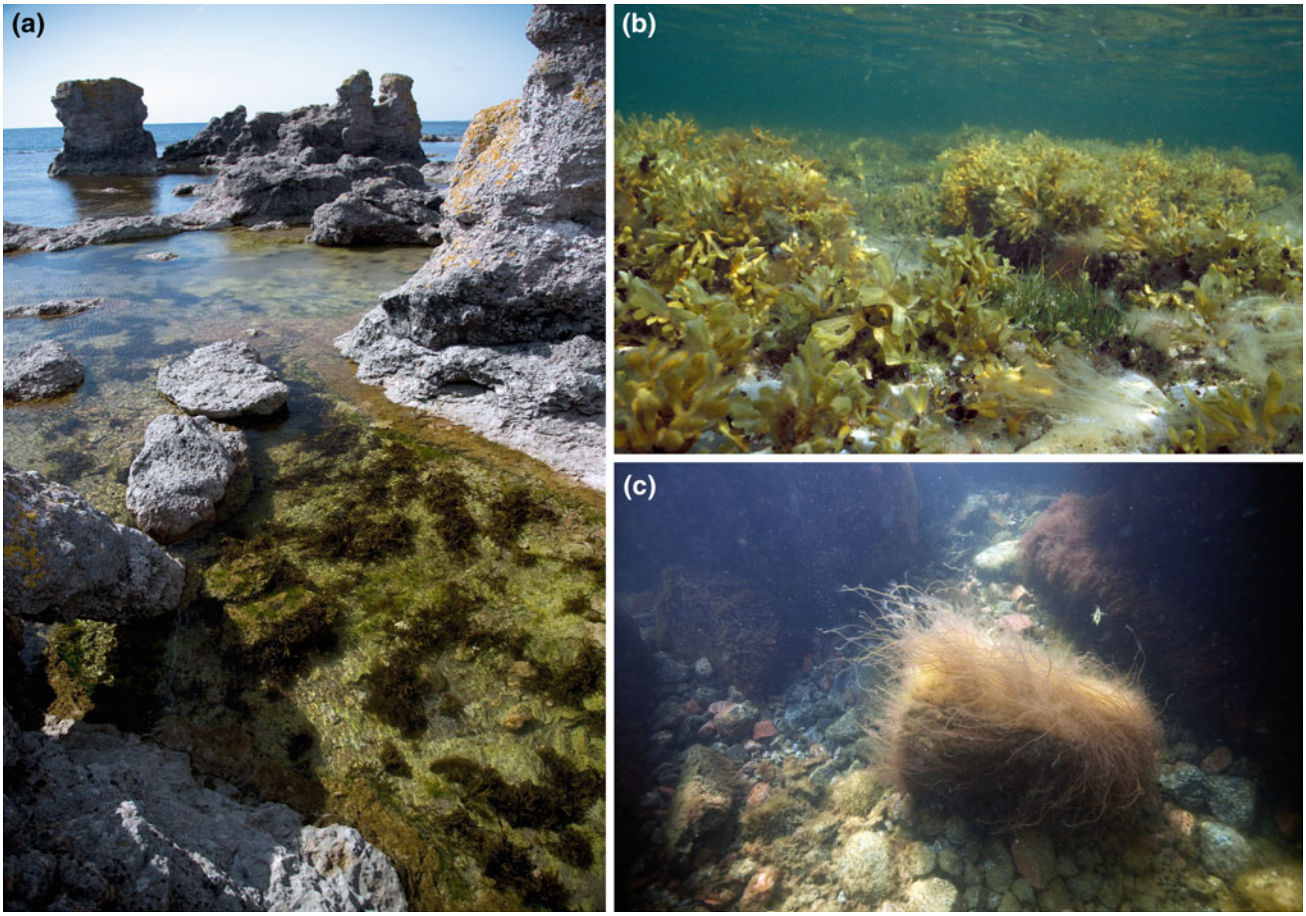


Fig. 11.8 Limestone cliffs and their submerged vegetation. (**a**) Limestone rauk coast at Gotland in the Baltic Sea proper, with *Fucus vesiculosus* in the small lagoons. (**b**) *Fucus vesiculosus*-dominated vegetation at a wave-exposed site with a small patch of *Ruppia spiralis*. (**c**) A limestone cliff exposed to strong wave action on the eastern coast of Gotland with an unstable substrate of rounded boulders and stones at a 2–3 m water depth. More stable boulders support a luxuriant growth of the annual brown algae *Chorda filum* and *Pylaiella littoralis*. The surrounding rock is covered by the red alga *Ceramium tenuicorne*. Photo: © Hans Kautsky

Limestone shows large variability in quality as the substrate type depends on the geological origin of the exposed layer, which determines the type of vegetation. However, it is the grain size and stability, not the chemistry, of the substrate that affects the species composition of the phytobenthic communities. A typical vegetation of the first klint consists of, *inter alia*, the brown macroalgae *Fucus vesiculosus*, *Chorda filum* and *Dictyosiphon foeniculaceus* and colonies of the cyanobacterium *Rivularia atra*. Also vascular plants, such as *Ruppia maritima*, *Ruppia cirrhosa* (syn. *Ruppia spiralis*), *Stuckenia pectinata* (syn. *Potamogeton pectinatus*) and *Zannichellia palustris*, as well as charophytes, grow here in limestone gravel. Limestone with substantial amounts of clay incorporated ("marl") is rather unstable and, therefore, a poor substrate for algae with large thalli such as *Fucus vesiculosus*, but it creates an excellent habitat for filamentous algae.

11.1.5 Substrates far away from coasts

Boulder fields deposited by the glacial ice have created submerged offshore stone reefs in the Baltic Sea Area, *e.g.* the Słupsk bank off the Polish coast, the Adlergrund in the Arkona Sea and Lilla Middelgrund, Stora Middelgrund, Morups bank and Fladen in the Kattegat (*cf.* Fig. 2.2; Pedersén and Snoeijs 2001; Andrulewicz et al. 2004; Zettler and Gosselck 2006). At these reefs, continuous currents prevent sedimentation so that macroalgae can attach, but the boulders and algae also create refuges where benthic organisms are protected from mechanical disturbance by the same currents.

Compared to the sand-dominated coasts of Poland and Germany, the Słupsk bank and the Adlergrund host communities with rich growth and high diversity of macroalgae, invertebrates and fish (Andrulewicz et al. 2004). Since these offshore stone reefs are unaffected by direct land-runoff and sedimentation, but are subject to strong currents, the algae are remarkably clean and healthy and may, if hard substrate is available, penetrate deeper than at most coastal sites. In the shallow Kattegat, the deep-water currents of the continuous inflow of saline water from the Skagerrak into the Baltic Sea (*cf.* Sect. 2.3.7) pass the offshore stone reefs below the halocline, which is probably an additional reason for the extremely high diversity and good condition of the algae at the offshore stone reefs in the Kattegat (Fig. 11.9).

Other shallow offshore areas in the Baltic Sea proper and the Gulf of Bothnia, *e.g.* the Hoburgs bank, Södra Midsjö bank and Norra Midsjö bank (*cf.* Fig. 2.2), are dominated by relatively unstable wave-sorted till deposits, although attached specimens of the red alga *Coccotylus truncatus* can be observed here at a ~32 m water depth. In contrast to the offshore stone reefs in the Kattegat, the Hoburgs bank and the Midsjö banks are low in biodiversity. Due to the rather unstable substrate, perennial species do not persist and annual species dominate. However, *Mytilus* beds with >3 kg dry weight m^{-2} can be found at the Hoburgs bank and the Midsjö banks (Kautsky 1984), and are a sign of the high productivity of these areas.

Of still lower diversity, due to continuous substrate instability, are the submerged sand banks in the Baltic Sea proper (*e.g.* the Odra bank) and the Bothnian Bay. Such sand banks lack attached vegetation and only a few invertebrate species can cope with the extreme environmental conditions

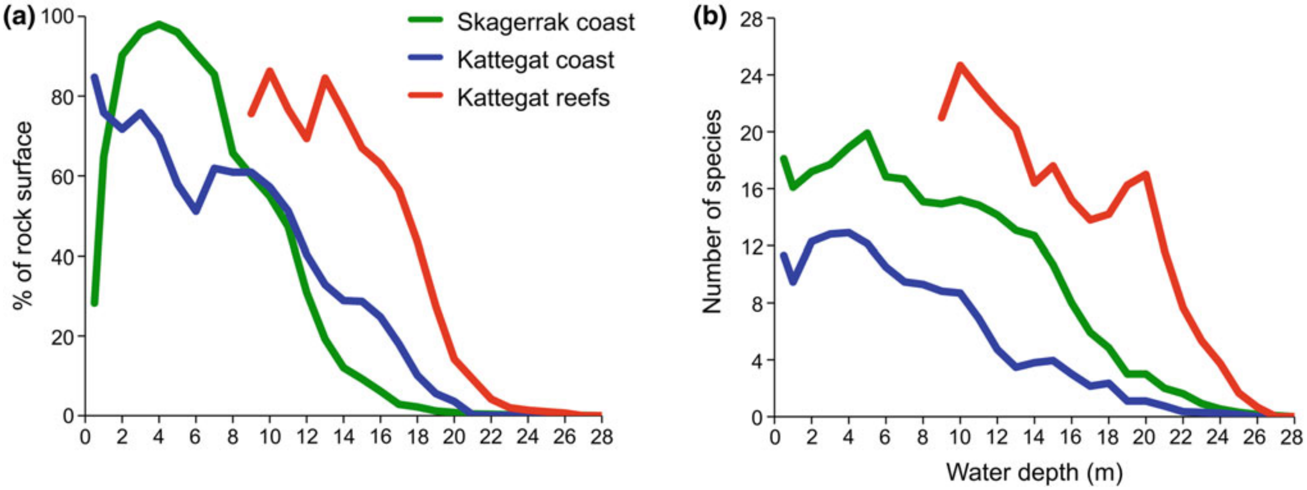


Fig. 11.9 Comparisons between the phytobenthic communities at offshore stone reefs in the Kattegat and those at wave-exposed coastal sites in the Kattegat and the Skagerrak. (**a**) Vegetation coverage. (**b**) Species richness. The higher diversity at the coastal sites in the Skagerrak is due mainly to the higher salinity. The higher diversity and cover at the reefs are caused by a combination of low sedimentation and higher salinity below the halocline (in the Kattegat situated at a 15–20 m water depth). The graphs represent means of 15 diving transects at coastal sites in the Skagerrak, 23 transects at coastal sites in the Kattegat and 12 transects at the offshore stone reefs in the Kattegat. Figure modified from Pedersén and Snoeijs (2001)

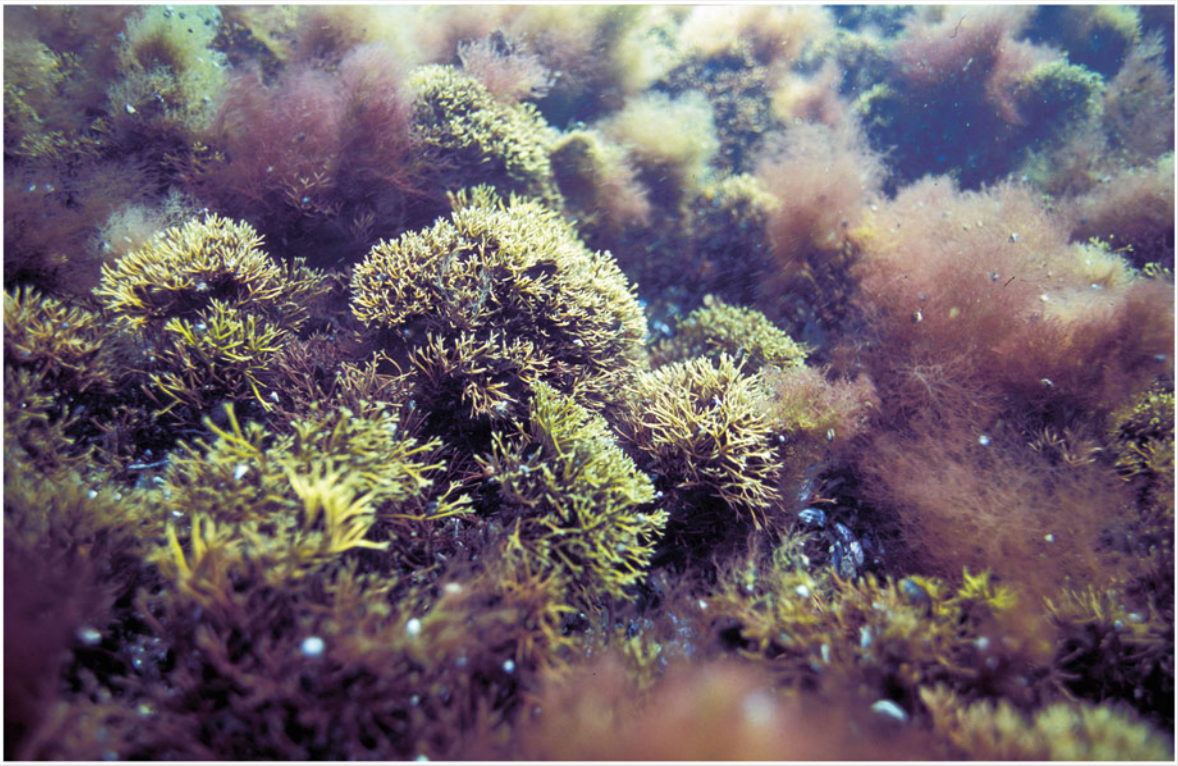
Box 11.4: Commercial harvest of macroalgae

The target compounds: polysaccharides

Polysaccharides are long molecules in which there are spaces that can be filled by water. This water-binding capacity is utilised when polysaccharides from algae are employed as additives to stabilise, thicken and smoothen human foods such as ice-cream, puddings, weight-loss products and as an alternative to gelatin for vegetarians (additives numbered E400-407a in the European Union classification). The algae use these polysaccharides to strengthen their cell walls as a protection against damage from being repeatedly thrown against the rocks by strong waves and to resist desiccation in the intertidal zone. The polysaccharides agar and carrageenan are extracted from red algae, and alginates are derived from brown algae. While no negative health effects have been reported for agar and alginates, the use of carrageenan in human food has been debated since the 1970s, especially in connection with colon cancer and diabetes (Tobacman 2001; Yang et al. 2012; Bhattacharyya et al. 2015), although food authorities in Europe and the USA consider it safe.

The algae harvested

Norway is one of the world's largest producers of alginates from Laminariaceae harvested in the wild along the Atlantic coast. In tropical countries, the red algae *Gracilaria* spp. (agar), *Eucheuma denticulatum* (carrageenan) and *Kappaphycus alvarezii* (carrageenan) are cultivated in large amounts, but in the Baltic Sea Area wild *Furcellaria lumbricalis* (Box Fig. 11.7) is harvested to obtain a product called "furcellaran", "Danish agar" or "Baltic agar", which is a form of carrageenan. The majority of the global *Furcellaria lumbricalis* harvest comes from Denmark and Canada, but the eastern coast of the Baltic Sea proper also hosts a large loose-lying *Furcellaria lumbricalis*-dominated community, which is commercially harvested in Estonia (Martin et al. 2006a, b; Bučas et al. 2009). In the early 1900s, large quantities of loose-lying *Furcellaria lumbricalis* occurred in the Kattegat (Austin 1959), but because of overexploitation this population has declined. *Furcellaria lumbricalis* was previously included in the HELCOM list of threatened or declining species in the Baltic Sea Area (HELCOM 2007), but is not on this list anymore (HELCOM 2013a). However, it is necessary to carefully monitor its standing stock and to decide if and how much can be sustainably harvested each year.



Box Fig. 11.7 *Furcellaria lumbricalis* is common along the northern European and Canadian marine coasts where it can be 30 cm in diameter. It is the largest red alga with a wide distribution in the Baltic Sea, although it is smaller in thallus size than on fully marine coasts. Together with other red algal species *Furcellaria lumbricalis* forms the red algal belt of the Baltic Sea proper. *Furcellaria lumbricalis* is a key species with an important structural role in the ecosystem, either attached to hard substrates or in loose-lying algal aggregates. Photo: © Hans Kautsky of high exposure to currents and low salinity due to runoff from local rivers. However, some species of suspension-feeding invertebrates can reach high densities at the Odra bank, *e.g.* the bristle worm *Pygospio elegans*, the amphipod *Bathyporeia pilosa*, the brown shrimp *Crangon crangon*, and the bivalves *Cerastoderma glaucum*, *Macoma balthica*, *Mya arenaria* and *Mytilus trossulus* (Zettler and Gosselck 2006). These high concentrations of invertebrates attract fish and waterbirds, as well as fisheries, which creates conflicting interests (Sonntag et al. 2012).

11.1.6 Macrophyte vegetation without a substrate

Macrophytes may be ripped off their substrate by wave forces and transported away with the currents. This is an important mechanism of vegetative dispersal for algae, and even for vascular plants, as they may find a new substrate elsewhere and grow further, often by first getting entangled in the attached vegetation. However, it is also common for the ripped-off macrophytes to end up on the shore and die (Fig. 11.10).

Some algae clearly have two different life forms: they occur both attached to a hard substrate or as loose-lying balls moving around with the prevailing currents. Examples of such species are the marine red alga *Furcellaria lumbricalis* (Box 11.4) in the Kattegat and the southeastern Baltic Sea proper and the freshwater green alga *Aegagropila linnaei* (syn. *Cladophora aegagropila*) in the Gulf of Bothnia.

In nutrient-rich places with weak water exchange, loose-lying algae may form aggregates called “algal mats”. These algal mats may be lying on the seafloor and/or float in the water column and form species-rich communities, often with macroalgae as a basis and accompanied by bacteria, cyanobacteria, protists and fauna. In nutrient-rich sheltered bays algal mats may be a natural phenomenon in summer, but the occurrence and abundance of algal mats increase with eutrophication and may become a nuisance, *e.g.* by preventing growth of an attached vegetation or by clogging of fishing nets. Furthermore, thick layers of decomposing algal mats can cause shallow-water anoxia, kill the benthic fauna, lead to the formation of hydrogen sulphide and the release of nutrients from the sediment in the same way as in the deep soft-bottom system of the Baltic Sea (*cf.* Fig. 10.12).

11.2 Vegetation changes along the large-scale Baltic Sea gradient

11.2.1 Loss of community diversity

Salinity is the most important factor for the macrophyte species distributions in the Baltic Sea on an ecosystem-wide scale (*cf.* Figs. 4.10a and 4.18b) and is based on the species’ salinity tolerances. The loss of marine macroalgal species along the Baltic Sea salinity gradient governs the structure and composition of phytobenthic communities to a large extent. Most phytobenthic vascular plant and charophyte species in the Baltic Sea are of freshwater origin, but, given their different substrate requirements, they cannot compensate for the loss of macroalgal species on hard substrates.

The changes in community composition from the Baltic Sea proper to the Bothnian Sea and further to the Bothnian Bay, are more stepwise than gradual, *i.e.* community composition changes radically at the sill areas of Södra Kvarken and Norra Kvarken because salinity conditions are relatively stable within each of the three basins, but there is a salinity gradient between them (*cf.* Fig. 4.2). Since there is no sill between the Gulf of Finland and the Baltic Sea proper the changes in community composition with salinity are more gradual here, but may be overshadowed by vegetation changes caused by the heavy eutrophication of the inner Gulf of Finland.

11.2.2 The “downward process” of marine macroalgae

When following the salinity gradient from the Skagerrak via the Kattegat, the Belt Sea and into the Baltic Sea, many marine algae that on the Atlantic and North Sea coasts are found in the intertidal and upper sublittoral zones occur in increasingly deeper water. For example, the mean upper depth limit of the relatively euryhaline species *Saccharina latissima* (syn. *Laminaria saccharina*) changes from a 1.5 m water depth in the Skagerrak to a 4 m depth in the Kattegat (Pedersén and Snoeijs 2001). Simultaneously, the less euryhaline species *Halidrys siliquosa* extends its depth range from 1 to 9 m and *Corallina officinalis* from 2 to 12.5 m.

The three canopy-forming brown algae: *Fucus vesiculosus*, *Fucus serratus* and *Saccharina latissima* differ in how far they penetrate into the Baltic Sea (Fig. 11.11). Of these three species, *Fucus vesiculosus* is best adapted to the low salinity of the Baltic Sea and *Saccharina latissima* least. At the inner Baltic distributional limit of *Saccharina latissima* in the southern Baltic Sea proper (the island of Bornholm, Denmark), its upper limit lies at the water depth of ∼20 m (Wærn 1965).

This phenomenon of successive downward dislocation with lower salinity is called “brackish-water submergence” or, as defined for the vegetation in the Baltic Sea, “the downward process” (Svedelius 1901; Wærn 1965). However, in the case of the large-scale Baltic Sea gradient, this process is more related to the horizontal salinity gradient than to a vertical salinity gradient in the water column. Initially, in the Skagerrak and Kattegat, the downward

Fig. 11.10 Algae washed ashore. (**a**) Red algae at the island of Gräsö in the southern Bothnian Sea. (**b**) The common gull *Larus canus* looking for something to eat among the algal debris in the Ekenäs archipelago in the Gulf of Finland. (**c**) Brown and red algae at the island of Gotland in the Baltic Sea proper. Photo: (**a**, **b**) © Pauline Snoeijs-Leijonmalm, (**c**) © Hans Kautsky

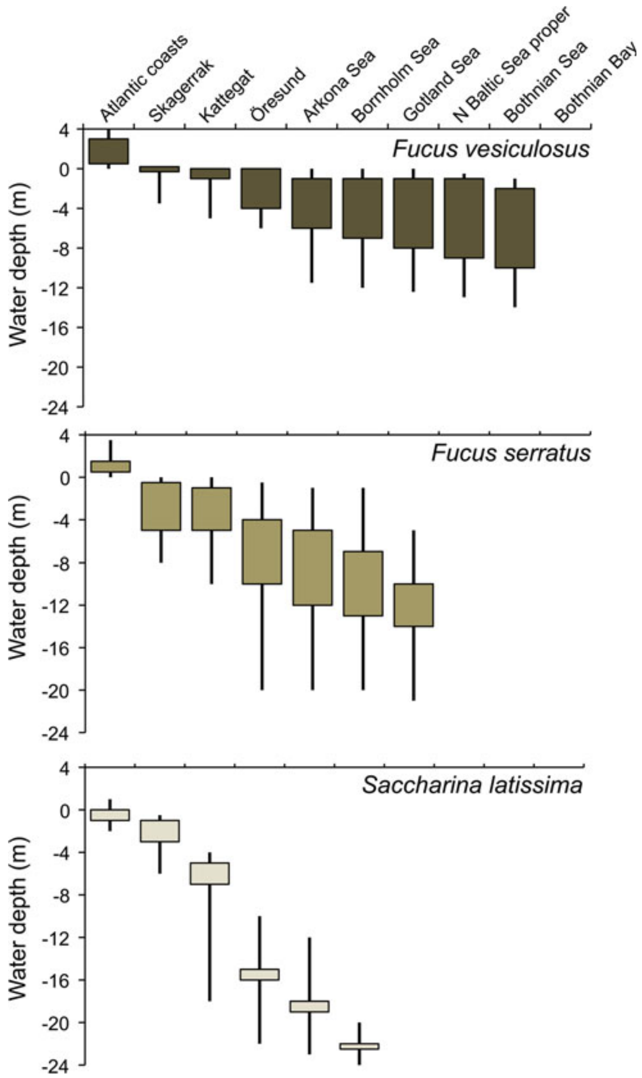


Fig. 11.11 Schematic summary of the downward process of the canopy-forming brown algae *Fucus vesiculosus*, *Fucus serratus* and *Saccharina latissima* along the large-scale Baltic Sea gradient. In the Bothnian Sea "*Fucus vesiculosus*" also includes *Fucus radicans*. The "zero" line is set at the waterline. Figure based on depth-distribution data from Wærn (1952, 1965), von Wachenfeldt (1975) and Pedersén and Snoeijs (2001)

process is obviously in some way, directly or indirectly, related to the reduction in surface-water salinity with water depth, as well as to the reduction of the tides towards the Baltic Sea (*cf.* Sect. 2.3.3). The Atlantic intertidal species *Fucus vesiculosus* and *Fucus serratus* live permanently submerged in the Baltic Sea and broaden their vertical distribution from 1–2 m to 15–20 m (Fig. 11.11). On the Atlantic coasts each of these two *Fucus* species is restricted to a specific narrow depth interval through competition with the species above and below them. Already in the Skagerrak they live submerged and extend deeper than many of their competitors, which are weakened by the low salinity.

11.2.3 The "downward process" inside the Baltic Sea

Inside the Baltic Sea the halocline is located far below the photic zone (*cf.* Fig. 2.15), and the downward process is driven by the tolerances of the algal species to low salinity, not by a vertical salinity gradient. From the Kattegat to the Bornholm Sea the depth extensions of *Fucus vesiculosus* and *Fucus serratus* maximise, but north of the Kalmarsund area and at the southern tip of the island of Gotland *Fucus serratus* has its northern limit.

Along the large-scale Baltic Sea gradient, *Fucus vesiculosus* seems to "press down" *Fucus serratus*, which in turn "presses down" *Saccharina latissima* and other species through competition (Fig. 11.11). This may partly be explained by a reduced competition when species diversity decreases successively along the Baltic salinity gradient (Torn et al. 2006a). However, at sites where *Fucus vesiculosus* and *Fucus serratus* occur together, *Fucus vesiculosus* grows from an ~0.5–1 m water depth and is joined by *Fucus serratus* at a ~3 m depth. The two species then grow together in approximately equal proportions down to the lower limit of *Fucus vesiculosus* at a 10–12 m water depth, and thereafter *Fucus serratus* is found deepest, usually a few metres deeper than *Fucus vesiculosus*. As they grow together in a broad belt, competition between these two *Fucus* species does not seem to be strong in the Baltic Sea. It is possible that *Fucus serratus* is better adapted to low irradiance, but this has not been proven.

11.2.4 Depth penetration – set by CDOM or eutrophication?

The attached vegetation in the Kattegat generally penetrates deeper (on average down to ~25 m) than it does in the Baltic Sea (on average down to 10–20 m) (Pekkari 1965; Wærn 1965; Kautsky 1995a; Pedersén and Snoeijs 2001). Exceptions are single specimens of *e.g.* the brown alga *Battersia arctica* (syn. *Sphacelaria arctica*) and some species of crustose algae, which may penetrate 5–10 m deeper than the lower limit of most other primary producers in the Baltic Sea.

It has been suggested that high concentrations of coloured dissolved organic matter (CDOM, *cf.* Sect. 15.2.6), which gives the water a yellowish-brown colour, limit the depth extension of attached growth of benthic primary producers

Box 11.5: The measurement of water movement

Different methods are used to measure or predict the forces of the wave action experienced by primary producers and animals in the phytobenthic communities at coastal sites. The method chosen depends on the focus of the study. The methods most frequently applied today involve *in situ* sensors and GIS-based modelling.

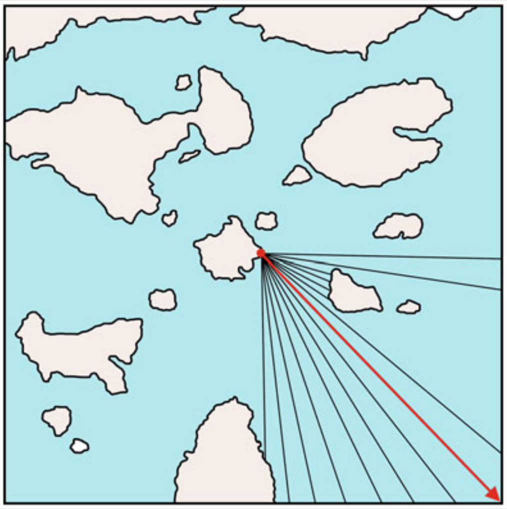
***In situ* sensors** perform direct measurements, thus providing the best information on the degree of water movement to which the organisms living at that spot are exposed. An abundance of instruments has been described in literature, from highly complicated expensive constructions to pieces of chalk that slowly dissolve in the water. Today, small cheap sensors are available that can be applied in the field. However, when employing instruments in the field, it is of course necessary to ensure that their mere presence does not alter the currents.

The Baardseth index is a simple cartographic measure of the "openness" of a coastal site (Baardseth 1970). It can be determined by placing the centre of a transparent circular disc with a radius of 7.5 km and subdivided into 40 sectors (each with an angle of 9°) at the study site on a 1:50,000 nautical chart (Ruuskanen et al. 1999). The Baardseth index represents the number of sectors without skerries, islands or mainland. Small solitary rocks at the periphery of the disc may be ignored. The Baardseth index varies between 0 and 40, where 0 indicates the extreme shelter and 40 denotes the maximum exposure.

The effective fetch is a cartographic measure that describes the average distance within which a wave can collect energy before it meets a coastal study site. This measure was originally designed for lakes, and is based on 15 measurements of the distance between the study site and the nearest skerry, island or mainland (Håkansson 1977). The central radius of a 90° fan shape is positioned from the study site towards the main wind direction (Box Fig. 11.8) and the distance (χ_i in km) from the study site to land is measured for each of the deviation angles from the central radius (γ_i) of −42°, −36°, −30°, −24°, −18°, −12°, −6°, 0°, 6°, 12°, 18°, 24°, 30°, 36° and 42°. The effective fetch (L_f) is then calculated as $L_f = (\sum \chi_i \cos|\gamma_i|)/(\sum \cos|\gamma_i|)$. The value of the effective fetch depends on the measured distances and is not restricted by a maximum value (if not defined). Additional calculations based on an effective fetch can be made by including *e.g.* wind speed and water depth.

GIS-based wave exposure models have been developed to provide estimations of water movement more precisely than the Baardseth index or the effective fetch (Ekebom et al. 2003; Isæus 2004). In the geographic information system (GIS), detailed wind direction, wind speed and water movement data from nearby meteorological stations are included in calculations for each angular section, and parameters such as wave height can also be estimated.

Microhabitats may have exposure conditions that differ substantially from cartographic measures and GIS-based models. Correct measurement of water movement in defined microhabitats can be obtained only with *in situ* sensors. It should be kept in mind that there are major differences in water movement on a small scale, *e.g.* between the top and the side of a boulder.



Box Fig. 11.8 The principle of calculating the effective fetch for a defined sampling station (red dot). The red arrow denotes the main wind direction. The black lines indicate the directions of the lines (each with a defined deviation angle). The lengths between the sampling station and the nearest land for all of these lines are used in the calculations. Figure: © Pauline Snoeijs-Leijonmalm as it does for phytoplankton (*cf.* Sect. 2.4.6). However, although CDOM does change light conditions in the water, some well-studied species (*e.g. Fucus vesiculosus*) grow generally deeper down in the CDOM-richer Bothnian Sea than in the Baltic Sea proper (Fig. 11.11). This is probably related to the lower degree of eutrophication (lower phytoplankton biomass) in the Bothnian Sea compared to the Baltic Sea proper.

The opposite is found in the eastern Gulf of Finland, where the lower limit of the vegetation is usually much shallower than in the Baltic Sea proper due to heavy eutrophication. Today the high phosphorus input from the city of Sankt-Petersburg has decreased, but there is still a high nitrogen input from Lake Ladoga via the Neva river. Eutrophication usually increases the turbidity of the water column by increasing phytoplankton growth, which decreases light availability on the seafloor (Kautsky et al. 1986). At the same time sedimentation increases and decreases the available area of hard substrate so that algae cannot attach with their holdfasts anymore. However, sedimentation is usually of lower importance than shading by phytoplankton because wind-induced waves do not change with eutrophication at a given site, *i.e.* at exposed sites the sedimented material is removed by water movement and at sheltered sites soft bottoms already occur.

11.2.5 Shading and scouring by ice

Further to the north of the Baltic Sea, in the Bothnian Bay, another factor that is thought to limit the depth distribution of the vegetation, probably much more important than the high CDOM concentrations here, is the ice cover that shades the seafloor for up to six months per year. Furthermore, at the northernmost latitudes of the Baltic Sea (64–66 °N) the lower declination of the sun causes a larger portion of the insolation to reflect due to higher albedo, despite long summer days with almost midnight sun. Thus, less light energy can penetrate deeper down into the water column in the Bothnian Bay than in the rest of the Baltic Sea, and the lower limit of the vegetation here is only ~10 m.

The scouring of ice can mechanically disturb the phytobenthic communities close to the water surface, usually down to a ~1 m water depth but occasionally deeper. The largest damage to the attached vegetation by ice scour is caused at wave-exposed open sites during ice break-up in spring. The influence of ice scouring is strongest in the northern Gulf of Bothnia and the eastern Gulf of Finland, where an ice cover occurs every year and lasts longer than in the south of the Baltic Sea (up to half a year in the Bothnian Bay, *cf.* Sect. 2.4.4). The most dramatic effects of ice scouring may be observed on some coasts in the Norra Kvarken area facing the Bothnian Bay, where land vegetation (including lichens on the rock) is destroyed for several metres high up on the shore (Fig. 11.12a). In this area, 17-m high ice piles from ridging have been observed on land, as well as substantial damage to the sublittoral phytobenthic communities (Fig. 11.12b, c).

11.3 Factors structuring the vegetation on local scales

11.3.1 Water movement

Besides its indirect effect on community composition by substrate sorting (*cf.* Sect. 11.1), water movement has a significant effect on macrophyte growth, both by its physical drag force and by its transport of nutrients and metabolites. At low to moderate velocities, currents typically stimulate both the biomass and diversity of the phytobenthic communities, but at higher velocities the macrophyte growth is reduced. For example, the tallest and widest *Fucus vesiculosus* thalli are found at the sheltered end of an exposure gradient and the smallest and narrowest thalli at the most exposed end (Ruuskanen et al. 1999).

The actual water movement at a given site (microcurrents, *e.g.* around a boulder) can be measured with *in situ* sensors (Box 11.5). Also, several exposure indices based on simple cartographic models, such as the Baardseth index and the effective fetch, have been designed to estimate the amount of water movement that is experienced by the phytobenthic communities. However, more detailed modelling, based on geography, wind and current data in the geographic information system (GIS-based), is often used today.

Extreme wave exposure can even turn boulders around at a substantial water depth and restrict macroalgal growth (Fig. 11.4b). On strongly wave-exposed bedrock, the algal vegetation is kept short by the constant mechanical disturbance and/or can only attach in sheltered microenvironments such as rock crevices (Fig. 11.13a–c). With less water movement, *e.g.* at the lee side of an island, or within archipelagos, conditions are more sheltered and the vegetation can grow higher and form more diverse phytobenthic communities.

Larger algae may utilise the forces of waves to control their filamentous algal competitors by the so-called “whiplash effect” (Dayton 1975; Kiirikki 1996a). For example, especially when the *Fucus vesiculosus* vegetation is sparse, filamentous epiphytes and undergrowth are continuously removed by the *Fucus* tufts as they are swept around by waves (Fig. 11.13d).

11.3.2 Light and substrate availability

In an archipelago area, the depth penetration of attached macroalgae usually increases from the inner archipelago to

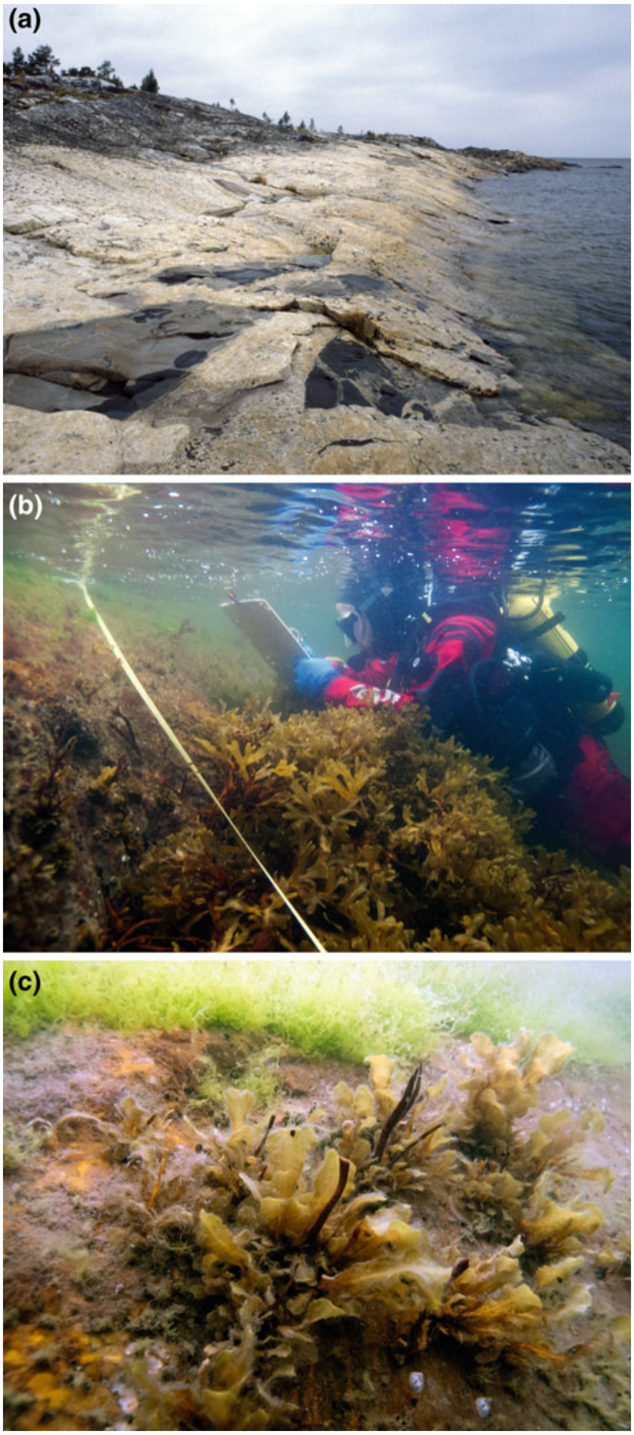


Fig. 11.12 Effects of the annual ice scouring on the coast of Holmöarna at the Norra Kvarken sill between the Bothnian Sea and the Bothnian Bay. (**a**) Enormous amounts of ice have been pressed on to the cliffs and have thereby scraped off the lichens several metres up on the shore. Only bare rock with some terrestrial vegetation in deep crevices is left. (**b**) A biologist documenting the effects of ice scouring on the *Fucus* vegetation. (**c**) Ice scouring has ripped off older *Fucus* plants and new recruits have started to grow. Photo: © Hans Kautsky

the islands furthest away from the coastline (Fig. 11.6). The reason for this is twofold. Firstly, an increase in wind-induced currents towards the outer archipelago increases the amount of suitable (hard) substrate deeper down. Secondly, the influence from terrestrial runoff, and thus the turbidity of the water, decreases.

The algal depth penetration at the outer archipelago is usually set by light availability. When hard substrate is available down to the deepest part the photic zone, the algae become smaller and darker with water depth through slow growth and high pigment concentrations proportional to the increasing light stress (Fig. 11.14a). In the case of a sudden disappearance of the algal vegetation with water depth, this is usually due to the lack of suitable substrate deeper down (Fig. 11.14b). With the decrease in water movement towards the inner archipelago, the hard substrate deeper down turns into mixed and soft substrates closer and closer to the water surface, limiting the algal depth penetration. It is not the light but the lack of suitable substrate deeper down that limits the depth penetration of the macroalgae, and they are replaced by rooted plants.

Sublittoral light quality depends on water depth. In coastal waters the maximum transmittance occurs at 500–575 nm (Jerlov 1976), *i.e.* in the green part of the energy spectrum, which means that green light penetrates deepest down in the water column. This has been used to explain why red algae occur deepest on *e.g.* Atlantic coasts according to the "theory of complementary chromatic adaptation", and even to explain why red algae have evolved red pigments in the form of phycobilins. However, the combined physiological evidence supports the notion that the changes in pigment composition that are observed with increasing depth in marine algae are largely adaptations to low irradiance, and not to the spectral composition of underwater light (Dring 1981). For example, increases in phycoerythrin concentrations in red algae are responses to low irradiances, and not to green wavelengths, of light. More important for algal zonation is that the photosynthetic apparatus of the species growing deeper down is more sensitive to low irradiance (Johansson and Snoeijs 2002) and that a thin thallus is essential for the growth and survival of marine macroalgae at great depths (Markager and Sand-Jensen 1992).

11.4 Microhabitats and biotic interactions

11.4.1 Vegetation layers

Like a terrestrial forest, the attached aquatic vegetation can be subdivided into several vertical layers that create

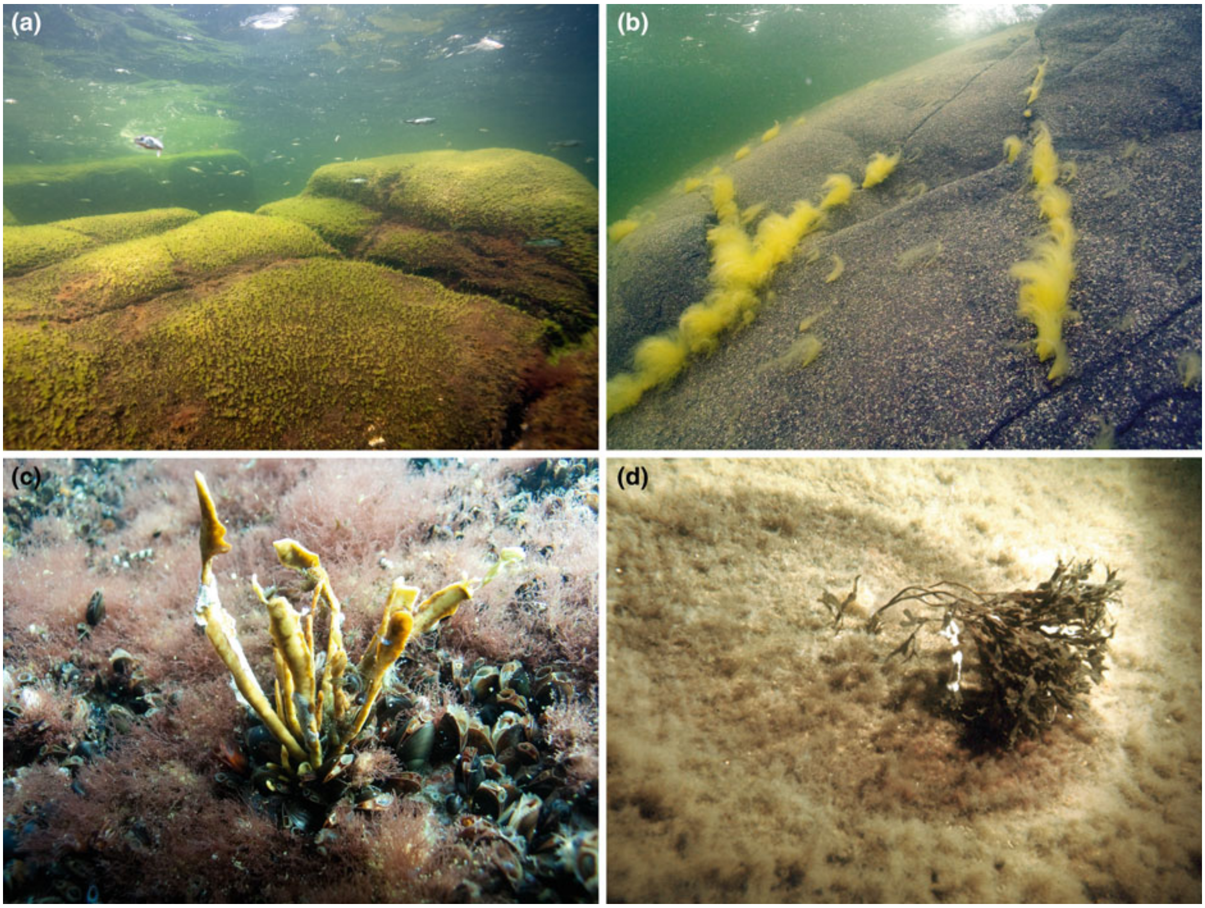


Fig. 11.13 Mechanical disturbances at sites exposed to strong wave action. (**a**) The *Cladophora glomerata* vegetation on the bedrock is kept short by the continuous mechanical forces on the algal thalli. (**b**) *Cladophora glomerata* can only attach in deep crevices in the bedrock. (**c**) The thallus of *Fucus vesiculosus* is continuously ripped off and only basal parts of the alga are left. Here the basal parts of *Fucus vesiculosus* are accompanied by *Ceramium tenuicorne* and *Mytilus trossulus*. (**d**) A *Fucus vesiculosus* tuft controlling the growth of filamentous algae (epiphytes and undergrowth) by the whiplash effect. Photo: (**a**–**c**) © Hans Kautsky, (**d**) © Svante Pekkari

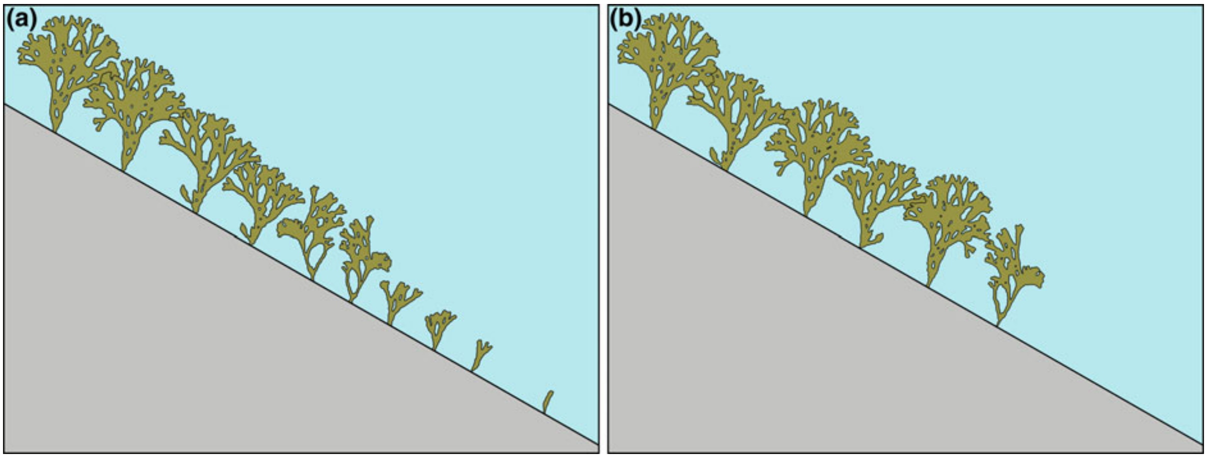


Fig. 11.14 The lower depth limit of *Fucus vesiculosus* can be set by light or by substrate. (**a**) Light penetration through the water column gradually decreases with increasing water depth, which produces a gradual decrease in the thallus size of *Fucus vesiculosus* and dwarf morphology of the lowermost individuals. (**b**) Lack of substrate below a certain depth, often caused by sedimentation, produces an abrupt elimination of the *Fucus vesiculosus* vegetation with no decrease in thallus size. Figure modified from Kiirikki (1996b)

microhabitats for other species in the phytobenthic communities (Fig. 11.15a). The canopy layer consists of large macrophytes such as the bladderwrack *Fucus vesiculosus* and the common eelgrass *Zostera marina*, with no other vegetation above them. The bush layer consists of smaller macrophytes such as *Ceramium tenuicorne*, *Furcellaria lumbricalis* and *Zannichellia palustris*, and the ground layer contains the species that are barely elevated above the substrate, such as crustose algae and *Rivularia atra*.

Each of these three layers supports epiphytes, *i.e.* all species (including animals) attached to the macrophytes. The different vegetation layers are not exactly defined by the macrophyte species in them and the same macrophyte species can create different microhabitat types. For example, the same macrophyte species can belong to different vegetation layers depending on the age of the algal tuft: an attached *Fucus* germling occurs in the ground layer, a first-year *Fucus* in the bush layer and an adult *Fucus* in the canopy layer. Filamentous algae such as *Pylaiella littoralis* and *Ceramium tenuicorne* can occur in the bush layer as well as epiphytically.

11.4.2 Diatoms: an integral part of all vegetation layers

Hundreds of diatom species occur in the sublittoral zone of the Baltic Sea (*cf.* Box Fig. 4.7) and form an important food source for invertebrates, *e.g.* for deposit-feeding snails, in the phytobenthic communities. The diatoms may belong to the inflora (*e.g. Campylodiscus clypeus*, *Martyana atomus*, *Surirella brebissonii*), ground layer (*e.g. Mastogloia smithii*, *Navicula perminuta*, *Nitzschia inconspicua*), epiphytes (*e.g. Cocconeis pediculus*, *Gomphonema olivaceum*, *Rhoicospenia abbreviata*), and some colony-forming diatoms can even belong to the bush layer (*e.g. Berkeleya rutilans*, *Encyonema silesiacum*, *Navicula ramosissima*) (Svensson et al. 2014).

Bush-layer diatom species often live in gelatinous tubes and the colonies can be several dm high, especially in spring (Snoeijs 1990a). At first sight, they look like brown filamentous algae, but when one tries to pick them they fall apart. In the early days of diatom research all colony-forming species were united in the genus *Schizonema* (Greek for "split thread", *cf.* Agardh 1824, 1830), but today they belong to many genera, *e.g. Berkeleya*, *Encyonema* and *Parlibellus*.

Another aspect that should be taken into account is that the biomass of epiphytic microalgae on macrophytes can be extremely high, especially on thin filamentous algae. For example, >95 % of the biomass of a "*Pylaiella littoralis*" sample can in fact consist of diatom cells (Snoeijs 1995). In such a case it would perhaps be fair to consider the algal tuft as a diatom colony instead of a macroalga.

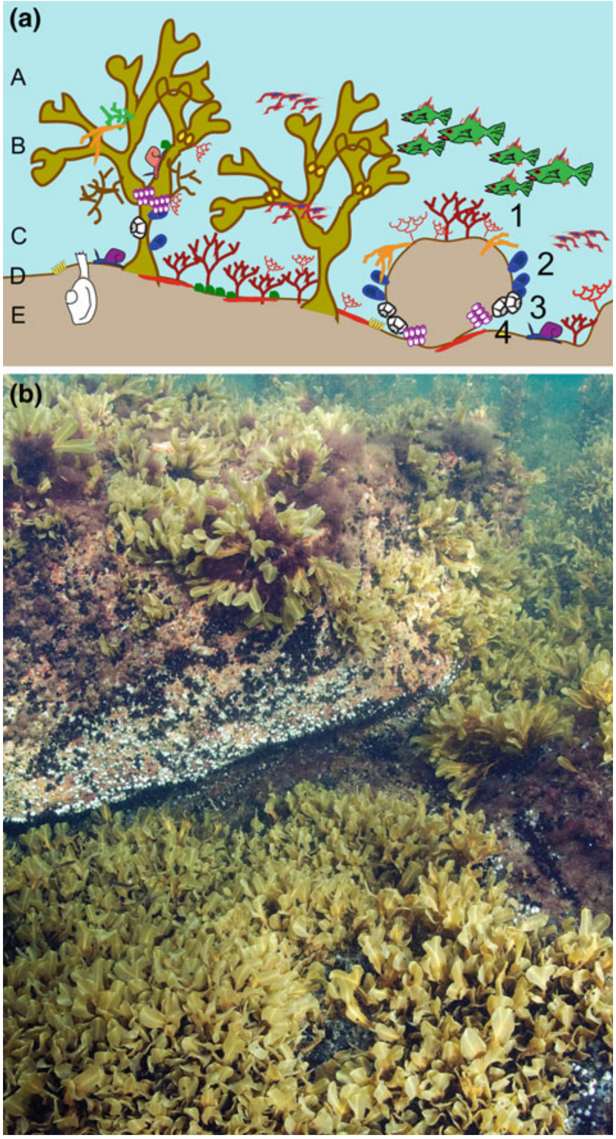


Fig. 11.15 Microhabitats in the phytobenthic zone. (**a**) Schematic summary, showing the different microhabitats: A = canopy layer, B = epiphytes, C = bush layer, D = ground layer, E = inflora and infauna in sandy and soft substrates. Free-living among the vegetation are *e.g.* gammarids, mysids and fish. (**b**) On larger boulders a distinct vertical microzonation pattern may be observed with algae on the top of the boulder, the blue mussel *Mytilus trossulus* (black) below the algae, followed by the balanoid *Amphibalanus improvisus* (white), and in the lowest, darkest places the hydrozoan *Cordylophora caspia* and the bryozoan *Einhornia crustulenta* are found. Besides this microzonation, the photograph also shows a large number of *Fucus vesiculosus* recruits, only a few of which will survive to reproduce after 5–10 years. Figure: (**a**) © Hans Kautsky, Photo: (**b**) © Hans Kautsky

11.4.3 Fauna abundance and species composition

Micro-, meio- and macrofauna organisms seek food, shelter and spawning habitats in the macrophyte vegetation. Some

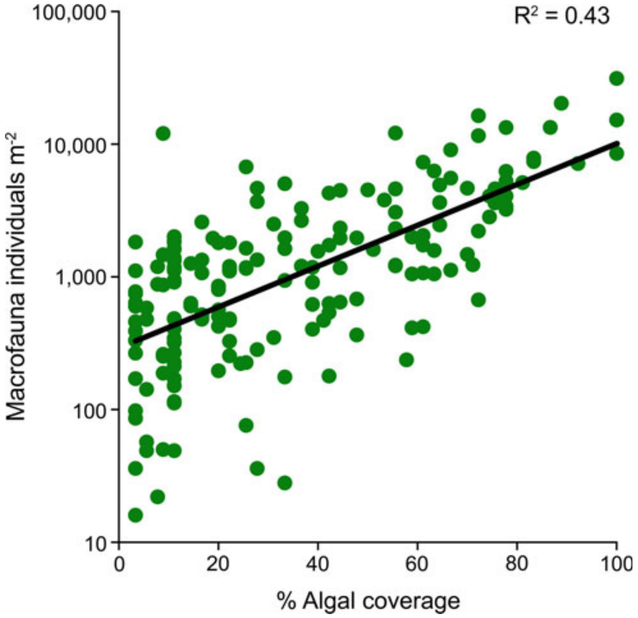


Fig. 11.16 The relationship between epilithic algal coverage and the density of the associated macrofauna (>1 mm) in the *Cladophora* belt at Forsmark in the southern Bothnian Sea (linear regression analysis). With an increase in algal coverage from 1 % to 100 %, the macrofaunal density increases from an average of ~300 individuals m^{-2} to an average of ~10,000 individuals m^{-2}. The data shown in this figure represent 11 sampling sites on 18 sampling occasions throughout one annual cycle. Note the logarithmic scale on the y-axis. Figure based on data in Snoeijs (1989)

animals stay in one of the vegetation layers, but many free-living animals, *e.g.* snails, gammarids, isopods, mysids and fish, move around between the different layers. Below the ground layer there is often a rich inflora and infauna, *i.e.* species living inside sandy or soft substrate below the seafloor, which also belong to the phytobenthic communities.

The number of animals associated with the vegetation is usually directly proportional to the abundance of the vegetation (Fig. 11.16). The species composition of the animals usually depends on the vegetation type. For example, in the western Gulf of Finland different *Gammarus* species prefer different microhabitats in the phytobenthic zone following the algal depth zonation. *Gammarus zaddachi* (Fig. 11.17a) lives mainly at a 0–1 m water depth between filamentous algae and in sheltered locations also in the *Fucus* vegetation, whereas *Gammarus oceanicus* (Fig. 11.17b) lives mainly at a 1–4 m water depth in the *Fucus* belt, and *Gammarus salinus* (Fig. 11.17c) occurs deeper than 4 m associated with red algae and *Mytilus trossulus*. A fourth gammarid abundant in the Baltic Sea, *Gammarus duebeni*, is a typical rock-pool species (Korpinen and Westerbom 2010).

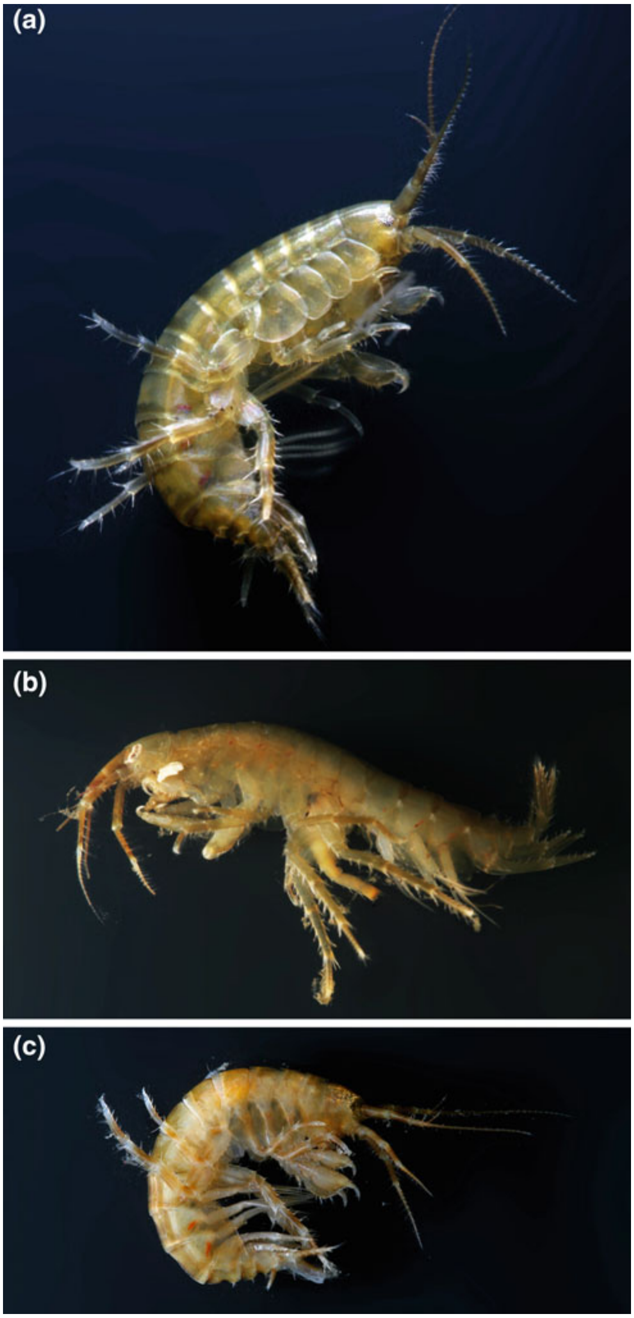


Fig. 11.17 The three native *Gammarus* species that are common in the phytobenthic zone of the Baltic Sea. (**a**) *Gammarus zaddachi* lives mainly at a 0–1 m water depth. (**b**) *Gammarus oceanicus* lives mainly at a 1–4 m water depth. (**c**) *Gammarus salinus* occurs deeper than 4 m. Photo: © Maria Włodarska-Kowalczuk and Piotr Bałazy

11.4.4 Biotic interactions

Biotic processes such as predation and competition operate on smaller scales than environmental drivers such as salinity or currents, *i.e.* at a patch or community scale. In comparison with fully marine systems, biotic interactions seem to be of lower importance in determining the community composition in the phytobenthic zone of the Baltic Sea (Kautsky and van der Maarel 1990; Nyström-Sandman et al. 2012). This is related to the loss of macroscopic species diversity along the large-scale Baltic Sea gradient (*cf.* Fig. 4.10). Thus, the current increase of the diversity of the Baltic Sea through introductions of non-indigenous species (*cf.* Sect. 5.1) has the potential to increase biotic interactions.

The absence of large predators such as starfish (*Asterias* spp.) and larger crabs (*Carcinus* spp.) in the major part of the Baltic Sea is probably the reason why *Mytilus trossulus* can become so abundant (Kautsky 1981). Also, major groups of large marine herbivores such as sea urchins, *Littorina* spp. and *Patella* spp. occur up to the Arkona Sea at most, which decreases the grazing pressure on the aquatic vegetation. However, the Baltic Sea hosts abundant populations of mesoherbivores that may regulate the density and species composition of the vegetation, especially at the early stage of algal colonisation.

An example of competition for space in the Baltic Sea is the distinct vertical microzonation that may be observed on larger boulders with macroalgae on top of the boulder, *Mytilus trossulus* on the side below the algae, the barnacle *Amphibalanus improvisus* below the blue mussel, and lowest down in crevices of the rock the hydrozoan *Cordylophora caspia* and the bryozoan *Einhornia crustulenta* (syn. *Electra crustulenta*) (Figs. 11.15b and 11.18). However, strong competition for space between different *Fucus* species as documented in the intertidal zone of Atlantic coasts (Hawkins and Hartnoll 1985) does not seem to take place in the Baltic Sea, where >10 m wide belts of mixed *Fucus serratus* and *Fucus vesiculosus* occur in the southwestern Baltic Sea proper and >10 m wide belts of mixed *Fucus radicans* and *Fucus vesiculosus* in the Bothnian Sea. On the other hand, *Fucus* recruits are sensitive to both intraspecific and interspecific competition. Out of a thousand established individuals only one or two will survive to reproduce 5–10 years later (Fig. 11.15b).

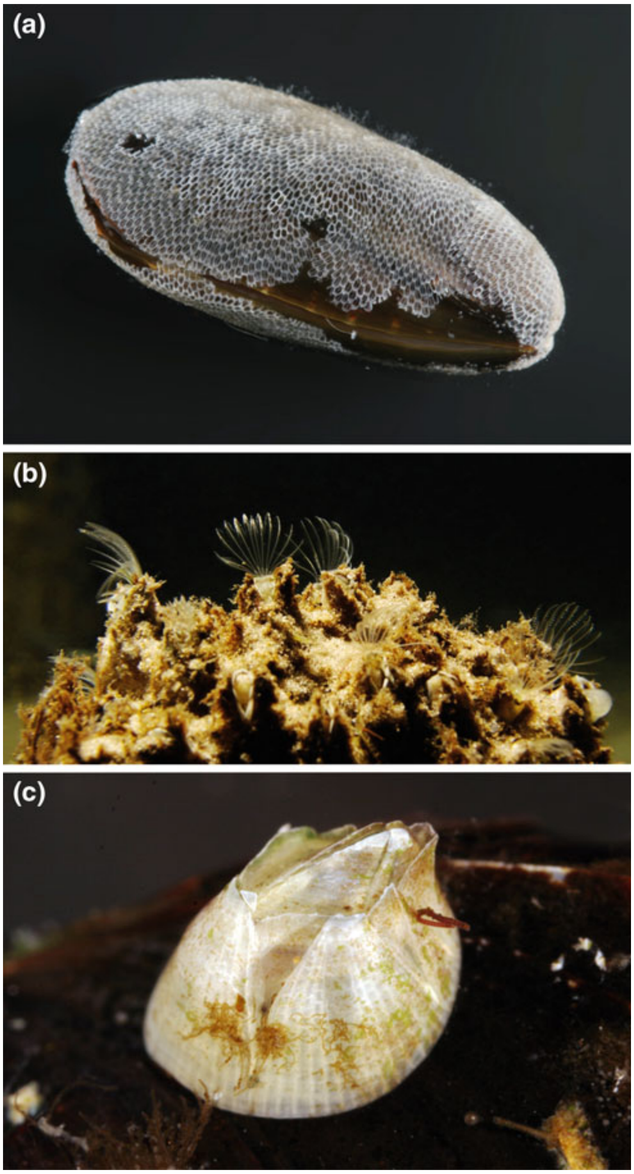


Fig. 11.18 Sessile filter-feeding animals that are common in the phytobenthic zone of the Baltic Sea. (**a**) The bryozoan *Einhornia crustulenta*. (**b**) The barnacle *Amphibalanus improvisus*. (**c**) A closed specimen of *Amphibalanus improvisus*. Photo: (**a**, **c**) © Maria Włodarska-Kowalczuk and Piotr Bałazy, (**b**) Piotr Bałazy

11.4.5 Experimental studies reveal biotic interactions

In general, biotic interactions in the phytobenthic zone are difficult to identify by field observations, and in most cases an experimental approach is necessary. Laboratory experiments neatly show the sensitivity of species and interaction mechanisms when factors such as population density, species richness or grazing pressure are varied under controlled conditions at different temperatures, nutrient concentrations and/or concentrations of hazardous substances. While the results obtained in such experiments often show clear cause-effect relationships, it is often more complicated to evaluate their relevance and/or importance for processes observed in nature. In the field there are so many factors that simultaneously influence biotic interactions in a community that they cannot be addressed in a single experimental set-up.

A compromise is to perform experimental manipulations of biotic factors (in combination with variation in environmental drivers) directly in the field or in mesocosms, *i.e.* in enclosures of a part of the ecosystem. In the phytobenthic zone, such field experiments are especially important for understanding recruitment mechanisms and interactions between the primary producers and the fauna. Field experiments have elucidated several crucial mechanisms that can regulate the abundance and species composition of the primary producers, such as recruitment of algae, nutrient recycling, food preference of grazers and trophic cascades governed by top predator abundances (Eriksson and Johansson 2003; Worm et al. 1999, 2001; Eriksson et al. 2006, 2009).

However, in a meta-analysis including a large number of the same type of experiments, the biotic interactions may not be so clear as in single experiments, or may even be contradictory (Lyons et al. 2014; Thomsen and Wernberg 2015). One of the reasons for such discrepancies is that no field experiments are carried out under exactly the same conditions because environmental conditions, species, life stages of species and/or genetic diversity within species, etc. may differ between experiments. To draw wider conclusions, *e.g.* for ecosystem management, it is necessary that support for the processes discovered in experiments is observed in nature. Thus, a combination of experiments and field observations is always recommended.

11.5 Biological traits and ecological strategies

11.5.1 Functional traits

To predict and assess community shifts and their consequences, ecologists are increasingly investigating how the functional traits of primary producers determine their relative fitness along environmental gradients (*cf.* Sect. 4.7). The trait-based approach in ecology offers the opportunity to tackle the complexity of species-rich communities by constructing simple taxon-independent models of community structure and community dynamics in relation to the environment. By defining species according to their form and function, communities with different species can be compared through the "common currency" of their traits. For macrophytes such traits include *e.g.* growth form, body size, life span, reproductive strategy, season, reproductive performance and fecundity.

11.5.2 Growth forms of macroalgae

Growth form groups of marine macroalgae are often used to functionally relate the vegetation to environmental change (Littler and Littler 1984). In such models, a wide range of ecological and physiological functions are assumed to be correlated with different categories of thallus morphology, *e.g.* crustose, filamentous, coarsely branched, foliose, and this occurs often in combination with thallus thickness, *e.g.* uniseriate (consisting of rows of single cells) filamentous, thin foliose, thick leathery foliose, etc.

Such classifications have been found appropriate in many cases, but not all, and measurements based on specific ecological functions, *e.g.* photosynthetic rate, nutrient uptake rate (Box 11.6) or resistance to disturbances (including *e.g.* grazing), rather than morphology grouping, may be more reliable (Padilla and Allen 2000). Measurements of variables such as photosynthesis or nutrient uptake also provide the advantage of interval-scale data, which are more rigorous in statistical analyses than nominal-scale data (using categories). On the other hand, it has to be taken into account that such measurements are often made in the laboratory from isolated thallus parts under quite different conditions than those in the field.

11.5.3 Life-history strategies

Traits such as body size, life span and reproductive strategy are often clustered and incorporated in theories to explain ecological patterns, *e.g.* "*r/K* selection" (*cf.* Box 4.14) and "life-history evolution" (Stearns 1989). Thin filamentous algae are mostly short-lived species categorised as *r*-strategists or "opportunists" with an exponential growth curve. Such species can quickly colonise new areas when the opportunity arises. In comparison, slow-growing, long-lived perennial species with larger thalli, which are categorised as *K*-strategists, remain at their site once they are established. These species are good competitors for space. Typical *r*-strategists in the Baltic Sea are ephemeral algae such as *Ulva linza* (syn. *Enteromorpha ahlneriana*) and *Spirogyra* sp., which can appear one week and disappear the next. Fast-growing annual filamentous algae that usually stay attached for longer periods during the growing season, *e.g.* *Ceramium tenuicorne*, *Cladophora glomerata*, *Polysiphonia fucoides* and *Pylaiella littoralis*, are still more *r*- than *K*-selected. Included in this group of "annual" algae are also "pseudo-annuals", *i.e.* they have seasonal growth, but can hibernate as dark, rigid basal parts of up to a few cm in length (*e.g.* *Cladophora glomerata*) and start to grow from there when conditions become favourable again. Typical *K*-strategists in the Baltic Sea, with slower growth rates and thicker and more complex thalli, are perennial species such as the brown algae *Fucus vesiculosus*, *Fucus serratus*, *Fucus radicans*, the red algae *Coccotylus truncatus*, *Furcellaria lumbricalis*, *Phyllophora pseudoceranoides*, *Rhodomela confervoides* and the vascular plants *Zostera marina* and *Ruppia maritima*.

An increase in the proportion between annual and perennial algae and plants may indicate a disturbance that benefits an *r*-strategy over a *K*-strategy. An *r*-strategist usually profits the most from growth-enhancing

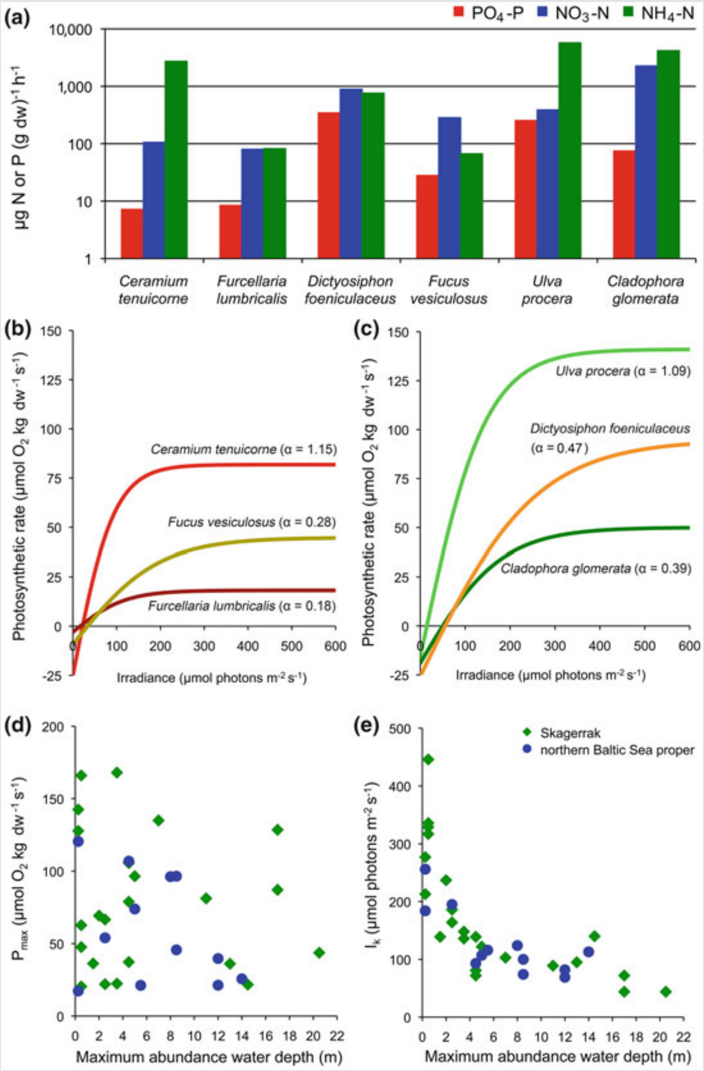
Box 11.6: Photosynthetic rates and nutrient uptake rates

Algal morphology and surface:volume ratio

Photosynthetic rate, nutrient uptake rate and growth rate are roughly related to algal growth form and life-history strategies, being lowest in slow-growing thick leathery algae (Box Fig. 11.9a, b) and highest in fast-growing thin filamentous algae (Box Fig. 11.9a, c). The differences in the rates between species are based on the relative cell surface area (surface:volume ratio) that has direct contact with the environment. For example, the maximum photosynthetic rates (P_{max}), as well as most of the maximum nutrient uptake rates (V_{max}) of the finely branched algae *Ceramium tenuicorne* (red) and *Dictyosiphon foeniculaceus* (brown) are higher than those of *Furcellaria lumbricalis* (red) and *Fucus vesiculosus* (brown) with coarser thallus morphology. However, when comparing the rates at which different algal species take up nitrate, ammonia and phosphate from the water (Wallentinus 1984), the red algae *Ceramium tenuicorne* and *Furcellaria lumbricalis* (with different morphologies) have lower phosphate and nitrate uptake rates than brown and green algae with comparable morphologies. On the other hand, the large differences in the ammonia uptake rate and photosynthetic rate between *Ceramium tenuicorne* and *Furcellaria lumbricalis* do reflect their respective morphologies.

The efficiency of photosynthesis

Uniseriate algae (consisting of rows of single cells) are expected to have the highest photosynthetic rates because they have the highest surface:volume ratio, but this is not necessarily so. In natural communities (Box Fig. 11.10a), many factors other than mere morphology are involved, including thallus self-shading, the abundance of microscopic

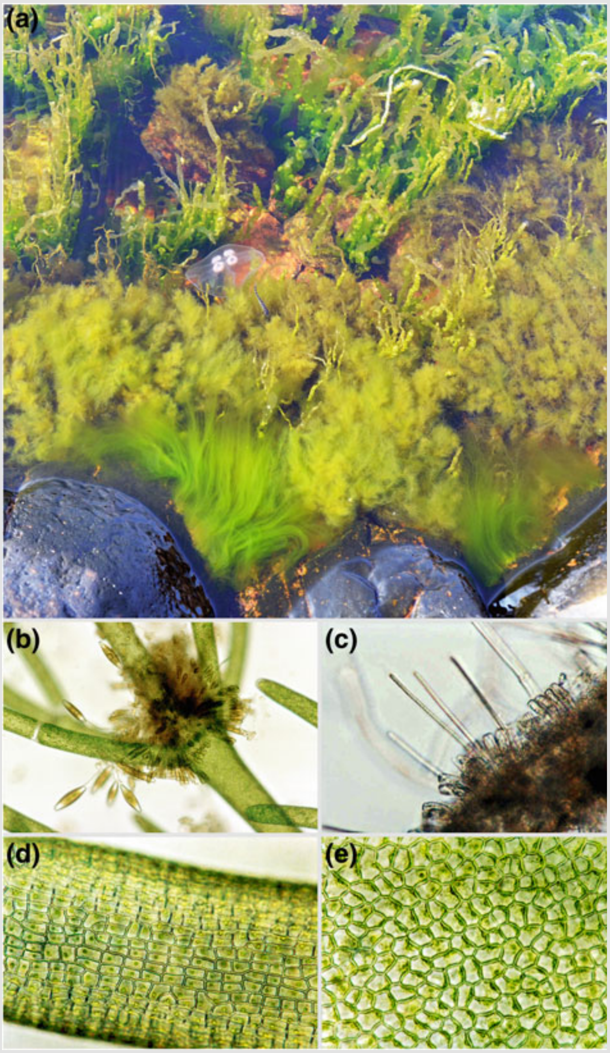


Box Fig. 11.9 Nutrient uptake rates and photosynthetic properties of different macroalgal species. (**a**) Maximum uptake rates (V_{max}) of the inorganic nutrients phosphate, nitrate and ammonia for the two red algae *Ceramium tenuicorne* (finely branched) and *Furcellaria lumbricalis* (coarsely branched), the two brown algae *Dictyosiphon foeniculaceus* (finely branched) and *Fucus vesiculosus* (flat thallus, young parts were used) and the two green algae *Ulva linza* (tube-shaped thin filaments) and *Cladophora glomerata* (uniseriate filaments) in the Baltic Sea proper at Askö (Sweden). Note that a logarithmic scale is used on the y-axis. (**b**, **c**) Photosynthesis-irradiance curves based on oxygen evolution measurements for the same six species as in (**a**), also from Askö. *Ulva linza* has the the highest photosynthetic rate at saturating light (P_{max}) and *Furcellaria lumbricalis* the lowest. α = initial slope at limiting irradiance levels [in μmol O_2 kg dry weight^{-1} (μmol photons m^{-2})$^{-1}$]. (**d**, **e**) P_{max} and the light saturation parameter I_k (= P_{max}/α) for 23 red and brown algal species in the Skagerrak at Fiskebäckskil (Sweden) and 12 red and brown algal species in the Baltic Sea proper at Askö. Figure (**a**) based on data in Wallentinus (1984), (**b**–**e**) based on data in Johansson and Snoeijs (2002) and Choo et al. (2005)

epiphytes and the efficiency of the photosynthetic apparatus. For example, the P_{max} and the initial slope at limiting irradiance levels (α) of the green alga *Cladophora glomerata* (uniseriate branched, Box Fig. 11.10b) is only slightly higher than that of young *Fucus vesiculosus*. Another example is the photosynthetic rate of the thin filamentous *Ulva linza* (Hayden et al. 2003), which is much higher than that of *Cladophora glomerata*, both when normalised to dry weight and when normalised to chlorophyll *a* content (Choo et al. 2005). These two green algal species often co-exist in the upper littoral zone of the Baltic Sea and, macroscopically, *Ulva linza* is easily confused with *Cladophora glomerata*. The older parts of *Cladophora glomerata* are usually completely overgrown by diatoms and the cyanobacterium *Heteroleibleinia* cf. *kützingii* (Box Fig. 11.10c) while *Ulva* is remarkably devoid of epiphytes (Box Fig. 11.10d, e), except when it is decaying. This is attributed to the release of large amounts of hydrogen peroxide as part of the alga's defence mechanism against oxidative stress in *Ulva linza* (Choo et al. 2005) and intercalary growth instead of apical growth. The low degree of shading by epiphytes of the *Ulva* species may partly explain their high photosynthetic rates.

Water depth

The P_{max} of the macroalgae in the Baltic Sea Area and the Skagerrak is independent of the water depth at which they are attached (Box Fig. 11.9d). However, the light saturation parameter I_k shows that the species growing deepest down in the sublittoral zone are more sensitive to light (Box Fig. 11.9e), *i.e.* their photosynthesis is more efficient at low irradiance levels compared with other species growing higher up in the sublittoral zone (Johansson and Snoeijs 2002). This is a physiological adaptation to low-light conditions that has nothing to do with algal morphology.



Box Fig. 11.10 Common green algae in the upper sublittoral zone of the Baltic Sea. (**a**) Bright green *Ulva linza* at the waterline, with *Cladophora glomerata* (coloured brownish-green by high abundances of microscopic epiphytes) and deeper down the tubular alga *Ulva intestinalis* with bright green lower parts and light green upper parts (from which spores have been released) in the Baltic Sea proper at Kråkelund (Sweden). Above the vegetation, the jellyfish *Aurelia aurita* and a three-spined stickleback *Gasterosteus aculeatus* are seen. (**b**) Light micrograph of *Cladophora glomerata* cells with the epiphytic diatoms *Brebissonia lanceolata* and *Gomphonema olivaceum*. (**c**) Light micrograph of old *Cladophora glomerata* cells completely overgrown with epiphytes, mainly the diatom *Rhoicosphenia abbreviata* (*cf.* Fig. 12.8) and the filamentous cyanobacterium *Heteroleibleinia* cf. *kützingii*. (**d**) Light micrograph showing cells of the branched tube-shaped alga *Ulva linza*, which are arranged in rows and have one pyrenoid. (**e**) Light micrograph showing cells of the unbranched tube-shaped alga *Ulva intestinalis*, which are not arranged in rows and have one pyrenoid. Photo: © Pauline Snoeijs-Leijonmalm environmental conditions that lead to an increase in the rate of supply of organic matter in an ecosystem (Nixon 1995), such as nutrient emissions, increased water temperature or the natural aging of a water body. Natural disturbances that favour *r*-strategists in the Baltic Sea are *e.g.* the irregular water level fluctuations following the frequency and intensity of weather disturbances in the upper sublittoral (*cf.* Sect. 2.3.4) and the harsh climate of the Bothnian Bay. Additionally, an unstable substrate (but not so unstable to totally prevent vegetation) usually benefits *r*-strategists that can recolonise fast.

11.5.4 Eutrophication indices

The ratio of annual to perennial macroalgae, as well as the ratio of filamentous algae to *Zostera marina*, can be used to indicate eutrophication because increased nutrient concentrations generally favour the growth of filamentous ephemeral algae (Korpinen et al. 2007). However, such indices should be used with great care because the abundance of filamentous algae depends not only on nutrient concentrations, but also on other factors such as salinity, grazing, season, sea level fluctuations and duration, thickness and ice-type of the winter ice cover. For example, in a broad salinity range, the fraction of opportunistic algae responds predominantly to salinity and not to eutrophication (Fig. 11.19). Thus, if a eutrophication gradient is accompanied by a salinity gradient, an index based on the proportion of filamentous algae is useless.

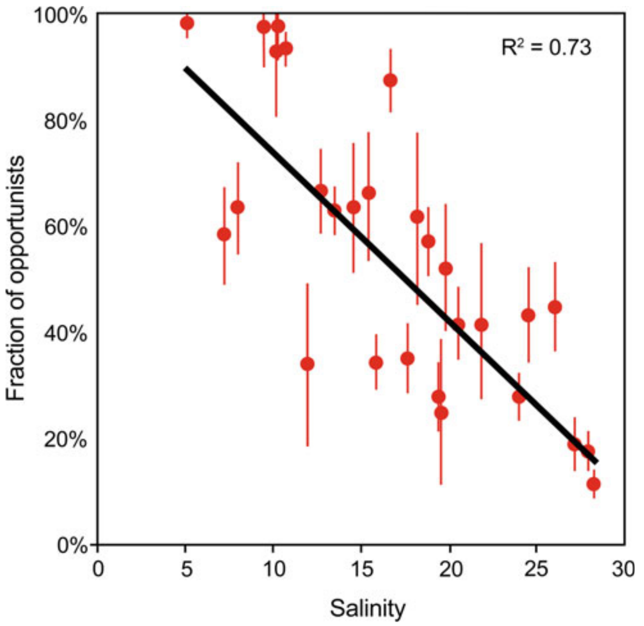


Fig. 11.19 Fraction of opportunistic algae as a function of salinity (linear regression analysis) in 28 brackish-water areas in the Bornholm Sea, Belt Sea, Kattegat, Limfjorden, Nissum Fjord and Ringkøbing Fjord. The red dots represent area-specific values, and error bars represent 95 % confidence intervals. Data from the National Danish monitoring programme. Figure modified from Krause-Jensen et al. (2007)

11.6 The epilittoral zone

11.6.1 Rock covered by lichens and cyanobacteria

The epilittoral zone of the Baltic Sea is the part of the coast that is influenced by waves and sea spray. The drier part of this zone is inhabited by lichens, which grow in distinct zonation patterns determined by the amount of sea spray they receive. The epilittoral lichen vegetation of the Baltic Sea Area is basically the same as that along other sea coasts in northern Europe (Ferry and Sheard 1969). The black tar lichen *Verrucaria maura* grows just above the waterline and orange sea lichen species of the genus *Caloplaca* are found slightly higher up on the shore (Fig. 11.20b, c). Species belonging to the green algal genus *Prasiola* can be found growing in shaded rock crevices some metres above the water line.

The black *Verrucaria maura* layer may be confused with the dark-green to black microbial layer dominated by the cyanobacterium *Calothrix scopulorum* (Fig. 11.20a). The two layers can be roughly distinguished by pure drastic experience: *Calothrix scopulorum* grows on sun-exposed parts and is extremely slippery, causing many unwanted baths, whereas *Verrucaria maura* is found on shaded parts of the shore and is not so slippery.

Common microbial species growing mixed with *Calothrix scopulorum* are the cyanobacteria *Gloeocapsopsis crepidinum* (syn. *Gloeocapsa crepidinum*) and *Phormidium* spp., and at the lower end of the layer (closest to the waterline) also *Rivularia atra* (Snoeijs and Prentice 1989). In contrast to *Rivularia atra*, *Calothrix scopulorum* does not live permanently submerged, except at a sudden high water level. Benthic diatoms typically occur associated with cyanobacteria (Snoeijs and Wakuru-Murasi 2004). At a low water level, this cyanobacteria-diatom layer dries out to form a distinct white crust, which mainly consists of the silica frustules of the diatoms. Also, dry *Cladophora glomerata* remnants at low water may be white from the silica frustules of its epiphytic diatoms.

11.6.2 Rock pools

Rock pools occur in depressions in the bedrock. These patchy habitats are characterised by a low temporal stability because daily temperature and salinity fluctuations (by evaporation or precipitation) may be large and smaller rock pools easily dry out during sunny days. Rock pools receive

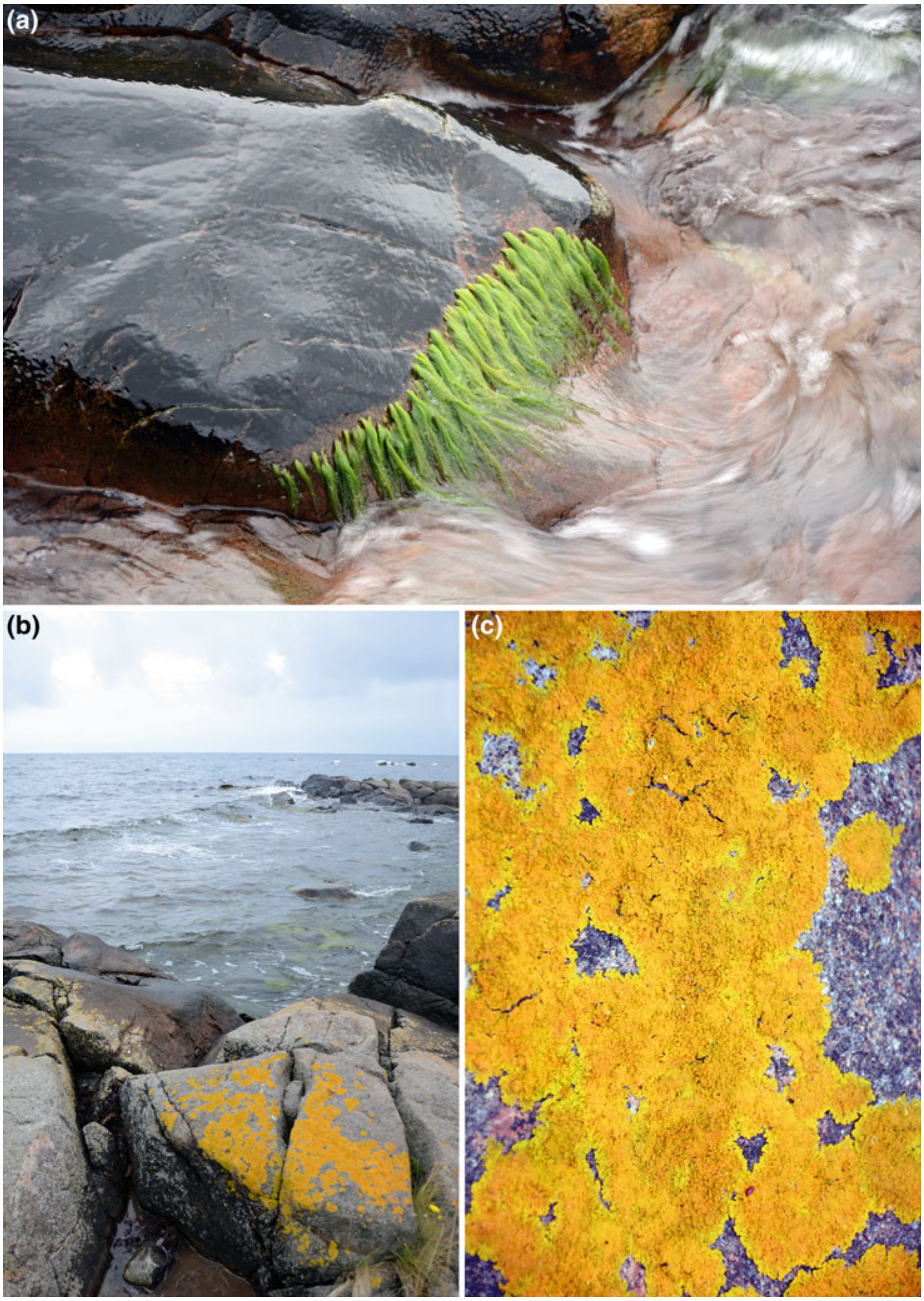


Fig. 11.20 Typical cyanobacteria and lichens in the epilittoral zone of the Baltic Sea. (**a**) At sites exposed to medium to strong wave action, a microbial layer dominated by the cyanobacterium *Calothrix scopulorum* (dark green - blackish) occurs just above the upper *Cladophora glomerata* tufts (light green). (**b**) The *Calothrix scopulorum* layer grows on sun-exposed parts of the shore closest to the waterline while the black tar lichen *Verrucaria maura* also grows close to the waterline, but on shaded parts of the shore (here on the front rock facing the photographer). Orange sea lichen species of the genus *Caloplaca* are found higher up on the shore. (**c**) Close-up of *Caloplaca* sp. Photo: © Pauline Snoeijs-Leijonmalm

water from surf, large waves and/or precipitation and can vary widely in salinity, temperature and nutrient concentrations depending on weather conditions, placement on the shore and pool size. Because of the large environmental variability between rock pools, they are inhabited by many different types of organisms, including microalgae, macroalgae, mosses, macrophytes and associated invertebrates (Fig. 11.21; Ganning 1971; Hällfors 1984). Within a rock pool, biological diversity is generally low (lowest in small pools) and with a simple food web structure.

When conditions deteriorate, rock pool organisms either have to escape from the habitat or survive the unfavourable

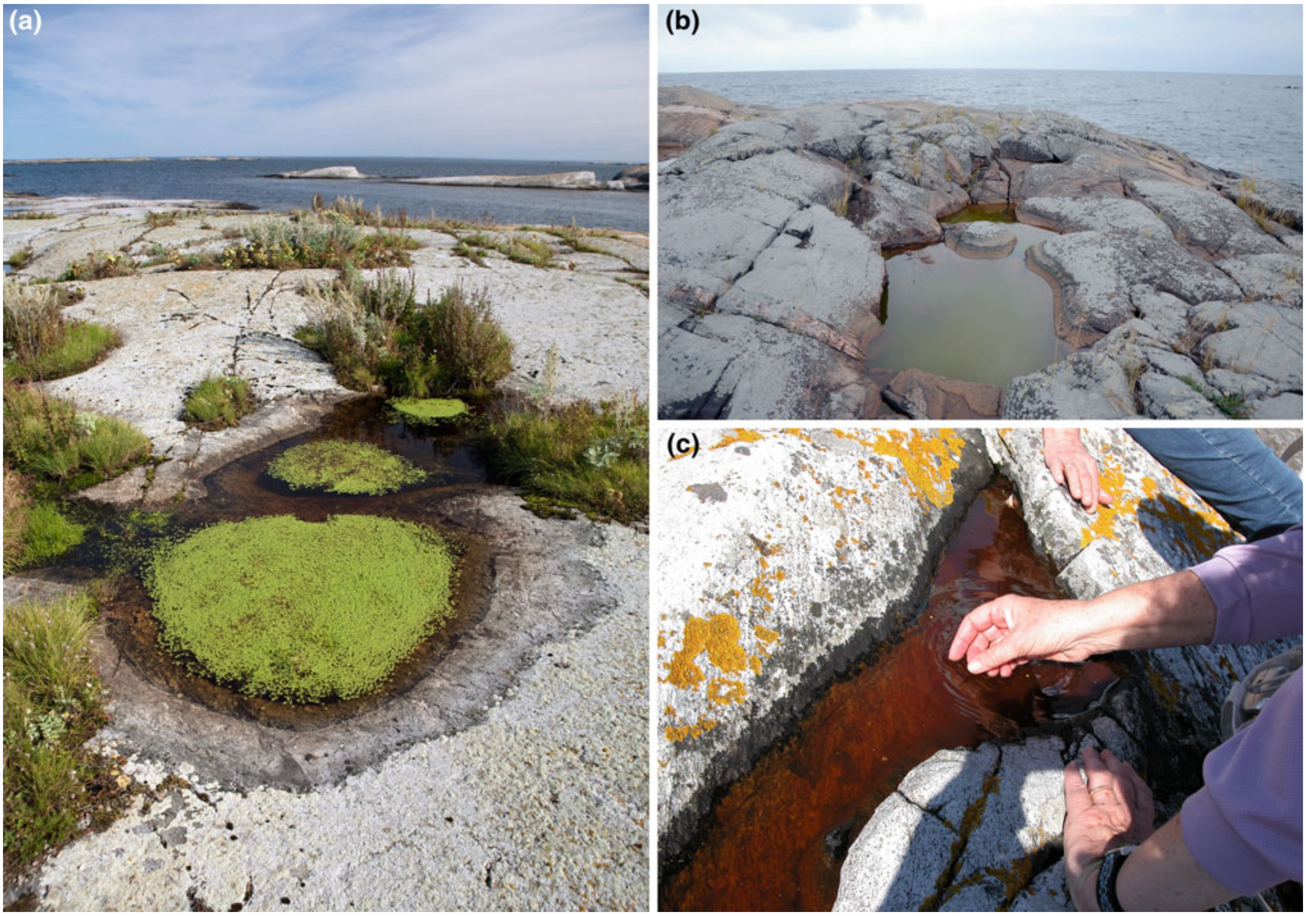


Fig. 11.21 Rock pools with different types of vegetation. (**a**) The vascular plant *Callitriche* sp. (**b**) Green filamentous algae. (**c**) Cysts of the green microalga *Haematococcus pluvialis*, which are coloured red by the carotenoid astaxanthin. Photo: (**a**) © Hans Kautsky, (**b**, **c**) © Pauline Snoeijs-Leijonmalm

period in a dormant state to stay alive. For example, the green alga *Haematococcus pluvialis* survives nutrient starvation and desiccation as red cysts filled with the antioxidant carotenoid astaxanthin (Fig. 11.21c) and cladocerans of the genus *Daphnia* can survive as dormant eggs. The production of dormant eggs in *Daphnia* spp. is induced by stimuli associated with deteriorated growth conditions (Pauwels 2007). The two species most commonly found in Baltic Sea rock pools, the green alga *Ulva intestinalis* (syn. *Enteromorpha intestinalis*) and the amphipod *Gammarus duebeni*, both display extremely wide environmental tolerances (Ganning 1971).

11.7 The *Cladophora* belt

11.7.1 *The green alga Cladophora glomerata*

The general lack of perennial vegetation down to a water depth of ~0.5–1 m found everywhere in the Baltic Sea is caused by the irregular water level fluctuations due to weather conditions (*cf.* Sect. 2.3.4) and not primarily by ice scouring. In this zone, the freshwater green filamentous alga *Cladophora glomerata* is an imperative habitat builder (Jansson 1974; Salovius and Kraufvelin 2004). During prolonged periods of high atmospheric pressure, often in combination with off-land wind, the upper ~0.5–1 m of the sublittoral desiccates and the algae in the *Cladophora* belt dry out and die (Fig. 11.22). Ephemeral algae (*Cladophora glomerata* and others) readily recolonise the upper sublittoral zone when the water level increases again or can start growing again from surviving basal cells of the old tufts. Perennial species are slower colonisers and/or are confined to colonisation in a specific season. The low water level occurs irregularly, and the few perennial specimens that may settle close to the water surface will sooner or later desiccate and disappear again.

Cladophora glomerata is widely distributed in the entire Baltic Sea, and globally it is perhaps the most common attached alga in temperate fresh and brackish waters (Zulkifly et al. 2013). Recruitment is mainly through diploid biflagellate zoospores that directly germinate into diploid filaments. Each *Cladophora glomerata* tuft has usually

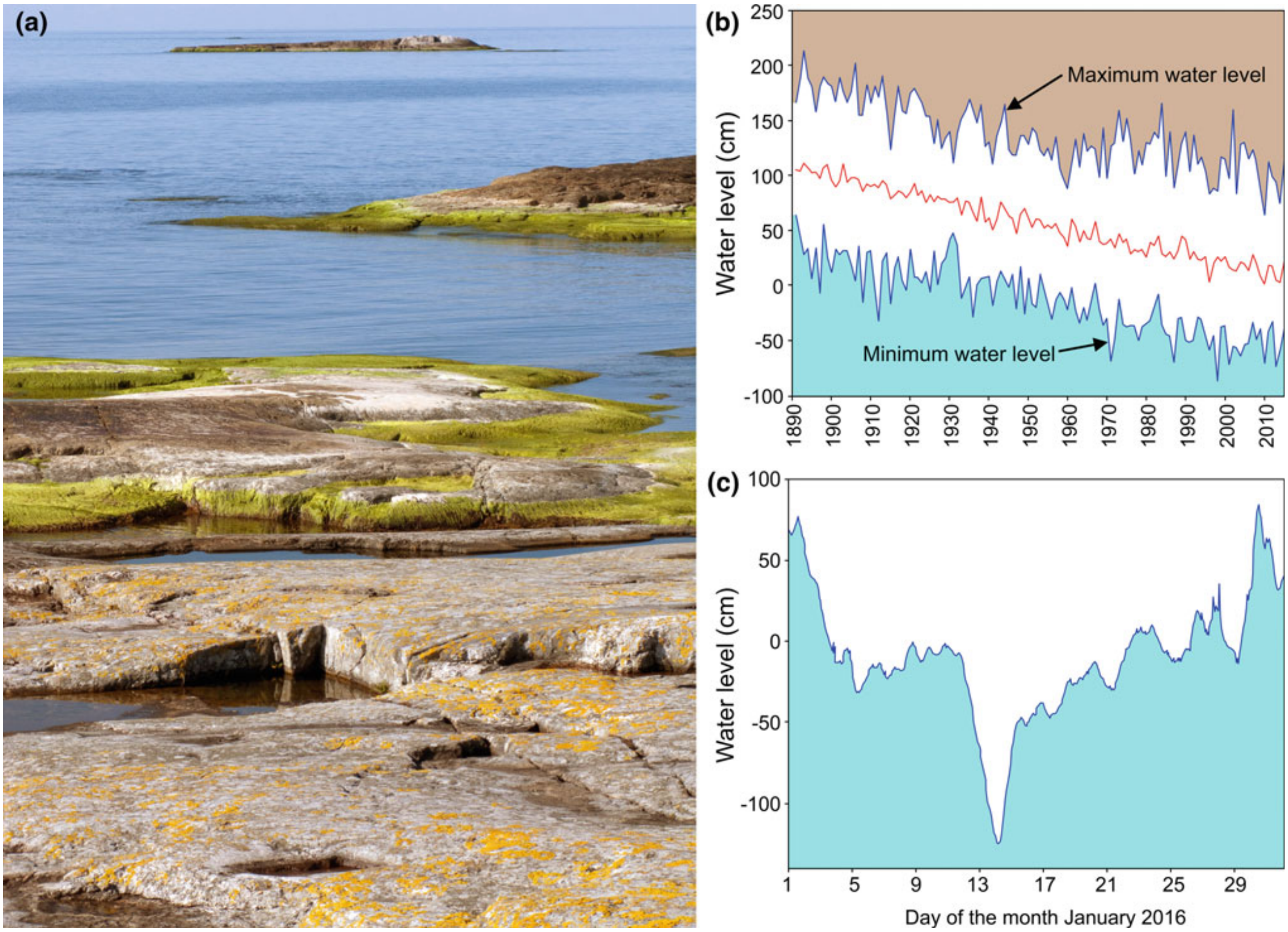


Fig. 11.22 Irregular changes in water level desiccate the algal vegetation in the upper littoral zone of the Baltic Sea. (**a**) A desiccated *Cladophora* belt at low water level at Askö, Baltic Sea proper. (**b**) The yearly minimum and maximum water levels at Ratan (63°59′ N, 20°54′ E, just north of Norra Kvarken) for the years 1891–2015 using the Swedish National RH2000 System. The amplitude between the minimum and maximum water levels is ~1.5 m. The red line is the yearly average water level. The downward trend with time is caused by the land uplift in the area (*cf.* Fig. 2.26b). (**c**) The daily mean water level at Haparanda (65°48′ N, 24°08′ E, northernmost Bothnian Bay). The amplitude between the minimum and maximum water levels is ~2.0 m and can change by more than 1.0 m from day to day. Photo: (**a**) © Hans Kautsky. Figures (**b**) and (**c**) based on data from the Swedish Hydrological and Meteorological Institute, SMHI (http://www.smhi.se)

grown from one zoospore (Figs. 11.20a and 11.23c). These zoospores are released throughout the growing season, from spring to autumn, and enable fast recruitment (Snoeijs and Prentice 1989; Hillebrand et al. 2010). Several generations of new asexual recruitment of *Cladophora glomerata* are often observed in horizontal rows above each other, reflecting past water level changes. In the low-salinity Bothnian Bay, a species related to *Cladophora*, *Aegagropila linnaei*, becomes belt-forming, but also here *Cladophora glomerata* dominates the upper sublittoral zone.

11.7.2 The *Cladophora* belt of the Baltic Sea proper

Like in the Skagerrak, the upper sublittoral zones of the Kattegat and Belt Sea are still inhabited by a *Fucus*-dominated vegetation. However, in the Baltic Sea proper the sublittoral zone between a 0 and 0.5–1 m water depth is dominated by filamentous algae. This zone is highly dynamic due to the irregular water level fluctuations typical of the Baltic Sea. *Cladophora glomerata* starts to colonise here in spring (April-May) and attains its full growth in early summer (June). Usually this species totally dominates the upper 0.5–1 m until September-October (Fig. 11.23), and this is the reason why this dynamic vegetation belt is called the “*Cladophora* belt” (Jansson 1974; Snoeijs 1990b)

The *Cladophora* belt shows a distinct seasonality where overwintering red algae are replaced sequentially by brown and green algae in spring and then finally by a pure green algal belt in summer. This cycle is partly triggered by repeatedly occurring longer low-water periods when this zone is desiccated, killing the standing population. When the water returns, the vegetation is replaced by the next

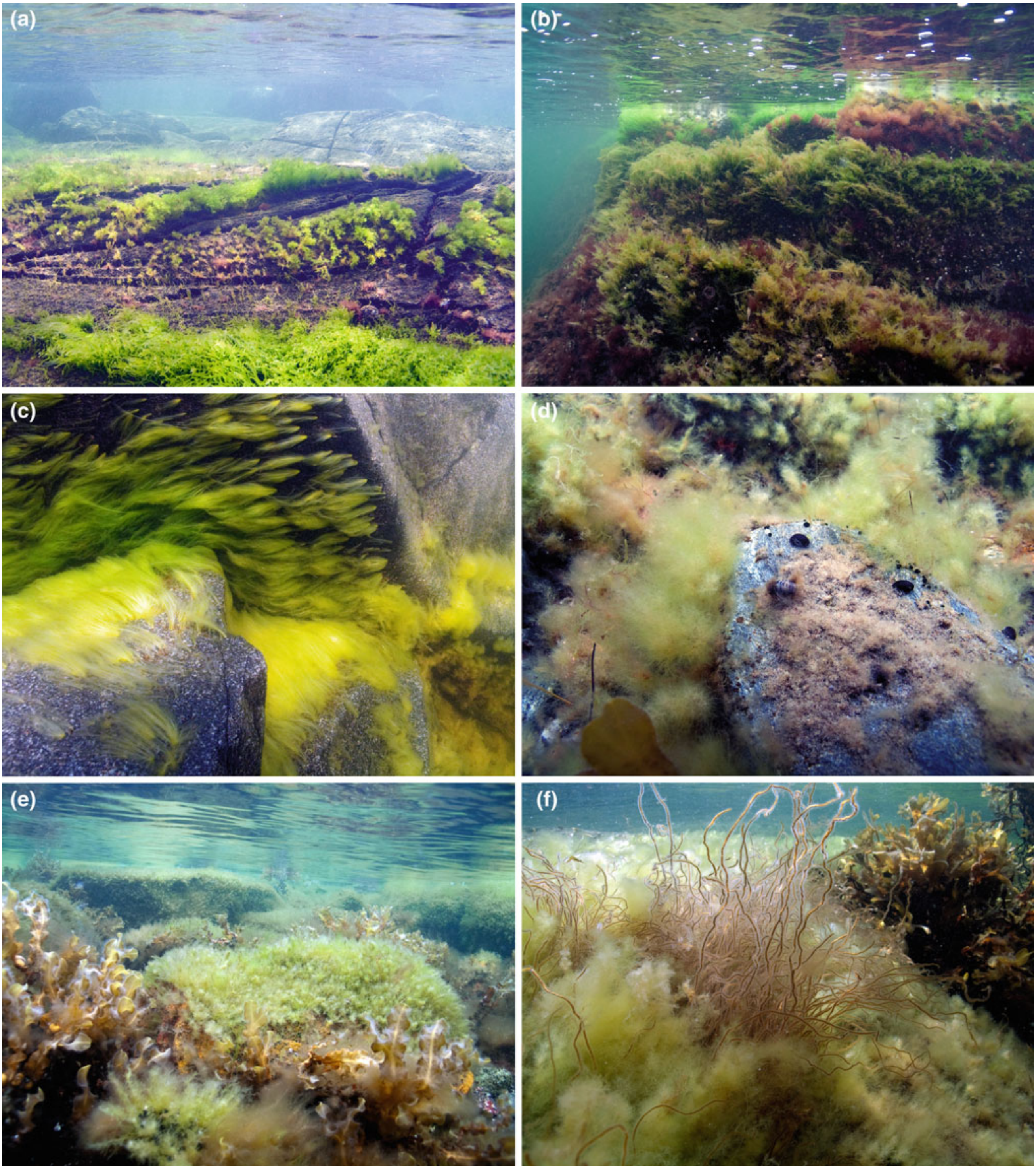


Fig. 11.23 Different appearance of the *Cladophora* belt of the Baltic Sea. (**a**) Down to a ~0.5–1 m water depth the rock is covered by filamentous algae; the green alga *Cladophora glomerata* dominates during summer often (like in this photograph) accompanied by *Ulva* spp. (**b**) In autumn *Cladophora glomerata* is replaced by the red alga *Ceramium tenuicorne*. (**c**) Exposure to strong wave action may hamper the growth of *Cladophora glomerata* as the tufts partly detach when they grow too large. (**d**) Filamentous algae are preferred food for grazers such as the snail *Theodoxus fluviatilis*, which can denude small patches of the substrate from vegetation. (**e**) *Cladophora glomerata* growing on the upper part of a boulder near the water level just above the *Fucus* belt. (**f**) *Cladophora glomerata* accompanied by the brown alga *Scytosiphon lomentaria*. Photo: © Hans Kautsky

"colour". In summer, other species common in the *Cladophora* belt of the Baltic Sea proper are the brown filamentous algae *Dictyosiphon foeniculaceus* and *Pylaiella littoralis*, different species of the green algal genus *Ulva*, as well as colonies of the cyanobacterium *Rivularia atra* (Fig. 11.24). In late summer-autumn, the red alga *Ceramium tenuicorne* (Fig. 11.24a), sometimes together with the brown algae *Scytosiphon lomentaria* (Fig. 11.23f) and *Spongomorpha aeruginosa*, colonises the upper sublittoral when *Cladophora glomerata* declines.

Ceramium tenuicorne persists through winter and dominates the upper sublittoral until spring. In early spring, it is joined by the green leaf-like alga *Ulvopsis grevillei*, green unbranched filamentous algae such as *Ulothrix* spp. and *Urospora penicilliformis*, and sometimes also by the red unbranched filamentous alga *Bangia atropurpurea* at the waterline. Later in spring, *Acrosiphonia centralis* (green) and *Pylaiella littoralis* (brown), followed by *Cladophora glomerata*, colonise. Also in late spring the brown algae *Dictyosiphon chordaria*, *Eudesme virescens*, *Halosiphon tomentosus* and *Scytosiphon lomentaria* can be found around a ~0.5 m water depth. *Bangia atropurpurea*, *Ulothrix* spp. and *Urospora penicilliformis* may reoccur in autumn.

11.7.3 The *Cladophora* belt of the Gulf of Bothnia

As in the Baltic Sea proper, the upper sublittoral of the Bothnian Sea is dominated by *Cladophora glomerata* from spring to autumn, mixed with *Pylaiella littoralis* (spring), *Ulva intestinalis* (spring-autumn), *Ulva flexuosa* (syn. *Enteromorpha flexuosa*, summer), *Ulva linza* (summer-autumn) and *Ceramium tenuicorne* (autumn). In the Bothnian Sea, *Cladophora glomerata* often extends deeper down than ~0.5 m because, due to ice scouring, the *Fucus* belt usually starts deeper down than in the Baltic Sea proper (Fig. 11.11).

In the Bothnian Bay *Fucus* spp. are absent. *Cladophora glomerata* totally dominates the upper sublittoral in summer, and below this *Aegagropila linnaei* forms a perennial vegetation all the way down to the lower depth limit of the vegetation at the water depth of ~10 m (Fig. 11.25). The green algae are usually completely overgrown by epiphytic diatoms, which gives them a yellowish appearance (Fig. 11.25c, d). An eye-catching species that occurs scattered in this vegetation type is the aquatic moss *Fontinalis dalecarlica* (*cf.* Fig. 11.31e). In the uppermost sublittoral zone, *Cladophora glomerata* is often accompanied by other green filamentous freshwater species such as *Ulothrix zonata*.

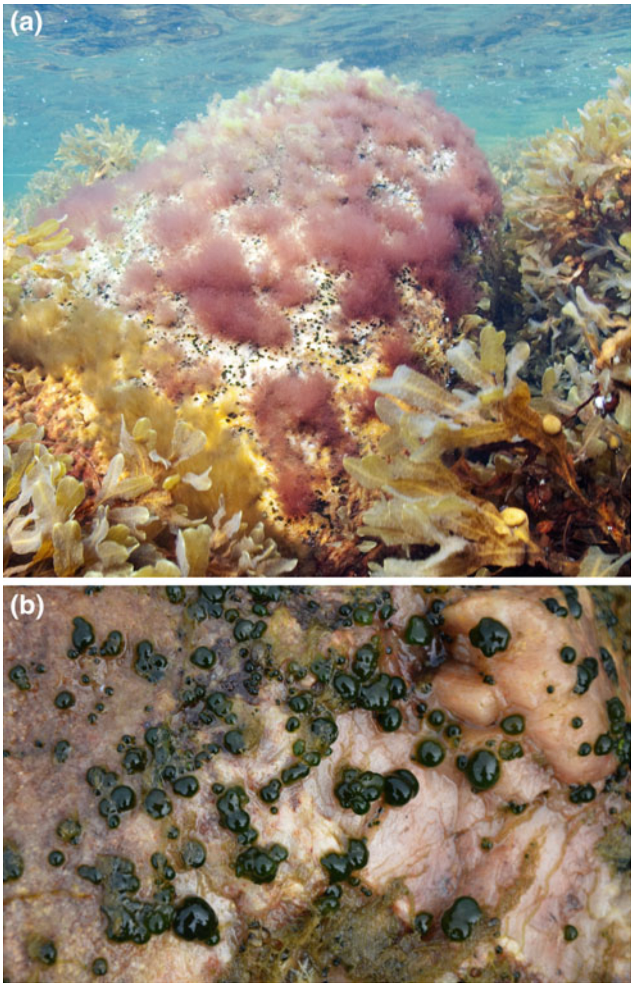


Fig. 11.24 In autumn the red alga *Ceramium tenuicorne* dominates the *Cladophora* belt. *Ceramium tenuicorne* is often associated with colonies of the cyanobacterium *Rivularia atra*. (**a**) A boulder with still some *Cladophora glomerata* on the top and *Ceramium tenuicorne* with *Rivularia atra* lower down. (**b**) Colonies of the cyanobacterium *Rivularia atra*, of the diameter up to ~6 mm, on a stone picked up from the *Cladophora* belt. Photo: (**a**) © Hans Kautsky, (**b**) © Pauline Snoeijs-Leijonmalm

11.8 The *Fucus* belt

11.8.1 Four *Fucus* species occur in the Baltic Sea Area

Globally, the bladderwrack *Fucus vesiculosus* is a widely distributed intertidal marine species in the northern hemisphere. In the Baltic Sea it lives permanently submerged and can become almost one metre high (Fig. 11.26). *Fucus vesiculosus* is considered the structurally most important phytobenthic alga in the Baltic Sea because it is the most widely distributed species with a larger thallus size. It is only

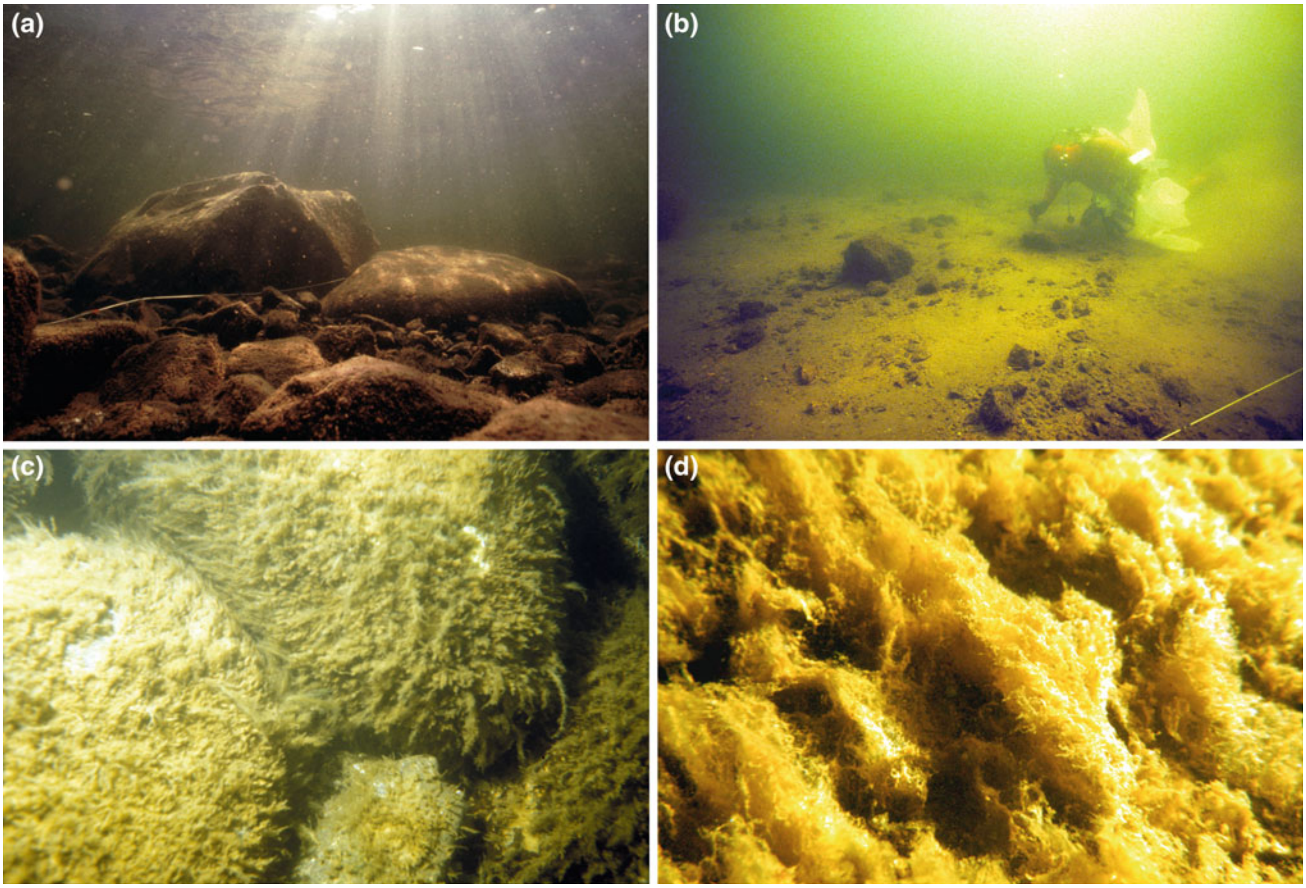


Fig. 11.25 The vegetation of the Bothnian Bay. (**a**) An *Aegagropila linnaei*-dominated vegetation covered with diatoms in the northernmost bay of the Baltic Sea (Töreviken) at a ∼3 m water depth. (**b**) A biologist working in a sublittoral environment typical of the Bothnian Bay. (**c**) A *Cladophora glomerata*-dominated vegetation covered with diatoms at a ∼3 m water depth. (**d**) A close-up of epiphytic diatoms completely covering filamentous algae. Photo: (**a**–**c**) © Hans Kautsky, (**d**) © Svante Pekkari

absent from the Bothnian Bay and coastal areas elsewhere in the Baltic Sea with salinity below ∼4. There are occasional reports of isolated and sparse populations or single individuals of *Fucus vesiculosus* found at salinities down to 2, but they concern the algae that grew within the radius <1 m around outlets of pipes releasing untreated sewage, which locally increased water conductivity (Wærn 1952; Pekkari 1965).

In the Bothnian Sea a "dwarf form" of *Fucus vesiculosus* has long been recognised (Wærn 1952; Kautsky et al. 1992). This form was recently described as a species of its own, *Fucus radicans* (*cf.* Fig. 6.2; Bergström et al. 2005). *Fucus vesiculosus* and *Fucus radicans* occur together in the Bothnian Sea and at the island of Saaremaa (Estonia). However, as *Fucus vesiculosus* decreases in size with decreasing salinity, it may be difficult to distinguish between the two species if they do not grow side by side (Fig. 11.26b).

Two other *Fucus* species occur in the Baltic Sea Area. *Fucus serratus* (*cf.* Fig. 4.27a) is belt-forming from the Skagerrak up to the Gotland Sea (Fig. 11.11). The non-indigenous species *Fucus evanescens* (an Arctic species) has been introduced to the Kattegat and the Belt Sea, where it has been observed to grow close to the water surface. Its occurrence is largely confined to harbour areas (being transported there by ships) and low salinity seems to restrict its further distribution into the Baltic Sea (Wennberg 1992; Wikström et al. 2002).

11.8.2 The key species *Fucus vesiculosus*

Fucus belts (Fig. 11.26) have high biomass and play an important structuring role in the phytobenthic zone of the Baltic Sea, except for the Bothnian Bay. *Fucus vesiculosus* creates habitats for species-rich communities of epiphytes and invertebrates, as well as for the recruitment of fish (Kautsky et al. 1992). In coastal areas of the Baltic Sea, fluctuations in the distribution and abundance of *Fucus vesiculosus* influence the ecosystem at all trophic levels. A species with these characteristics is called a "key species", an "engineering species", or simply a "dominating species".

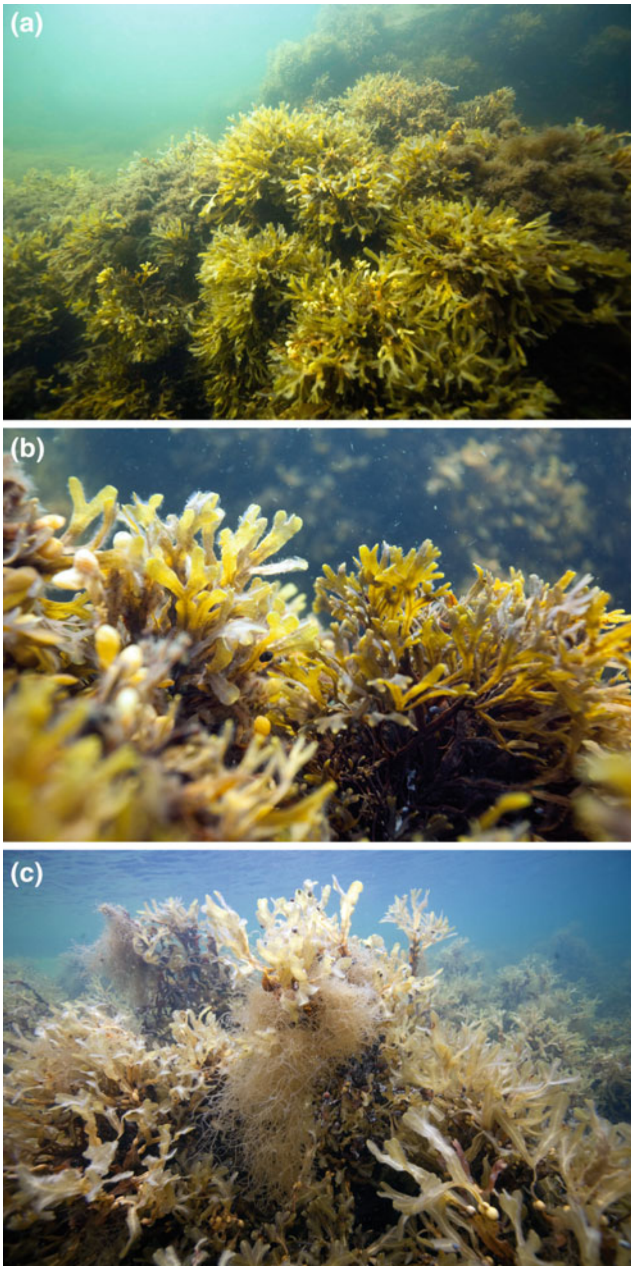


Fig. 11.26 Different appearance of the *Fucus* belt of the Baltic Sea. (**a**) A dense *Fucus* vegetation. (**b**) Co-occurrence of *Fucus vesiculosus* (to the left) and *Fucus radicans* (to the right). (**c**) *Fucus vesiculosus* with *Dictyosiphon foeniculaceus* as an epiphyte. (**a**, **b**) Höga Kusten, Bothnian Sea, (**c**) Askö, Baltic Sea proper. Photo: © Hans Kautsky

All of these terms indicate the importance of *Fucus vesiculosus* for the structure of the ecosystem. *Fucus vesiculosus* is not a "keystone species", which by definition is a species that, relative to its abundance, has a disproportionately large effect on community structure, usually a predator (Paine 1966, 1995).

Although the habitat requirements of *Fucus vesiculosus* with respect to salinity are fulfilled almost everywhere in the Baltic Sea, rich *Fucus* belts grow only on stable substrates at sites not exposed to strong wave action. *Fucus vesiculosus* has air bladders that keep the thalli upright in the water towards the light. With increasing wave exposure, the air bladders decrease in size and are absent at the most exposed sites where *Fucus vesiculosus* can grow. At high wave exposure there is no need to keep the thalli upright and bladders increase the drag force of waves with the risk of damaging and ripping off the algae. Deeper down in the sublittoral zone at exposed sites, where the forces of the waves are smaller, bladders still occur. Furthermore, detached *Fucus vesiculosus* is kept floating by means of the air bladders, and this is thought an advantage for long-distance dispersal of the species (van den Hoek 1987).

11.8.3 The *Fucus-Ascophyllum* belt of the Kattegat

The Atlantic intertidal species *Fucus vesiculosus* lives permanently submerged already in the Kattegat. It grows just below the water surface, with *Fucus spiralis* above it and *Ascophyllum nodosum* and *Fucus serratus* below it. These four perennial species form the *Fucus-Ascophyllum* belt in the Kattegat, together with many annual and pseudo-annual species that have seasonal abundance maxima in this belt. For example, in the end of February *Dumontia contorta* and *Ulvopsis grevillei* occur just beneath the water surface. Towards summer they give place to *Nemalion multifidum* in July and August, followed by *Polysiphonia fibrillosa* from October to February. *Fucus serratus* stretches from a 0.5–1 m down to ~4–5 m water depth, often accompanied by *Chondrus crispus* and *Chorda filum*. Filamentous algae such as *Ceramium* spp., *Cladophora* spp., *Dictyosiphon foeniculaceus*, *Ectocarpus* spp., *Pylaiella littoralis* and *Ulva* spp. start to grow in spring, epiphytic on *Fucus* or directly on the rock.

If an ice cover has been present in the Kattegat during the winter, the upper perennial algae may have been ripped off and the bare rock left is often colonised by *Osmundea truncata* and *Scytosiphon lomentaria* in spring. When they die off in May, regeneration of *Fucus* and *Ascophyllum nodosum* starts by colonisation of germlings in the gaps where the perennial vegetation was damaged by the ice.

11.8.4 The *Fucus* belt of the Baltic Sea proper

In the southern Baltic Sea proper, the sublittoral zone between a 0.5–1 m and 4–5 m water depth is characterised by belt-forming *Fucus vesiculosus* (Fig. 11.26), except for sheltered sites and sites heavily exposed to wave action. Up to a line between just north of the island of Öland (Sweden) and the southern part of the island of Gotland (Sweden), the *Fucus* belts also contain *Fucus serratus* (Fig. 11.11). In the northern Baltic Sea proper *Fucus serratus* does not occur anymore and *Fucus vesiculosus* is the only *Fucus* species left here.

The lower depth limit of *Fucus vesiculosus* in the northern Baltic Sea proper varies between 4 and 9 m, but it has been found attached down to a ~14 m water depth. In archipelago areas, the lower depth limit extends deeper towards more exposed and cleaner sites in the outer archipelago. Typical epiphytes on *Fucus vesiculosus* are filamentous algae such as *Ceramium tenuicorne*, *Elachista fucicola* (obligate on *Fucus* spp.), *Pylaiella littoralis* (especially in spring and early summer), *Ectocarpus siliculosus* (in summer), *Dictyosiphon foeniculaceus* (in late summer).

The *Fucus vesiculosus* thalli support a high diversity of animals living on and in between them. Typical attached faunal species are *Amphibalanus improvisus* (Fig. 11.18b, c), *Einhornia crustulenta* (Fig. 11.18a) and *Mytilus trossulus* (*cf.* Fig. 4.29). High abundances of gammarids and isopods are also common, as well as grazing snails such as *Theodoxus fluviatilis*, *Ecrobia ventrosa* (syn. *Hydrobia ventrosa*) and *Peringia ulvae* (syn. *Hydrobia ulvae*). Below the *Fucus vesiculosus* canopy, an understory bush vegetation of *Ceramium tenuicorne*, *Cladophora rupestris*, *Furcellaria lumbricalis*, *Polysiphonia fucoides* and *Stictyosiphon tortilis* is found. *Chorda filum* usually occurs as single threads, but may occasionally form dense bundles on less stable substrates such as small stones and gravel (Fig. 11.8c).

11.8.5 The *Fucus* belt of the Bothnian Sea

In the low salinity (~5) of the Bothnian Sea, *Fucus vesiculosus* continues to grow in dense stands until close to its northern limit at Norra Kvarken (at salinity ~4). *Fucus vesiculosus* is in the Bothnian Sea accompanied by *Fucus radicans* (Fig. 11.26b), which has its northern limit of occurrence only ~20 km north of that of *Fucus vesiculosus*. Furthermore, detached, up to football-sized floating bundles of *Fucus* can cover large areas of the shallow sandy sublittoral zone of the western Bothnian Sea.

In the Bothnian Sea, the *Fucus* belt usually starts deeper down than in the Baltic Sea proper due to ice scouring. However, in protected places, *e.g.* behind large boulders, the two *Fucus* species can be found already at a ~0.5 m water depth. Like in the *Cladophora* belt, the aquatic moss *Fontinalis dalecarlica* (*cf.* Fig. 11.31e) is a conspicuous species in the Bothnian Sea *Fucus* belt. The distribution of this moss in the Baltic Sea stretches from the Gräsö area in the southern Bothnian Sea up to the northernmost Bothnian Bay. In the Södra Kvarken area, *Fontinalis dalecarlica* can be used as an indicator of Bothnian Sea water, *e.g.* areas of the Åland Sea that are affected by Bothnian Sea water may be classified as belonging to “the *Fontinalis* district” due to the occurrence of this moss (Wærn 1952).

Other species in the *Fucus* belt of the Bothnian Sea are the green algae *Aegagropila linnaei* and *Cladophora glomerata*, the brown algae *Chorda filum* and *Pylaiella littoralis*, and the red algae *Ceramium tenuicorne*, *Coccotylus truncatus*, *Furcellaria lumbricalis*, *Phyllophora pseudoceranoides* and *Polysiphonia fucoides*. At the lower end of the *Fucus* belt, in the whiplash zone where the *Fucus* vegetation is less dense, *Cladophora rupestris* and *Rhodochorton purpureum* are frequently found, together with the belt-forming species *Battersia arctica*.

11.9 The red algal belt

11.9.1 The red alga *Furcellaria lumbricalis*

The marine red alga *Furcellaria lumbricalis*, with a rather stable, leathery thallus (Fig. 11.27), is the largest red alga with a wide distribution in the Baltic Sea. It occurs up to Norra Kvarken at the islands of Holmöarna (Sweden) and the Vaasa archipelago (Finland). *Furcellaria lumbricalis* is belt-forming in two forms, either attached to a stable hard substrate in the lower part of phytobenthic zone (Kautsky 1995a) or in loose-lying aggregates at a 4–10 m water depth (Martin et al. 2006a; Bučas et al. 2009).

Together with other red algal species, *Furcellaria lumbricalis* forms the “red algal belt” of the Baltic Sea. Its morphology is governed by salinity and light and the maximum size of the *Furcellaria lumbricalis* tufts in the Baltic Sea is ~12 cm in diameter, which is much smaller than on fully marine coasts. At its lower depth limit (stressed by low irradiance), and at its northern limit of occurrence in the Baltic Sea (stressed by low salinity), *Furcellaria lumbricalis* tufts are only a few cm in diameter, almost black in colour and with thin branches (Box 11.7).

11.9.2 The red algal belt of the Baltic Sea

Many marine red algae cannot survive the low salinity of the Baltic Sea. Species common at Atlantic coasts, such as *Corallina officinalis*, *Dilsea carnosa*, *Odonthalia dentata*, *Osmundea truncata*, *Phyllophora crispa*, *Polysiphonia brodiei*, *Porphyra umbilicalis*, *Pterothamnion plumula* and *Scagelothamnion pusillum* (syn. *Antithamnion boreale*) are still found in the lower sublittoral of the Belt Sea, but do not enter the Baltic Sea (HELCOM 2012). Some others, *e.g.* *Brongniartella byssoides*, *Palmaria palmata*, *Plumaria plumosa* and *Spermothamnion repens* occur in the Arkona Sea but do not penetrate further into the Baltic Sea.

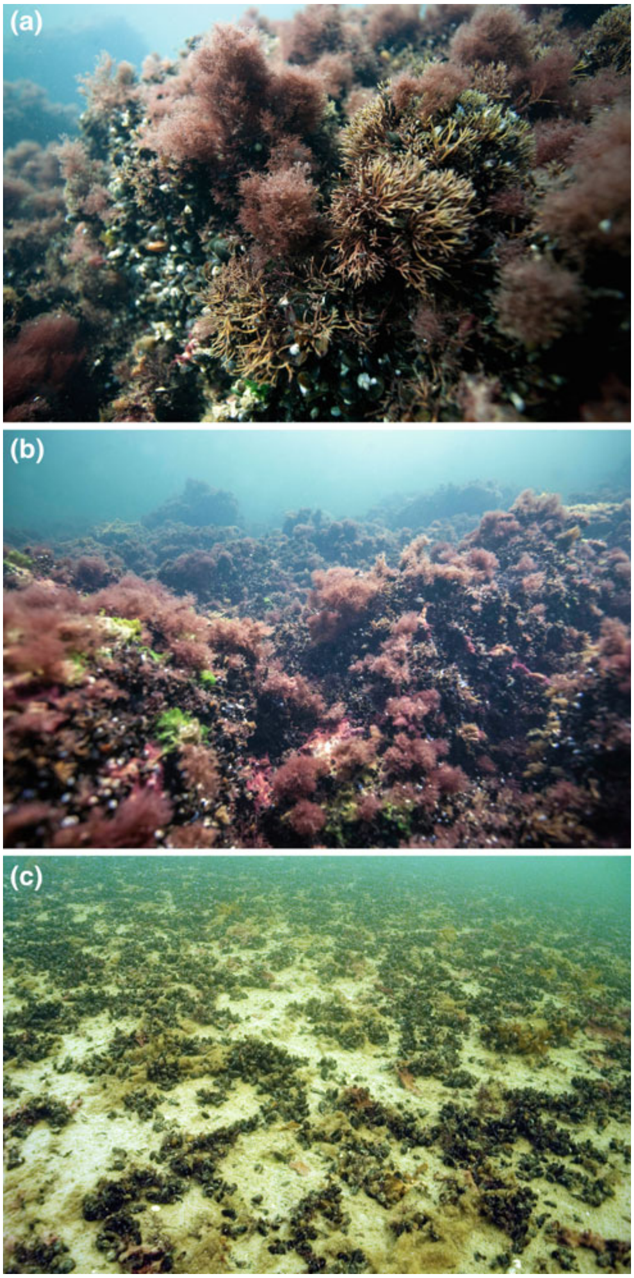


Fig. 11.27 Different appearance of the red algal belt of the Baltic Sea. (**a**) *Furcellaria lumbricalis* with *Ceramium tenuicorne* as an epiphyte, growing together with *Polysiphonia fucoides* and the animals *Mytilus trossulus*, *Amphibalanus improvisus* and *Einhornia crustulenta* at a ~4 m water depth. (**b**) *Furcellaria lumbricalis*, *Polysiphonia fucoides* and *Mytilus trossulus* at a ~7 m water depth; the green algae are patches of *Spirogyra* sp. (**c**) A loose-lying *Mytilus trossulus* community with intertwined *Furcellaria lumbricalis*, *Coccotylus truncatus* and other algae at a ~10 m water depth. (**a**–**c**) Askö, Baltic Sea proper. Photo: © Hans Kautsky

Consequently, the distinct "red algal belt" of the Baltic Sea proper (Fig. 11.27) consists of only nine commonly occurring species. The dominant species, *i.e.* that with the highest biomass, is usually *Furcellaria lumbricalis*. It is accompanied by *Ceramium tenuicorne*, *Ceramium virgatum* (syn. *Ceramium rubrum*), *Coccotylus truncatus*, *Phyllophora pseudoceranoides*, *Polysiphonia fibrillosa*, *Polysiphonia fucoides* and *Rhodomela confervoides*, and rarely also by *Ahnfeltia plicata*. The red algae successively disappear when the *Battersia arctica* belt takes over in the northern Baltic Sea proper.

In the Bothnian Sea some red algae, *e.g. Furcellaria lumbricalis* and *Coccotylus truncatus*, may still grow in a narrow belt below the *Fucus* belt. However, they usually occur here in the lower part of the *Fucus* belt or the upper part of the *Battersia* belt and not in a red algal belt of their own. All red algal species have smaller thalli in the Bothnian Sea than in the Baltic Sea proper.

The only frequently occurring marine species left in the Bothnian Bay is *Ceramium tenuicorne*, but it has to be searched for since it is small and often overgrown by epiphytic diatoms. The marine crustose alga *Hildenbrandia rubra*, which still occurs in the Bothnian Sea, is in the Bothnian Bay replaced by its freshwater relative *Hildenbrandia rivularis* (Pekkari 1965). The latter species occurs on hard substrates from the low water line down to the water depth of ~10 m, and it may, especially in deeper water, become well developed and up to 2–3 dm^2 large (Forsberg and Pekkari 1999).

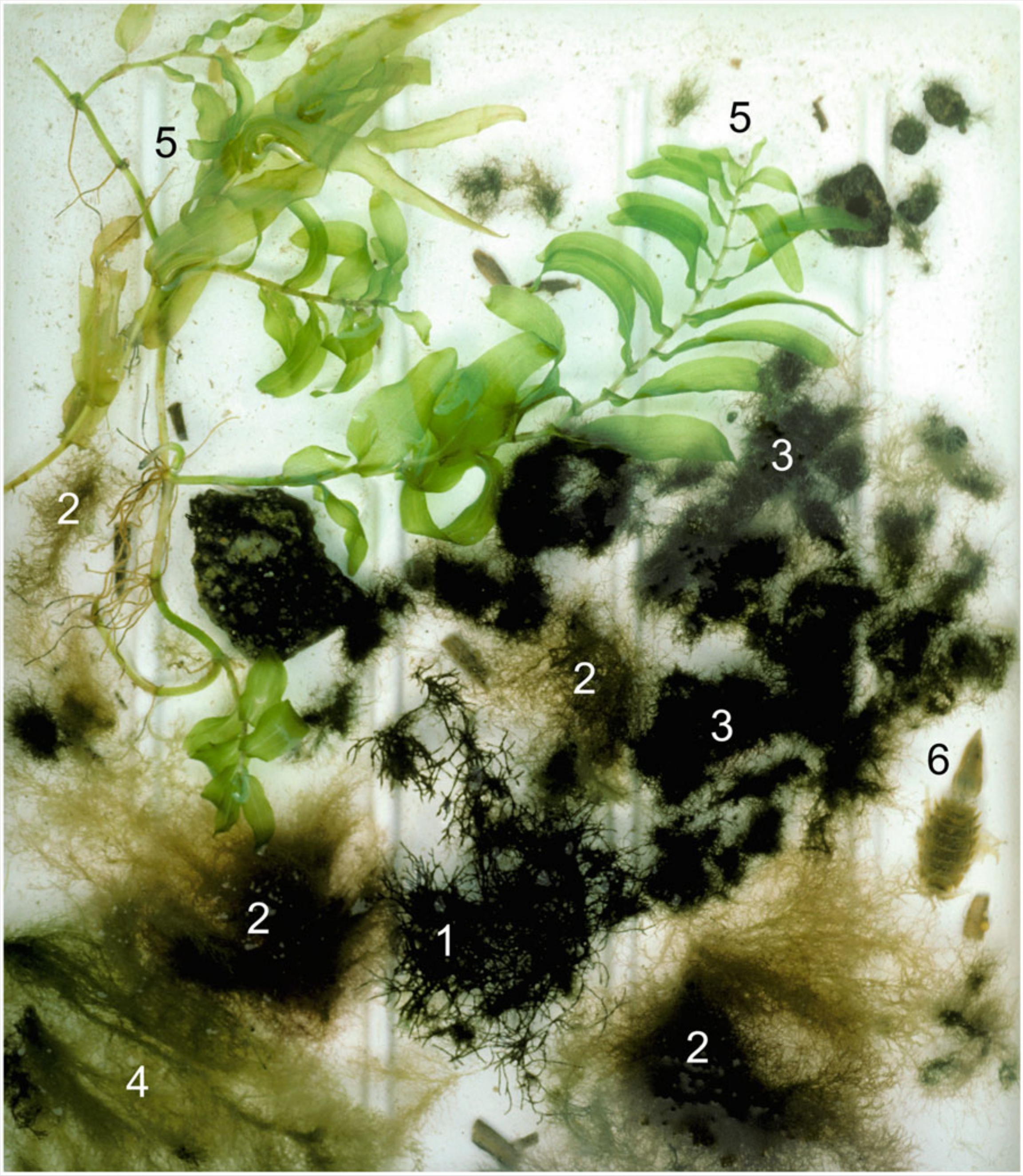
11.9.3 Red algae and *Mytilus*

The red algal belt of the Baltic Sea proper is often associated with *Mytilus trossulus*. Aggregates of *Furcellaria lumbricalis* are attached to the blue mussel shells or entangled in the byssus treads. Other red algae that are habitually associated with these *Furcellaria*-*Mytilus* aggregates (Fig. 11.27c) are *Coccotylus truncatus*, *Phyllophora pseudoceranoides* and *Rhodomela confervoides*. This community type forms distinct high-diversity patches on flat, soft substrates. For example, in the northern Baltic Sea proper a total of 24 associated macrofaunal species were identified in such patches, 11 of which were not present on the bare sediment outside the patches (Norling and Kautsky 2008).

In the eastern Baltic Sea proper, small areas densely vegetated with red algae are valuable marine biodiversity hotspots surrounded by vast areas with sandy substrate. The Estonian coast hosts a large loose-lying *Furcellaria lumbricalis*-dominated community, which is commercially harvested (Box 11.4). *Furcellaria lumbricalis*, mixed with *Coccotylus truncatus*, covers up to 120 km^2 of the seafloor with more than 140 kilotonnes of wet weight biomass in Kassari Bay between the islands of Saaremaa and Hiiumaa (Martin et al. 2006a, b). Also along the coasts of Latvia and Lithuania a loose-lying *Furcellaria lumbricalis* dominated vegetation is abundant (Bučas et al. 2009).

Box 11.7: Norra Kvarken: the northern distributional limit of marine algae

In the Bothnian Sea with salinity ~5, most marine algae that occur in the northern Baltic Sea proper are still found, but their thallus size tends to be smaller. Along the Bothnian Sea coast some marine species reach the northern limit of their distribution. However, the bulk disappearance of marine species occurs in the Norra Kvarken area at salinity ~4. Within a few tens of km almost all marine species are gone and freshwater species take over completely (Box Fig. 11.11).



Box Fig. 11.11 Marine macroalgae reach the northern limit of their distribution in the Baltic Sea at the islands of Holmöarna in the Norra Kvarken area as shown by a sample taken in this area including *Furcellaria lumbricalis* (1) with entangled *Coccotylus truncatus*, *Ceramium tenuicorne* (2) and *Battersia arctica* (3). They occur together with the freshwater green alga *Cladophora glomerata* (4), the freshwater vascular plant *Potamogeton perfoliatus* (5) and the isopod *Saduria entomon* (6). Photo: © Hans Kautsky

11.10 The *Battersia* belt

11.10.1 The brown alga *Battersia arctica*

The marine brown alga *Battersia arctica* is an Arctic species that has not been reported on coasts south of northern Norway, except in the Baltic Sea Area. *Battersia* occurs from the Kattegat to the Norra Kvarken area, down to the salinity of ~3–4 (Wærn 1952, 1965). Tufts of this slow-growing perennial species are usually 2–5 cm high, but may grow up to 8 cm (Fig. 11.28a).

Battersia arctica has a rather stiff thallus, which is probably the reason why this alga is able to cope with moderate amounts of sedimentation. Especially the deepest-growing *Battersia arctica* specimens may be periodically almost completely covered with sediment with only the upper shoots protruding above the sediment surface (Eriksson et al. 1998).

11.10.2 The *Battersia* belt of the Baltic Sea

The *Battersia* belt, completely dominated by *Battersia arctica*, forms the deep-water vegetation on hard substrates below the red algal belt in the Baltic Sea proper and immediately below the *Fucus* belt in the Bothnian Sea (Fig. 11.28). Only some crustose algae, *e.g. Hildenbrandia rubra* (red) and *Pseudolithoderma rosenvingei* (brown), can penetrate deeper down in the sublittoral zone than *Battersia arctica*.

In the Bothnian Sea, a vegetation dominated by *Battersia arctica* may occur below ~10 m when substrate is available (Wærn 1952, 1965). For example, in the Öregrund archipelago (southern Bothnian Sea), *Battersia arctica* is the most common alga, covering more than half of the phytobenthic zone (Wærn 1945, 1952). However, population size seems to vary over time (Kautsky et al. 1986, Eriksson et al. 1998).

11.11 *Zostera* meadows

11.11.1 The distribution of *Zostera marina*

The only truly marine vascular plant with a wide distribution in the Baltic Sea is the seagrass *Zostera marina* (common eelgrass). This is the most common marine vascular plant in the cooler coastal waters of the northern hemisphere. The plants are anchored by roots and rhizomes in soft or sandy substrates. Contrary to the more marine areas in the Skagerrak and Kattegat, where it mainly grows on soft substrates, *Zostera marina* seems to prefer sand and sand mixed with gravel in the Baltic Sea. A smaller relative of

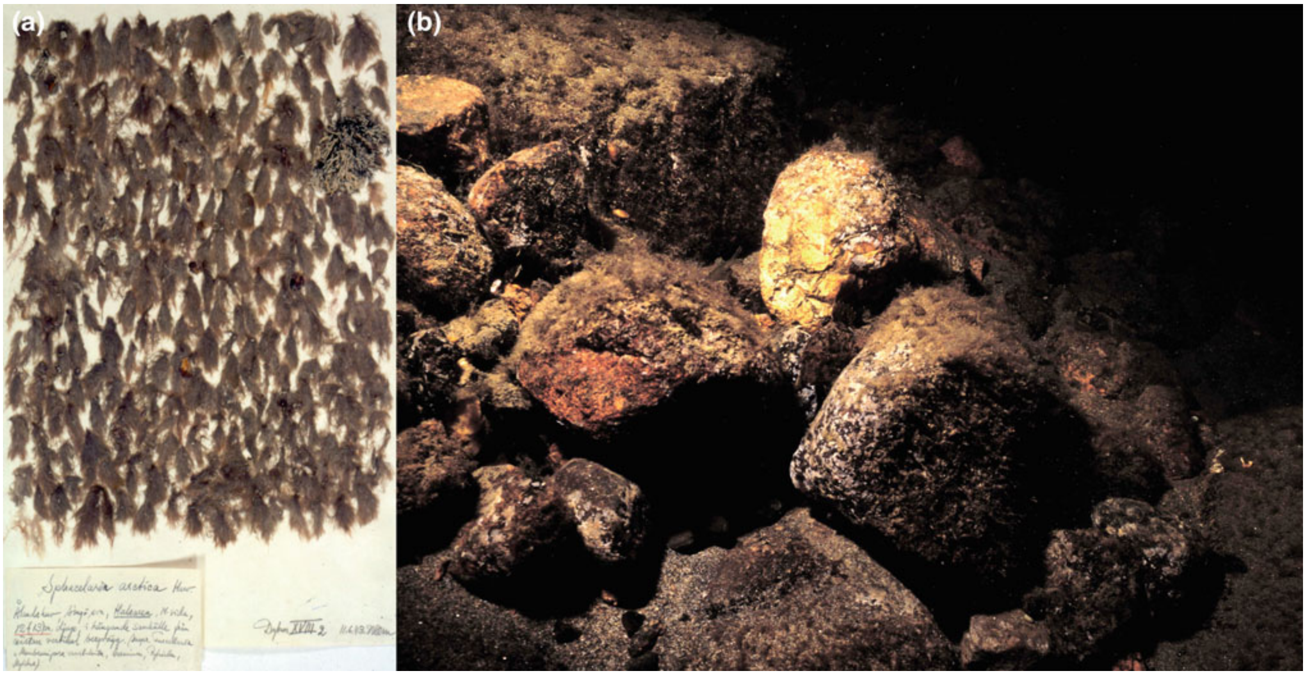


Fig. 11.28 The *Battersia* belt of the Baltic Sea. (**a**) A herbarium sheet of material sampled from an almost vertical bedrock cliff at a ~12–13 m water depth during a dive by Mats Wærn at Halsaren (Åland Sea) on 11 June 1943. The dominant species on the herbarium sheet is *Battersia arctica* (syn. *Sphacelaria arctica*), accompanied by *Ceramium tenuicorne*, *Furcellaria lumbricalis* (with epiphytic *Einhornia crustulenta*), *Pylaiella littoralis* and *Mytilus trossulus*. (**b**) *Battersia arctica* growing on boulders at a ~15 m water depth at Höga Kusten in the Bothnian Sea. Photo: (**a**) © Marianne Hielm Pedersén, (**b**) © Hans Kautsky

Zostera marina, the dwarf eelgrass *Zostera noltei*, which is widely distributed along the European Atlantic coasts, the Mediterranean Sea and the Black Sea, is rare in the Baltic Sea Area and restricted to the Belt Sea west of the Darß sill.

The range of *Zostera marina* in the Baltic Sea Area extends from the Kattegat to a line from the northern Stockholm archipelago to Rauma in southwestern Finland, with its main distribution along the ice-marginal Salpausselkä end moraines (Boström et al. 2006). The lower limit of its salinity distribution in the Baltic Sea is ~5 (Boström et al. 2014). The total areal cover of *Zostera marina* in the Baltic Sea Area is estimated at a minimum of 1,222 km^2, ~74 % of which is situated in the Kattegat and the Belt Sea and ~26 % in the Baltic Sea proper (Boström et al. 2014). This estimate is largely influenced by Danish cover data, which range from 673 to 1,345 km^2, assuming the present covers constituting 10 % to 20 % of the historical distribution, respectively. Thus, when using the more optimistic estimate for Denmark, the total eelgrass area in the Baltic Sea Area would be almost 1,900 km^2.

The most luxuriant *Zostera* meadows in the Baltic Sea Area, with plants over half a metre high, are found in the Belt Sea, as well as on the west coast of the island of Öland and around the island of Gotland in the Baltic Sea proper. In these areas sandy substrates prevail, and almost pure stands of *Zostera marina* may form extensive underwater meadows of several km^2 in size (Fig. 11.29a, b).

Shoot density at the time of maximum above-ground biomass is highly variable (72–3,948 shoots m^{-2}) but does not show significant differences between the different regions in the Baltic Sea Area (Boström et al. 2014). Although there is no significant relationship between salinity and shoot density within the salinity range 5–26, the shoot density is generally highest in shallow water and decreases exponentially with depth. However, the *Zostera* meadows in the northern Baltic Sea proper tend to develop smaller shoots, and the above-ground biomass is lower (range 37–73 g dry weight m^{-2}) than in the Skagerrak and the Kattegat - Belt Sea area (average 281 g dry weight m^{-2}), where shoots are generally larger (Boström et al. 2014).

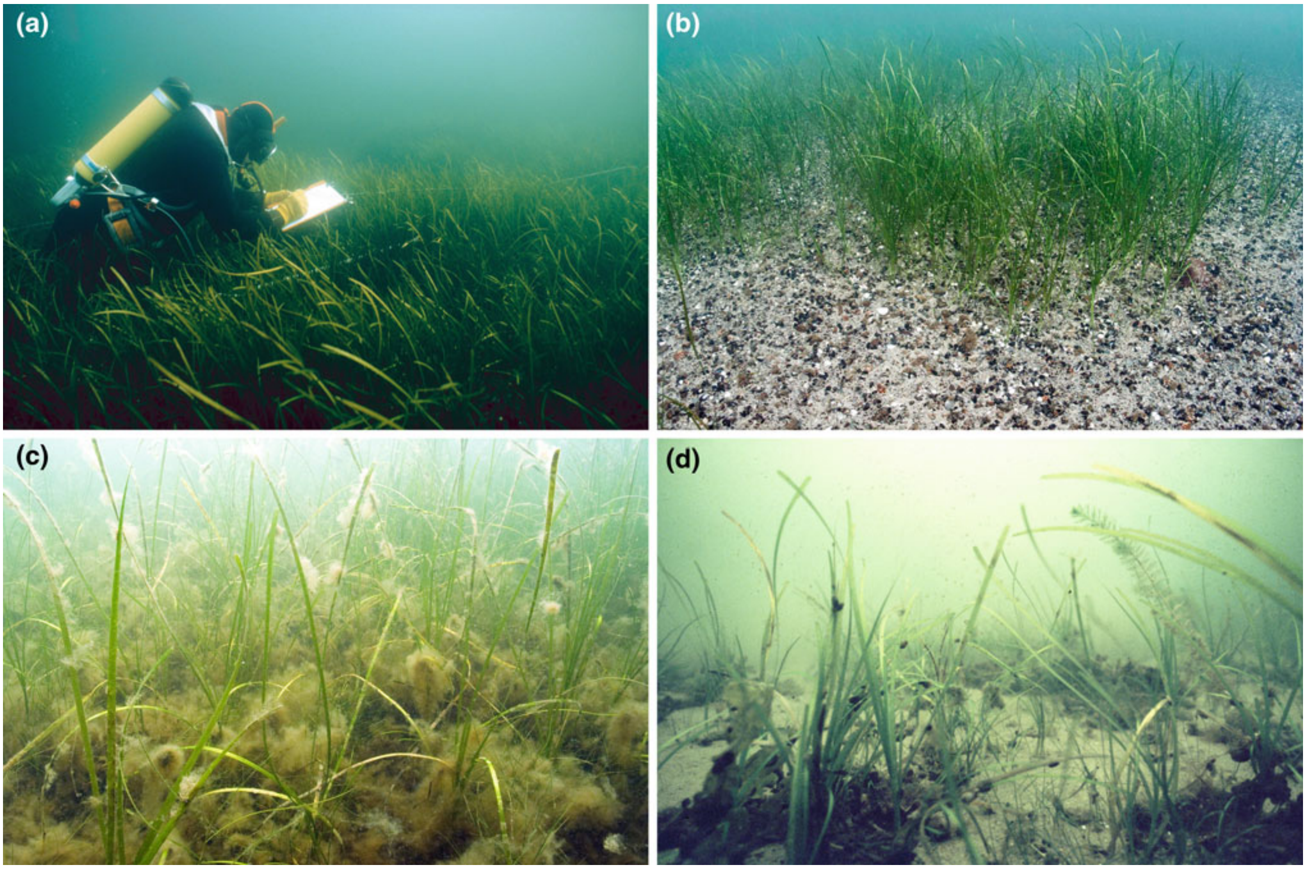


Fig. 11.29 *Zostera* meadows in the Baltic Sea. (**a**) A biologist (the late Bengt-Owe Jansson) working in a dense *Zostera* meadow in the Baltic Sea proper at the northeastern coast of the island of Gotland (Baltic Sea proper) at a ~4 m water depth. (**b**) *Zostera marina* on a substrate of sand, gravel and mollusc shells. (**c**) *Zostera marina* in a vegetation on mixed substrates, growing together with the brown alga *Pylaiella littoralis* and the hydrozoan *Cordylophora caspia*. (**d**) *Zostera marina* growing together with other vascular plants at the northern limit of its extension a few km north of Stockholm (northern Baltic Sea proper). Photo: © Hans Kautsky

11.11.2 The key species *Zostera marina*

Similarly to *Fucus vesiculosus* on hard substrates, *Zostera marina* plays critical structural and functional roles in the Baltic Sea ecosystem on sandy substrates, and is therefore considered a key species within its distributional range. On the otherwise species-poor sandy substrates, *Zostera marina* communities have high biomass with a positive effect on biodiversity by creating habitats for epiphytes, invertebrates and fish reproduction. In addition, the complex rhizome and root system of *Zostera marina* stabilises the substrate and facilitates the existence of diverse infaunal communities (Boström et al. 2002).

The higher-salinity areas in the Kattegat and the Belt Sea support monospecific meadows, with higher productivity (3–10 g dry weight m^{-2} d^{-1}) and higher genetic connectivity. In the Baltic Sea proper, *Zostera marina* productivity is generally low (<2 g dry weight m^{-2} d^{-1}) and meadows are isolated and genetically impoverished (Boström et al. 2014). Close to the limit of its salinity tolerance in the Baltic Sea, *Zostera marina* mainly grows vegetatively; flowering shoots are rare, and seeds do not ripen during the season. As a consequence, a *Zostera* meadow may consist of a single genotype (individual) and these mega-clones can reach an age of >1,000 years (Reusch et al. 1999).

A large proportion of the total faunal biomass associated with the *Zostera marina* vegetation in the Skagerrak and the northern Belt Sea consists of fish, ~70 % and ~40 %, respectively (Fig. 11.30). In the southern Belt Sea, fish make up as little as a few % at most of the total faunal biomass, and in the Baltic Sea even less. Omnivorous crustaceans decrease in relative abundance along the large-scale Baltic Sea gradient northward and are replaced by grazing crustaceans and gastropods. This dominance of grazers within the communities in the northern Baltic Sea proper appears to constitute an important buffer against epiphytic overgrowth of the *Zostera marina* plants.

11.11.3 *Zostera* meadows support high diversity

In the Baltic Sea proper, the epifaunal diversity in the *Zostera* meadows seems to be as high as in the *Fucus*-dominated vegetation (Kautsky and van der Maarel 1990). However, as a diverse infaunal community thrives in the organic-rich sediments among the seagrass roots, the total invertebrate diversity of *Zostera* meadows is usually higher than on rocky coasts. Except for pipefish (*Nerophis ophidion* and *Sygnathus typhle*), no associated species seem to be specific for the *Zostera* meadows in the Baltic Sea proper, probably because most species in the Baltic Sea proper are generalists rather than specialists.

The highest diversity of the *Zostera marina* communities in the Baltic Sea proper is found in areas with mixed substrates. The plants are often rooted next to patches of hard substrate with attached algae (Fig. 11.29c) and may provide a secondary hard substrate for epilithic species that already

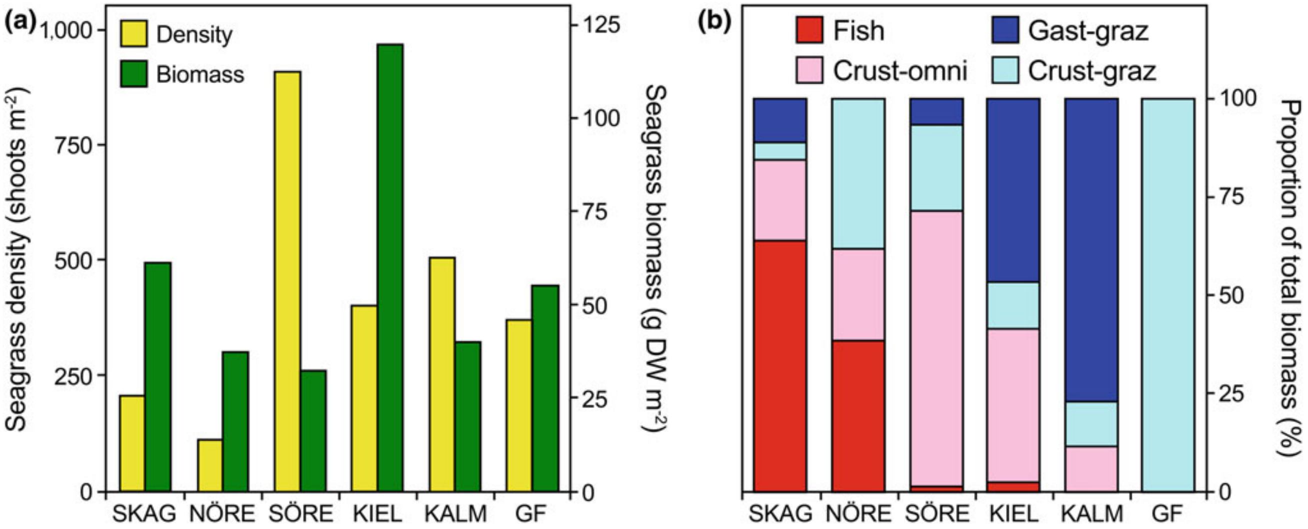


Fig. 11.30 The structure of *Zostera* meadows and their main epifaunal groups in six regions of the Baltic Sea Area. (**a**) Habitat complexity (expressed as shoot density) and the biomass of *Zostera marina* from which the epifauna was sampled. Note that this graph is not representative for shoot density or biomass differences between the six regions. (**b**) Relative biomass contribution (% of wet weight) of different groups of macrofauna to the total biomass of epifauna and fish. Crust-omni = omnivorous crustaceans, Crust-graz = grazing crustaceans, Gast-graz = grazing gastropods. SKAG = Skagerrak, NÖRE = northern Öresund (transition zone), SÖRE = southern Öresund (transition zone), KIEL = Kiel Bay (transition zone), KALM = Kalmarsund (Baltic Sea proper), GF = Gulf of Finland. Figure modified from Boström et al. (2014)

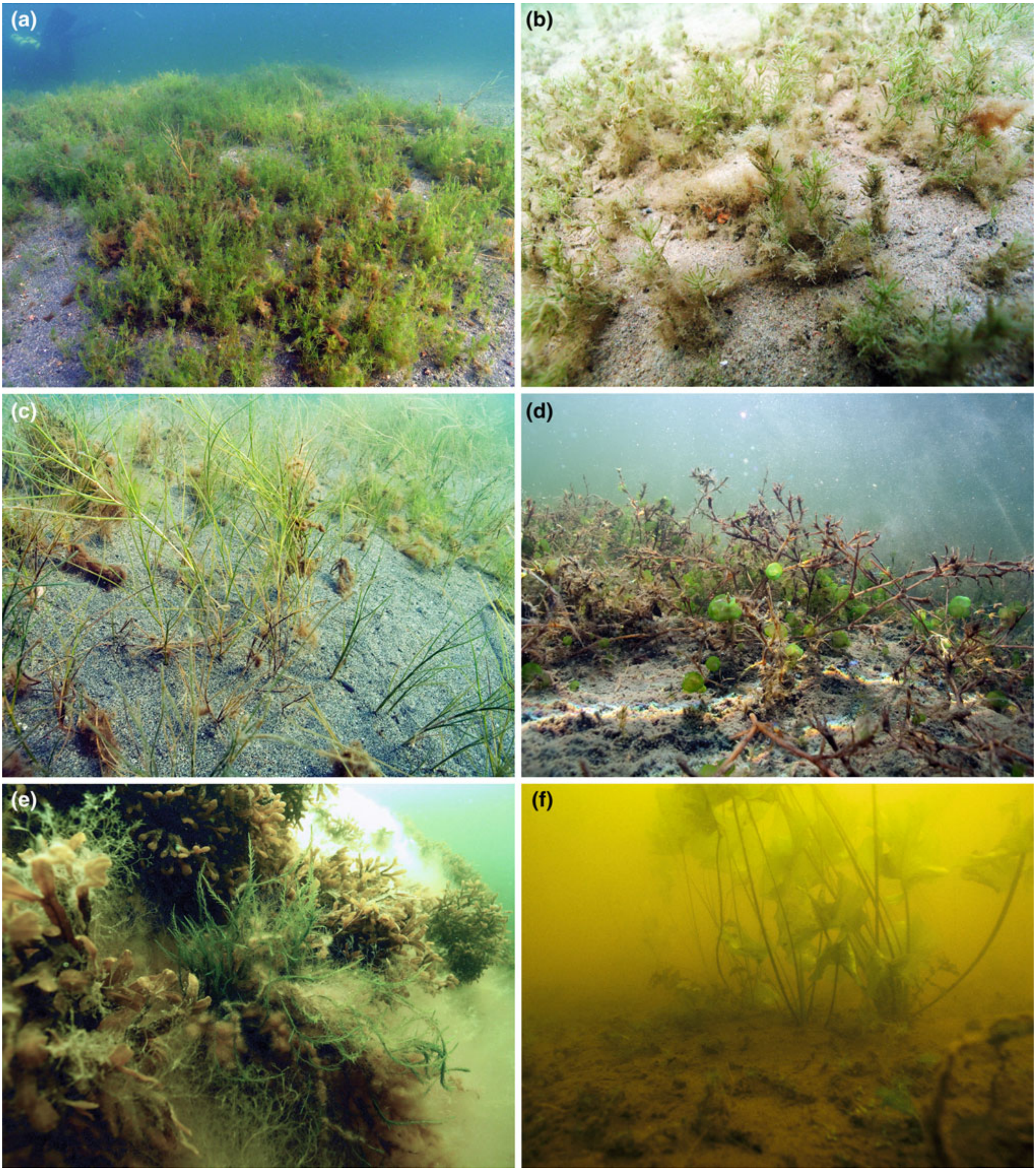


Fig. 11.31 Examples of freshwater species in the vegetation of the Baltic Sea. (**a**) The charophyte *Chara aspera*. (**b**) The charophyte *Chara tomentosa*. (**c**) The vascular plant *Stuckenia pectinata*. (**d**) *Najas marina* with epiphytic green colonies of the colonial ciliate *Ophrydium versatile*, which congregates in large mucilaginous masses. (**e**) The epilithic moss *Fontinalis dalecarlica* growing together with *Fucus*. (**f**) The vascular plant *Nuphar lutea* growing in the mouth of the Råneå river in the Bothnian Bay. The water is yellowish from high concentrations of coloured dissolved organic matter (CDOM). Photo: © Hans Kautsky

occur in the area (Boström and Bonsdorff 1997; Möller et al. 2014). Additionally, in the Baltic Sea proper *Zostera marina* often grows in mixed stands with other vascular plants such as *Myriophyllum spicatum*, *Potamogeton perfoliatus*, *Ruppia maritima*, *Stuckenia pectinata* and *Zannichellia palustris*, which also increases community diversity. The growth of *Zostera marina* seems to be positively influenced by these other vascular plants as it produces more shoots and biomass in mixed stands (Salo et al. 2009; Gustafsson and Boström 2010, 2013; Fig. 11.29d).

11.12 Freshwater influences in the vegetation

11.12.1 Vascular plants in the Baltic Sea proper

A major difference in the vegetation on mixed, sandy and soft substrates between the Kattegat area and the Baltic Sea proper is the higher abundance of freshwater vascular plant and charophyte species in the latter (Fig. 11.31). The vegetation of the Baltic Sea proper often consists of mixed stands of *Zostera marina*, the brackish-water species *Ruppia cirrhosa*, and freshwater vascular plants such as *Myriophyllum spicatum*, *Potamogeton perfoliatus*, *Stuckenia pectinata* and *Zannichellia palustris* (Luther 1951a, b; Wallentinus 1979; Kautsky 1989). In the Kattegat-Belt Sea area these freshwater vascular plants are restricted to bays with a strong freshwater influence.

11.12.2 Vascular plants in the Bothnian Sea

The dominating coast type in the Bothnian Sea, except for the rocky coasts of Höga Kusten (Sweden), is a flat coast with mixed, sandy and soft substrates. Flushed till from the last glaciation characterises the landscape below the sea surface (seascape) in the Bothnian Sea and this type of substrate supports abundant *Myriophyllum spicatum*, *Potamogeton perfoliatus*, *Stuckenia pectinata*, and *Zannichellia palustris*. *Zostera marina* and *Ruppia cirrhosa* are absent, but the brackish-water species *Ruppia maritima* (which despite its Latin name is not a marine species) still occurs in the southern half of the Bothnian Sea, up to Höga Kusten. A number of additional freshwater vascular plants emerge in the Bothnian Sea, *e.g.* *Callitriche* spp., *Isoetes echinospora*, *Subularia aquatica*, as well as the submerged aquatic bryophytes *Drepanocladus* spp. and *Fontinalis dalecarlica* (Fig. 11.31e).

11.12.3 Vascular plants in the Bothnian Bay

Exposed bedrock is rare in the Bothnian Bay and mixed, sandy and soft substrates dominate the shallow coastline. The long winter period makes it difficult for perennial species to survive. However, sites sheltered from ice scouring may host the luxuriant growth of vascular plants, with *Potamogeton perfoliatus* and *Stuckenia pectinata* as dominants, accompanied by *Myriophyllum spicatum*, *Ranunculus palustris* and others. Some additional freshwater vascular plants that occur in the phytobenthic vegetation here, but not in the Bothnian Sea, are *Limosella aquatica* and the red-listed species *Alisma wahlenbergii* (HELCOM 2013a), as well as some mosses (*Fissidens fontanus*, *Fontinalis* spp.). *Limosella aquatica* and *Alisma wahlenbergii* seem to be even more abundant in the Bothnian Bay than in freshwater, perhaps due to lower competition.

Obligate freshwater species such as *Nuphar lutea* (Fig. 11.31f) occur only in almost pure freshwater in river mouths. The more wave-exposed coasts in the Bothnian Bay are often characterised by extensive sand fields, which are mainly inhabited by benthic diatoms and meiofauna. On boulders and stones, short tufts of *Aegagropila linnaei*, benthic diatoms and freshwater bivalves (*Anodonta* sp., *Pisidium* spp., *Sphaerium* sp.) and freshwater snails such as *Radix balthica* (syn. *Radix ovata*), *Radix labiata* (syn. *Radix peregra*), *Theodoxus fluviatilis* and *Valvata piscinalis*, may occur.

11.12.4 Charophytes

Charophytes may occur in high abundances and cover large areas on sandy and soft bottoms in shallow sheltered bays (Fig. 11.31a, b). The distribution of charophytes in the Baltic Sea is mainly governed by salinity, water depth, sediment type and exposure to wave action (Schubert and Blindow 2003; Torn and Martin 2004). The most widely distributed *Chara* species in the Baltic Sea are *Chara aspera* and *Chara baltica* (Torn 2008), but *Chara tomentosa* may also form high-biomass nearly monospecific aggregations locally in the northeastern Baltic Sea proper. Here the primary productivity of *Chara tomentosa* can be as high as ~30 µmol O_2 (kg dry weight)$^{-1}$ s^{-1} in July (Torn et al. 2006b), which is similar to that of *Cladophora glomerata* and *Fucus vesiculosus* (Box 11.6).

In recent decades, the number of species, distribution area and biomass of charophytes have significantly declined in the Baltic Sea. Declines have been described for several

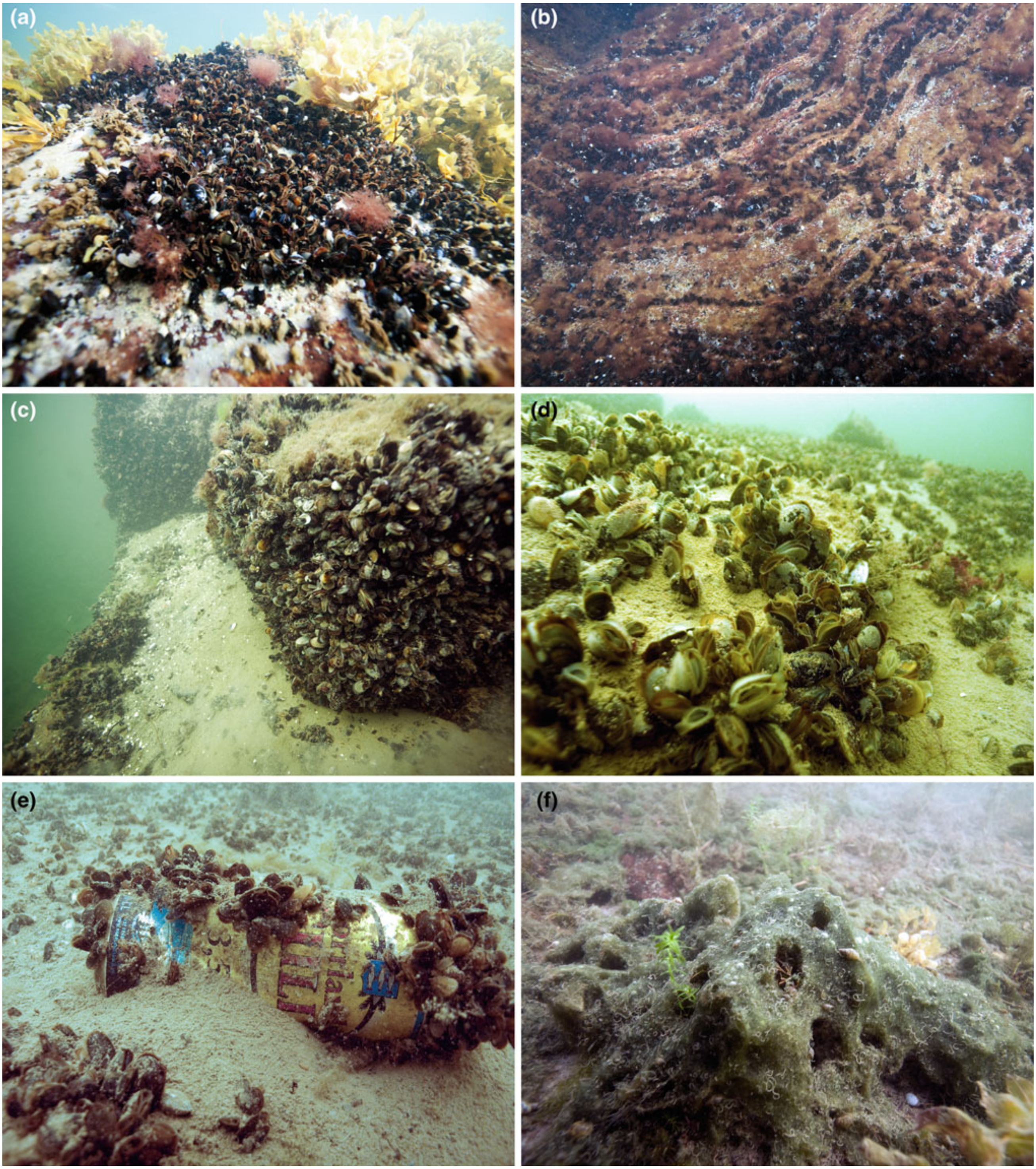


Fig. 11.32 *Mytilus trossulus* at Askö, Baltic Sea proper. (**a**) A dense patch of *Mytilus trossulus* in the *Fucus* belt, growing together with *Ceramium tenuicorne* and *Einhornia crustulenta* at a ~2 m water depth. (**b**) *Mytilus trossulus* growing together with short tufts of *Ceramium tenuicorne* at a ~2 m water depth at an exposed site where *Mytilus trossulus* can only stay attached in the crevices of the rock. (**c**) *Mytilus trossulus* on bedrock cliffs at a ~4 m water depth. Here *Mytilus trossulus* can attach to vertical surfaces only because the horizontal surfaces hold too much silt for the byssus to anchor. (**d**) Loose-lying *Mytilus trossulus* aggregates on sandy-soft substrate at a ~7 m water depth. (**e**) *Mytilus trossulus* attaches to any hard substrate, including beer cans. (**f**) *Mytilus trossulus* covered by an algal mat of decaying *Spirogyra* sp. at a ~4 m water depth. The decay process creates hypoxic conditions, but *Mytilus trossulus* individuals pump oxygenated seawater to the seafloor through the craters in the algal mat. A bright green branch of *Callitriche hermaphroditica* grows on the algal mat. Photo: © Hans Kautsky

subregions of the Baltic Sea, *e.g.* the coastal waters of Schleswig-Holstein (Germany), the Swedish west coast and the Hanko Peninsula in southwestern Finland (Blindow 2000; Schubert and Blindow 2003; Munsterhjelm 2005). Such declines are related to increased anthropogenic pressure (Torn 2008), and they may occur in other (less investigated) areas of the Baltic Sea as well. Charophytes are especially sensitive to mechanical stress (habitat destruction) as well as to eutrophication (Yousef et al. 2001; Schubert and Blindow 2003; Munsterhjelm 2005).

11.13 The role of the fauna in the phytobenthic zone

11.13.1 The key species *Mytilus trossulus*

The blue mussel *Mytilus trossulus* is a highly abundant habitat-forming key species in the Baltic Sea proper from just below the water surface down to a ~20 m water depth, but it can live at greater depth as well (Fig. 11.32). A biomass of ~300 g dry weight m^{-2} is common along the western coast of the Baltic Sea proper where 80–90 % of the total animal biomass in the sublittoral zone consists of *Mytilus trossulus* (Jansson and Kautsky 1977). In the Baltic Sea it is found up to the northernmost part of the Bothnian Sea with salinity ~4, but at this low salinity it seldom reaches high biomass. In the Gulf of Finland *Mytilus trossulus* extends to the central parts, down to salinity ~4.5 (Westerbom et al. 2002).

The energy demand for coping with osmotic stress makes the Baltic Sea blue mussel *Mytilus trossulus* smaller in body size (*cf.* Fig. 4.5b), with thinner shells (*i.e.* more easily predated) and byssus weaker (*i.e.* easily detached from the substrate) than its North Sea counterpart (Tedengren and Kautsky 1986; Tedengren et al. 1990). In the Åland Sea the shells are so thin that the mussel is an easy prey for fish and waterbirds. Therefore, *Mytilus trossulus* is usually rare in the entire Bothnian Sea, and scattered individuals are mainly found sheltered under boulders and stones where predators cannot reach them.

The high biomass of *Mytilus trossulus* in the Baltic Sea proper is also an important food source for fish and waterbirds, but here predators usually have little effect on the *Mytilus trossulus* population (Kautsky 1981). This is in contrast to more marine habitats where *Mytilus edulis* is constantly preyed upon by benthic predators (*cf.* Fig. 4.32) and the high biomass of the mussel is restricted to places where these benthic predators cannot reach them, *e.g.* high up on piers exposed to strong wave action.

Mytilus trossulus is a filter feeder that consumes both plankton and suspensions of benthic microorganisms directly, and is an important link between the benthic and pelagic components of the Baltic Sea ecosystem in channelling the matter and energy flows. In nearly all habitat types, pelagic feeding by *Mytilus trossulus* exceeds that of benthic feeding (Lauringson et al. 2009). One blue mussel individual is estimated to filter 5 L of seawater per hour and, theoretically, the *Mytilus trossulus* population of the entire Baltic Sea could recirculate the entire water column four times per year (Kautsky and Wallentinus 1980; Kautsky and Evans 1987). The recirculation of nitrogen and phosphorus from pelagic production by *Mytilus trossulus* is sufficient to support the phytobenthic system and also to export back nutrients to the pelagic system.

11.13.2 Substrate, wave exposure and the distribution of *Mytilus*

The lower depth limit of the blue mussel *Mytilus trossulus* in the sublittoral zone is usually set by the lack of suitable substrate (Fig. 11.32c). Close to the water surface the mussel attaches to any hard substrate, including *Fucus vesiculosus*. Where there are fewer algae, the competition for space between algae and the bivalve is lower and *Mytilus trossulus* can dominate the substrate. Therefore, the mussel may form belts that cover 100 % of the hard substrate below the algal belts or on vertical rock surfaces. On gently sloping seafloors, *Mytilus trossulus* is commonly found in clusters lying scattered on the substrate, which may be everything from gravel to soft substrate, often associated with red algae (Figs. 11.27c and 11.32d)

Water circulation is of major importance for food supply to *Mytilus trossulus*, *e.g.* an extremely high biomass of >3.5 kg dry weight m^{-2} (including shells) has been recorded at blue mussel beds on the strongly exposed offshore Sandö bank (Sweden) at an ~18 m water depth (Kautsky 1984). Along a wave-exposure gradient in the Archipelago Sea (Finland), the lowest densities and biomass of *Mytilus trossulus* were found in the innermost archipelago (Vuorinen et al. 2002). Most of the populations in the inner archipelago consisted of small, 4–6 mm long individuals. In the middle and outer archipelago areas they were twice that size, and the average growth rate was highest in the middle archipelago. Similar observations were made in the Ekenäs archipelago (Gulf of Finland) where the *Mytilus trossulus* density also increased steadily with increasing wave exposure towards the outer archipelago, but biomass was highest at intermediate exposure (Fig. 11.33, Westerbom and Jattu 2006). This suggests that *Mytilus trossulus* may be sensitive to intraspecific competition towards the outer archipelago since density increases but biomass decreases (*i.e.* body size decreases).

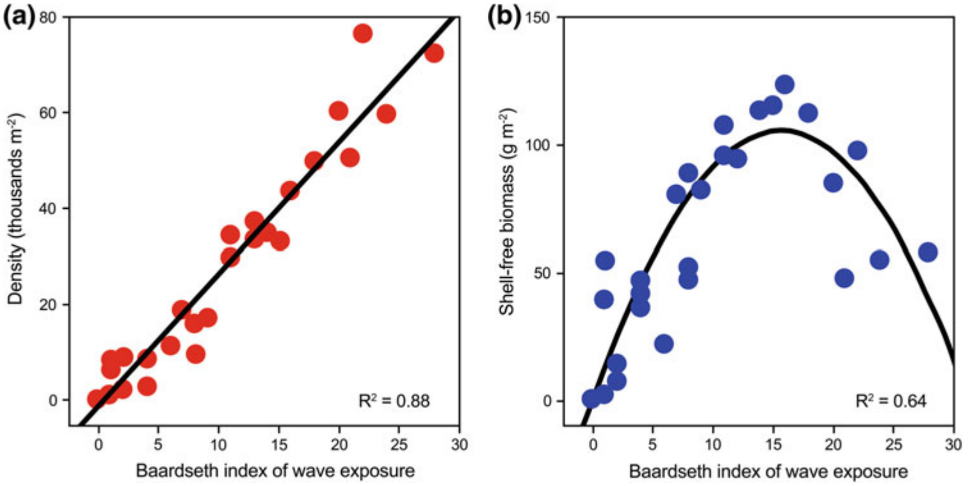


Fig. 11.33 Density and biomass of *Mytilus trossulus* in relation to wave exposure (Baardseth index, *cf.* Box 11.5) at a water depth of 8 m for 30 sampling stations near Tvärminne close to the entrance to the Gulf of Finland. (**a**) Relationship between the mean density of *Mytilus trossulus* per station and wave exposure. (**b**) Relationship between the mean shell-free biomass per station and wave exposure. Figure modified from Westerbom and Jattu (2006)

11.13.3 Invertebrate grazers

Grazers can have a direct negative grazing effect on macrophytes, but in the Baltic Sea it is rare for grazers to crop down entire phytobenthic communities because the grazer populations are usually not abundant enough. Rather it seems that grazing mainly keeps the growth of algal epiphytes down to the advantage of the phytobenthic communities' key species (Boström et al. 2014). Dominant perennial algae in the Baltic Sea, *e.g. Fucus vesiculosus*, *Fucus serratus*, *Furcellaria lumbricalis* and *Phyllophora pseudoceranoides*, have been shown to use chemical defences against grazing by the isopod *Idotea balthica* (Rodhe et al. 2004; Rodhe and Wahl 2008).

Typical grazers in the Baltic Sea are snails (*e.g. Bithynia tentaculata*, *Radix labiata* and *Theodoxus fluviatilis*, Fig. 11.34a), which mainly consume diatoms and filamentous algae. However, it has been demonstrated that the radula of the snails can also damage the thallus of robust algae, including the stiff leathery thallus of *Fucus vesiculosus*. Also, isopods (*e.g. Idotea* spp., Fig. 11.34b, c) and amphipods (*e.g. Gammarus* spp., Fig. 11.17) are grazers on diatoms, macroalgae and/or vascular plants. An exception is the large isopod *Saduria entomon*, which is basically a detritivore but also a carnivore.

Species of the marine genus *Idotea* can attain impressive feeding rates on a range of macroalgae and vascular plants (Vesakoski et al. 2008; Leidenberger et al. 2012). The three *Idotea* species that occur in the Baltic Sea exhibit a habitat segregation according to their lower salinity limit and preference for vegetation type and exposure to wave action. *Idotea balthica* (Fig. 11.34b) occurs down to salinity ~ 2.7 and is often dominant in the *Fucus* belt at varying exposure, *Idotea chelipes* (Fig. 11.34c) occurs down to salinity ~ 3.2 and is often dominant in *Zostera* meadows at varying exposure while *Idotea granulosa* occurs down to salinity ~ 4.6 and is restricted to fully exposed coasts (Leidenberger et al. 2012).

11.13.4 Grazing in the *Fucus* belt

An early model of the general decline of *Fucus* in the Baltic Sea in the 1970s suggested that filamentous algal epiphytes on *Fucus* would benefit from eutrophication and that these epiphytes would outcompete *Fucus* in the competition for light and nutrients (Kangas et al. 1982). Furthermore, the filamentous algae were thought to increase the abundance of grazers (notably *Idotea balthica*), which then also crop down the *Fucus* vegetation.

In the early 1990s, *Fucus* disappeared from the deeper parts of the sublittoral and also from whole depth transects in the Kalmarsund area (Sweden) in the Baltic Sea proper, which coincided with a mass occurrence of *Idotea balthica* (Engkvist et al. 2000). Experimental studies demonstrated the isopod's voracious feeding on *Fucus* and showed that 800 individuals, but not 600 or fewer, of *Idotea balthica* kg^{-1} of *Fucus* wet weight are able to graze down the *Fucus* vegetation (Engkvist et al. 2000; Svensson et al. 2004). However, such high abundances of *Idotea balthica* are extremely rare in nature (Leidenberger et al. 2012).

Furthermore, multiple choice experiments showed that *Idotea balthica* in fact prefers the green filamentous algae

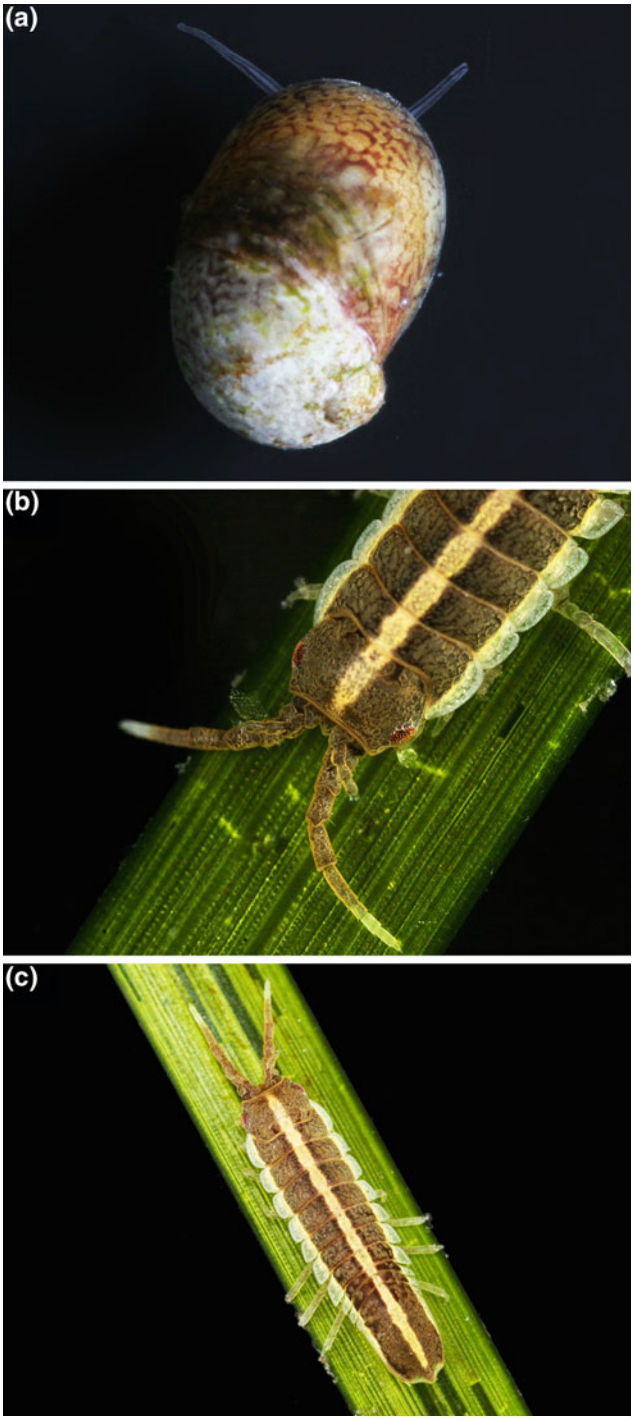


Fig. 11.34 Three species of grazers that are common in the phytobenthic zone of the Baltic Sea. (**a**) The snail *Theodoxus fluviatilis* (**b**) The isopod *Idotea balthica*, see also Fig. 6.1. (**c**) The isopod *Idotea chelipes*. Photo: © Maria Włodarska-Kowalczuk and Piotr Bałazy

Cladophora glomerata and *Ulva intestinalis* above the leathery thallus of *Fucus vesiculosus* (Goecker and Kåll 2003). Other experiments confirmed that *Idotea balthica* prefers *Cladophora glomerata* above *Fucus vesiculosus* as a food item, but that vascular plants are even more appealing. The preferred food items of *Idotea balthica* can be arranged in the following series: *Stuckenia pectinata* > *Zannichellia palustris* > *Zostera marina* > *Cladophora glomerata* > *Fucus vesiculosus*, while this isopod's habitat preference order is *Fucus vesiculosus* > *Stuckenia pectinata* > *Zostera marina* > *Zannichellia palustris* > *Cladophora glomerata* (Vesakoski et al. 2008).

Other experiments have shown that moderate abundances of grazers are beneficial for the growth of *Fucus vesiculosus* during nutrient enrichment since they crop down filamentous epiphytes, which lowers shading by epiphytes and decreases competition for nutrients (Worm et al. 1999). Furthermore, it was shown that grazers may even enhance *Fucus vesiculosus* recruitment by selective consumption of filamentous algae (Worm et al. 1999, 2001). Thus, the effect of grazers on *Fucus vesiculosus* in eutrophic environments may be negative or positive, depending on the local characteristics, the life stage of *Fucus vesiculosus* and the magnitude of grazing.

11.13.5 Bottom-up and top-down control of grazers

Theoretically, eutrophication would support higher grazer densities by increasing the availability and quality of algal food to the grazers (Hemmi and Jormalainen 2002). This would lead to an increasing density of grazers such as snails, isopods and amphipods (bottom-up control). The abundance of epiphytic diatoms and filamentous algae in the phytobenthic community would decrease to a point where they switch to feed on *Fucus*. This would then damage the *Fucus* thallus so that it is more easily torn away from its substrate by wave action and there would be a loss of *Fucus* biomass.

The top-down approach postulates that when a piscivorous fish (*e.g.* the Atlantic cod *Gadus morhua*) decreases in abundance, the population sizes of its prey (invertivorous fish) will increase and the population sizes of the invertebrate grazers (snails, amphipods, isopods) will decrease, which leaves the filamentous alga to grow freely with low grazing pressure. Experimental evidence for this mechanism has been presented for the Baltic Sea Area (Moksnes et al. 2008; Baden et al. 2010; Eriksson et al. 2009, 2011).

Both the bottom-up and top-down mechanisms cannot be confirmed by long-term field observations in the Askö area in the Baltic Sea proper. While eutrophication decreased and the cod collapsed in this area between 1993 and 2012, there were increasing trends in both grazer biomass and *Fucus* biomass, whereas filamentous algae did not show any particular trend (Fig. 11.35a–c). This suggests that the grazer pressure in the Askö area is not high enough to damage the *Fucus* vegetation.

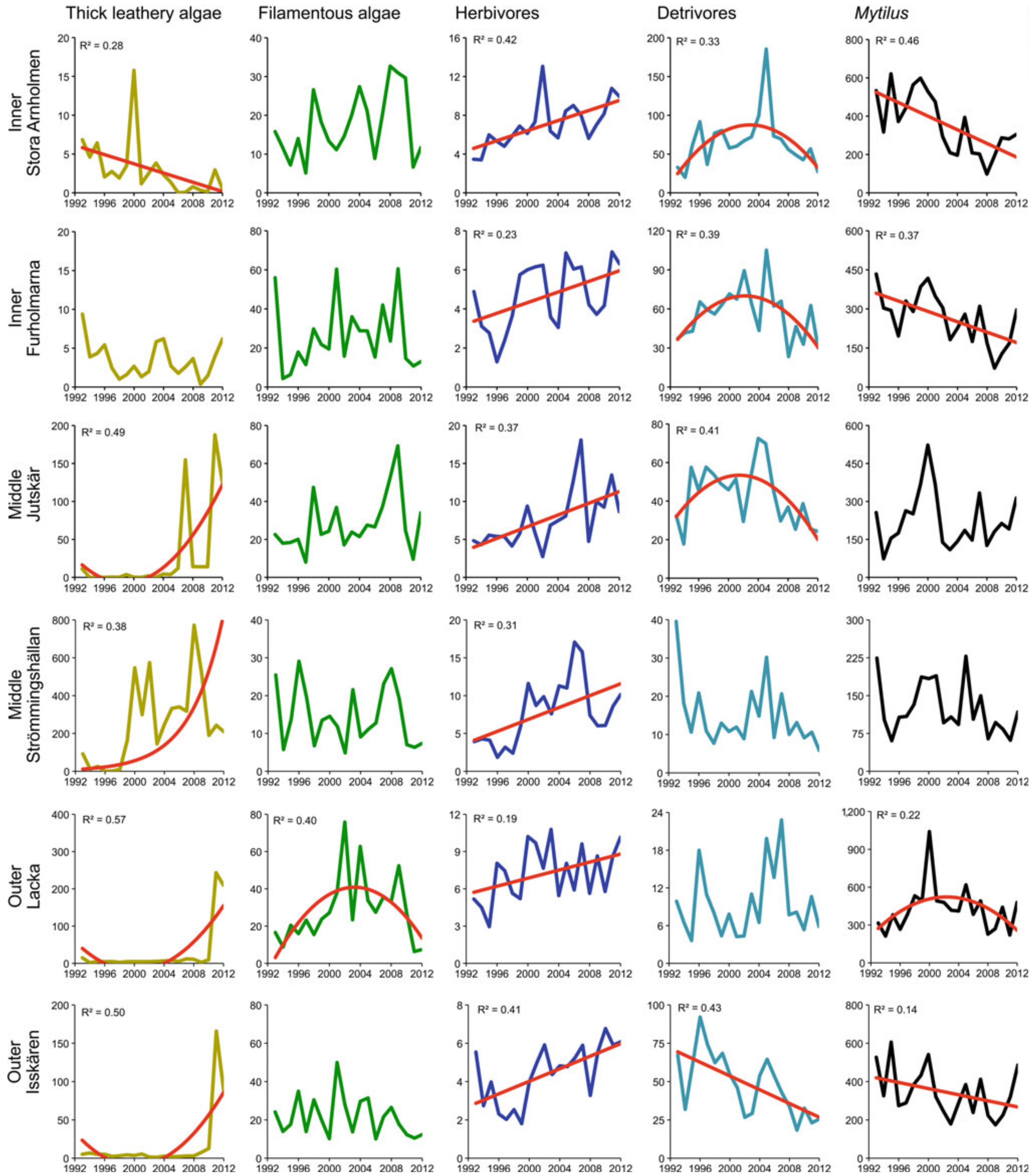


Fig. 11.35 Long-term field observations (1993–2012) on the phytobenthic communities, including the associated macrofauna, in the Askö area (Baltic Sea proper) at two stations in the inner archipelago (Stora Arnholmen, Furholmarna), two stations in the middle archipelago (Jutskär, Stömmingshällan) and two stations in the outer archipelago (Lacka, Isskären). This is shown as the mean dry weight m^{-2} per station for thick leathery algae (mainly *Fucus*), filamentous algae, herbivores, detritivores and *Mytilus trossulus* (including shells) at each station. Figure based on data in Kautsky et al. (2011) and additional unpublished data from the Swedish monitoring programme for phytobenthos

11.13.6 Invertebrate carnivores and omnivores

There are many invertebrate carnivorous species that pick their prey within the phytobenthic communities. Many of these species are not obligate carnivores as they can also eat algae and plants, and are thus in fact omnivores. Some of them eat invertebrate prey as well as detritus. The polychaete *Hediste diversicolor* and several insect larvae (*e.g.* the Polycentropodidae, Tanypodinae, Zygoptera) are carnivores, but many insect larvae are herbivores, and some even breed and harvest their own food (*e.g.* some tube-dwelling Chironomidae and Trichoptera larvae, Hasselrot 1993). None of the carnivorous or omnivorous invertebrate species in the phytobenthic zone of the brackish Baltic Sea occur in abundances high enough to alter the community composition like large predators such as starfish (*Asterias* spp.) and larger crabs (*Carcinus* spp.) are able to do in marine areas (*cf.* Fig. 4.32).

11.13.7 Invertebrate detritivores

Most of the energy fixed in the phytobenthic zone is not consumed directly. Most primary producers are first decomposed and then consumed as detritus (dead organic matter). Decomposition rates can be so high that hypoxic (<2 mL O_2 L^{-1}) and anoxic conditions occur as patches in the phytobenthic zone. This is often shown as white patches of bacteria belonging to the genus *Beggiatoa*, which oxidise hydrogen sulphide (H_2S) as an energy source, or as a purplish to wine-red or blue-green layer of the cyanobacterium *Spirulina*, which covers patches of decaying primary producers on the seafloor.

The detritivores, which recirculate the nutrients, have a key function in the ecosystem. The detritivores are scavengers, deposit feeders and suspension feeders and are represented in most invertebrate groups. Abundant detritivores in the phytobenthic communities of the Baltic Sea are the bivalves *Cerastoderma glaucum* and *Macoma balthica*, which filter suspended matter from the water or consume the organic matter from the seafloor.

11.13.8 Fish

Small fish species and juvenile fish seek shelter from predators and find their food in the phytobenthic communities (Aneer 1985; Kautsky et al. 1992; Rönnbäck et al. 2007). The two perhaps most common benthic fish in the shallow waters of the Baltic Sea, the sand goby *Pomatoschistus minutus* and the common goby *Pomatoschistus microps*, are difficult to observe without diving (Nellbring 1985). However, other common inhabitants of the phytobenthic zone, the three-spined stickleback *Gasterosteus aculeatus* (Fig. 12.15a) and the common minnow *Phoxinus phoxinus*, can be easily observed swimming among the vegetation close to the water surface.

One of the dominant pelagic fish in the Baltic Sea, the Atlantic herring *Clupea harengus*, has its spawning habitats among the macrophytes (*cf.* Fig. 4.28), while the Atlantic cod *Gadus morhua* seeks its prey fish here. Freshwater piscivores such as European perch *Perca fluviatilis* and northern pike *Esox lucius* use the shallow bays of the Baltic Sea as spawning habitats because they are rich in vegetation and warm up quickly by the sun during the day (*cf.* Box 4.9). Restoration of these habitats is nowadays being carried out to stop the decline of the benthic fish populations of the Baltic Sea proper.

In open coastal waters of the southwestern Baltic Sea proper, the coastal predators, the perch and the pike, have decreased markedly in abundance while small fish species such as sticklebacks have increased (Ljunggren et al. 2010). One hypothesis claims that the now numerous sticklebacks induced the decline of their predators by eating their eggs (Nilsson et al. 2004; Nilsson 2006), but this was based on the stomach content of the sticklebacks and not so much on their actual numbers in field. An alternative hypothesis proposes that the decline of the perch and pike in the phytobenthic zone are caused by a trophic cascade in the Baltic Sea offshore pelagic system where the European sprat *Sprattus sprattus* has caused a decline in the mesozooplankton populations (*cf.* Sect. 8.9.5) and thus limiting food for young recruits of perch and pike (Ljunggren et al. 2010). Thus, the dramatic change in the offshore system may have propagated to the coast.

The ground-dwelling fish all have their microhabitat preferences, and in general their diversity increases with the heterogeneity of the substrate (Fig. 11.36). These fish species are usually stationary and may reflect the local environmental conditions. For example, the viviparous eelpout *Zoarces viviparus* is used in environmental monitoring along the Baltic Sea coast as a bioindicator (*cf.* Sect. 14.6.2). The male black goby *Gobius niger* is easily observed on mixed substrates where it defends its nest below a boulder. The well-camouflaged European bullhead *Cottus gobio* is more difficult to see as it lies still among stones and algae, waiting for its prey to swim just in front of its large mouth. The pipefish *Syngnathus typhle* floats around in an upright position and sucks in small animals or nibbles off the siphons of hydrobiid snails. Small schools of the common

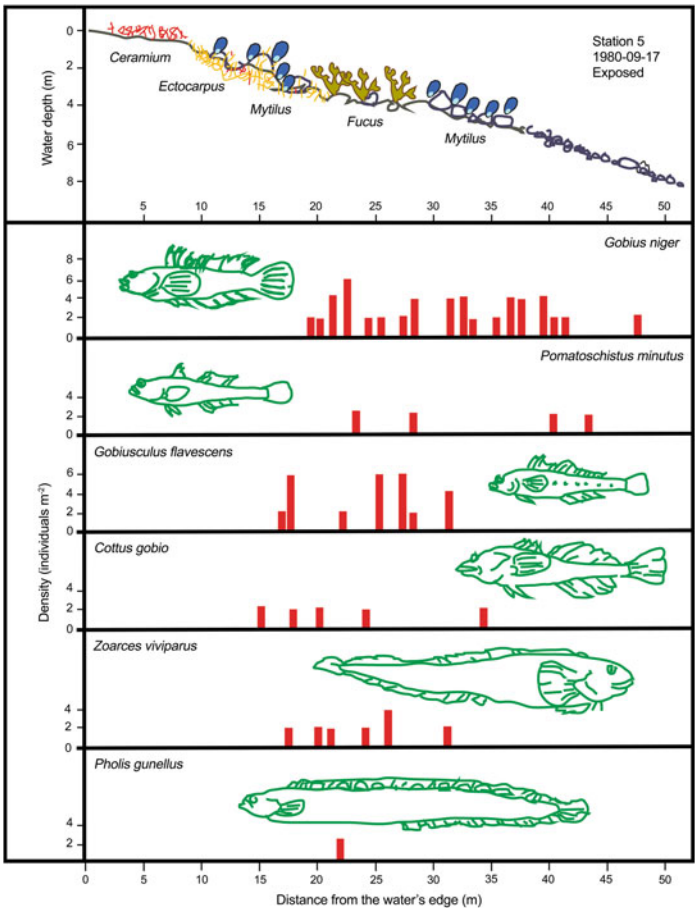


Fig. 11.36 Spatial distribution of demersal fish in the phytobenthic zone of the Askö area in the Baltic Sea proper. Figure modified from Jansson et al. (1985)

minnow *Phoxinus phoxinus* hunt for large schools of mysids that live on invertebrate prey found within the *Fucus* belt.

11.13.9 Birds

Several species of diving waterbirds feed in the phytobenthic zone either close to the coast or at shallow offshore banks far from land. Some species of diving ducks and especially the sea ducks feed to a large extent on mussels, clams and other benthic fauna. For example, in winter a single common eider *Somateria mollissima* may consume up to two kilogram wet weight blue mussels per day and the smaller long-tailed duck *Clangula hyemalis* (*cf.* Box Fig. 11.12) may consume one kilogram or more blue mussels per day. In total, two to three million sea ducks, including Arctic-breeding long-tailed ducks, common scoters *Melanitta nigra* and velvet scoters *Melanitta fusca* as well as the Baltic-breeding common eiders and velvet scoters spend the non-breeding season in the Baltic Sea (Skov et al. 2011). Marine areas with dense populations of blue mussels of high quality and of right size are therefore needed to support the European sea duck populations (Box 11.8).

Fish-eating waterbirds such as cormorants and grebes are often found foraging in the phytobenthic zone. These bird species catch both pelagic and benthic fish and in some cases also benthic invertebrates. Among the auks, the feeding behaviour of black guillemot *Cepphus grylle* differs from the more offshore and pelagic feeding common guillemot *Uria aalge* (*cf.* Fig. 16.2) and razorbill *Alca torda*. In winter, the black guillemot mainly occurs at offshore banks and at coastal areas which indicate that they primarily search for fish and invertebrates in the benthic zone.

11.14 Biomass and productivity in the phytobenthic zone

11.14.1 Macrophyte and macrofauna biomass

The average biomass in the phytobenthic zone, both that of the macrophytes and of the associated fauna, is about the same in the Baltic Sea proper as in the Kattegat, ~50–300 g dry weight m^{-2} for both groups (Fig. 11.37). However, extremely high biomasses of ~2 kg dry weight of primary producers m^{-2} and ~6 kg dry weight of animals including shells m^{-2}, such as those recorded *e.g.* in the marine Gullmarsfjorden in the Skagerrak, are not found in the Baltic Sea.

In the Bothnian Sea the average biomass is less than one-third of that in the Baltic Sea proper. In the Bothnian Bay the average biomass becomes extremely low, ~100 times lower than in the Baltic Sea proper, even if these data were collected in patches sheltered from ice; thus, in practice, the average biomass is even lower. The large differences in the biomass of the primary producers between the three major basins of the Baltic Sea are also reflected in the biomass of the animals (Figs. 11.37 and 11.38).

The reasons for the drastic decrease of primary production in the phytobenthic zone from the Baltic Sea proper to the Bothnian Bay are, in the first place, a lack of nutrients, and secondly, the increasingly harsh climatic conditions towards the north with ice scouring, shading by ice and a short growing season. The Bothnian Bay could be considered ultra-oligotrophic because of its low phosphate concentrations in the water. Also, while the Bothnian Sea is oligotrophic, the Baltic Sea proper has higher nutrient concentrations and is classified as mesotrophic (*cf.* Figs. 3.24 and 3.25).

11.14.2 Microphytobenthic biomass

A diatom spring bloom does not only occur in the pelagic zone (*cf.* Sect. 8.2.4), but also in the phytobenthic zone. In the upper sublittoral zone, before *Cladophora glomerata* colonises, these diatom blooms may consist of dense 10–30 cm high colonies of tube-dwelling diatoms such as *Berkeleya rutilans* and *Navicula ramosissima* (Snoeijs and Kautsky 1989) and biomass can be as high as 570 g dry weight m^{-2} after a warm winter with little ice cover in the Bothnian Sea (Snoeijs 1990a). This is higher than the average biomass in the entire phytobenthic zone in summer (*cf.* Sect. 11.14.1).

After an average winter, the biomass of diatoms and filamentous algae (mainly *Pylaiella littoralis*) on rocks in the upper sublittoral zone (0.2–0.7 m of water depth) during the benthic spring bloom of diatoms in April-May (about three weeks after ice break) is ~100–200 g dry weight m^{-2} along the Baltic Sea gradient from the Öresund to the northern

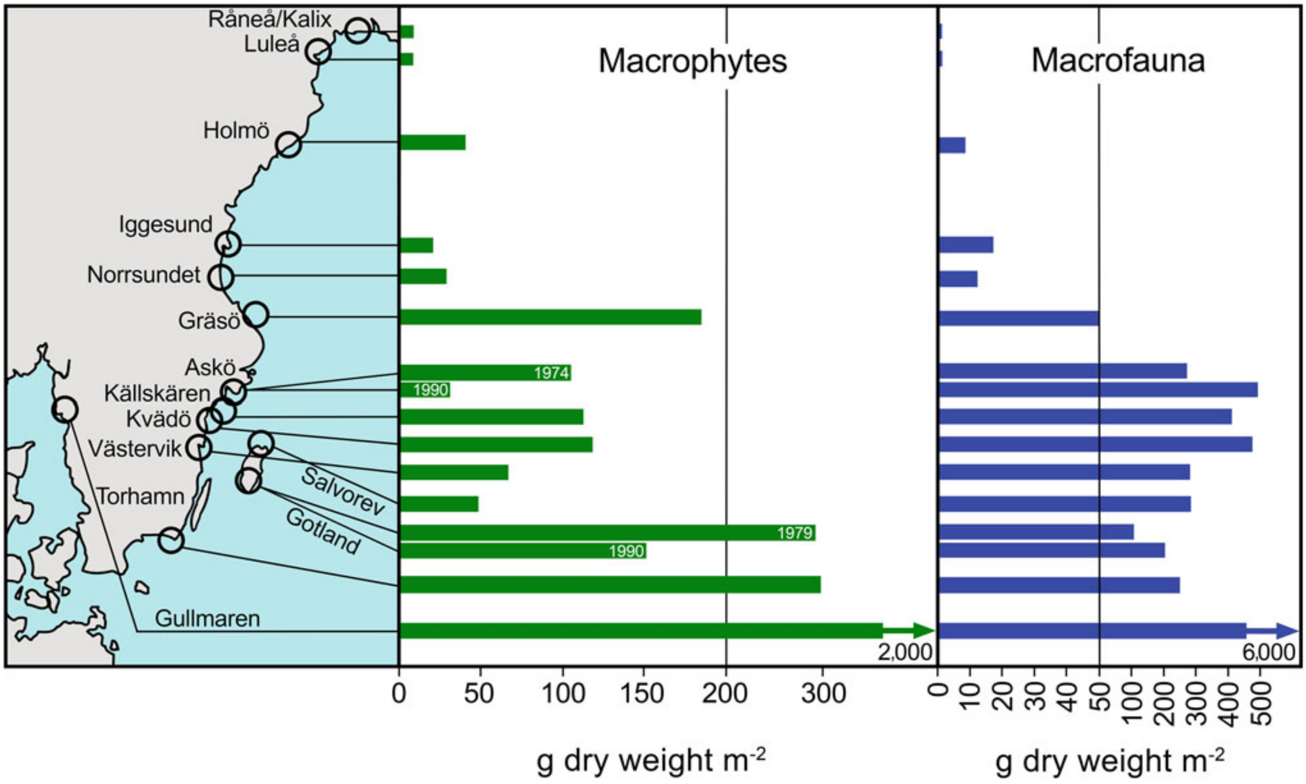


Fig. 11.37 The average total biomasses of macrophytes and associated macrofauna in the phytobenthic zone along the large-scale Baltic Sea gradient. Variation between years can be large as shown for Askö (1974 and 1990) and Gotland (1979 and 1990). In the Skagerak (Gullmarsfjorden) biomass is much higher than in the Baltic Sea for both macrophytes and macrofauna. The fauna dry weight includes shells. Note the change of scale above 200 g and 50 g of macrophytes and macrofauna, respectively. Figure modified from Kautsky (1995a)

Box 11.8: The Baltic Sea is an important wintering area for waterbirds

Kjell Larsson

Waterbirds rely on marine food all year round

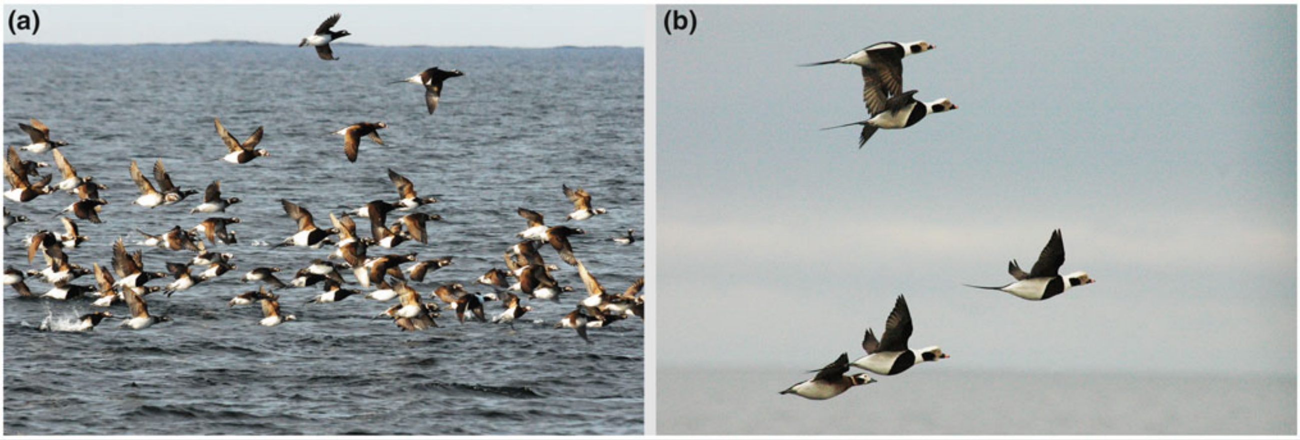
Waterbird populations are fascinating elements of the Baltic Sea ecosystem. In summer, several species of diving and dabbling ducks, gulls, terns, auks, grebes, mergansers, other waterfowl as well as waders breed along the Baltic Sea coast. However, the Baltic Sea is not just an important breeding area. Several million waterbirds are observed in the Baltic Sea in the non-breeding season when Arctic breeding species have returned from the north, and birds that mainly breed in inland freshwater lakes have moved to the coast.

Many waterbirds feed on fish or benthic fauna

About 30 waterbird species in the Baltic Sea region are completely or to a very large extent dependent on fish, mussels or other marine invertebrates as food in winter and spring. Auks, cormorants, divers, grebes, mergansers, terns and some species of gulls are specialised fish predators. Auks such as the common guillemot *Uria aalge* and the razorbill *Alca torda* and the wintering black- and red-throated divers *Gavia arctica* and *Gavia stellata* usually forage in the pelagic zone far from land. Auks may dive to 25 m depth or more, and occasionally even down to 100 m, in search for schooling fish such as sprat and herring. Great cormorants *Phalacrocorax carbo sinensis* predate on a whole range of fish species, usually in more shallow coastal waters, but can easily dive to 10 m depth. Gulls and terns, on the other hand, catch fish that swim close to the surface. Wintering diving ducks such as the tufted duck *Aythya fuligula*, the common goldeneye *Bucephala clangula* and the greater scaup *Aythya marila* and sea ducks such as the common eider *Somateria mollissima* (*cf.* Box 4.10), the common scoter *Melanitta nigra*, the velvet scoter *Melanitta fusca* and the long-tailed duck *Clangula hyemalis* (Box Fig. 11.12) feed to a very large extent on benthic fauna, especially on mussels and clams but also on crustaceans and other invertebrates.

Wintering areas

The major part of the European long-tailed duck population winter at offshore banks far from land in the central and southern Baltic Sea. In mid-winter the most important sites are the Hoburgs bank, Södra Midsjö bank, Norra Midsjö bank, Odra bank, Adlergrund and Słupsk bank (*cf.* Fig. 2.2). There the long-tailed ducks regularly dive down to 10–25 m depth to feed mainly on *Mytilus trossulus* but also to some extent on *Macoma balthica* and *Saduria entomon*. Wintering common eiders and common and velvet scoters prefer offshore *Mytilus* beds and coastal waters in the southern and southwestern parts of the Baltic Sea, for example at the Odra bank and in Danish waters. In general, the common eider and scoters prefer somewhat shallower areas than the long-tailed duck. The wintering tufted duck, common goldeneye and greater scaup feed mainly on small bivalves and invertebrates in coastal waters less than 10 m deep. In late March and April, the Baltic common eider population starts migrating northward to their main breeding areas in Sweden and Finland. In late April and the beginning of May, the long-tailed ducks and common and velvet scoters aggregate in large flocks in the Gulf of Riga and Gulf of Finland before they leave the Baltic Sea in mid-May for their northward migration to their Arctic breeding grounds (Box Fig. 11.12a).



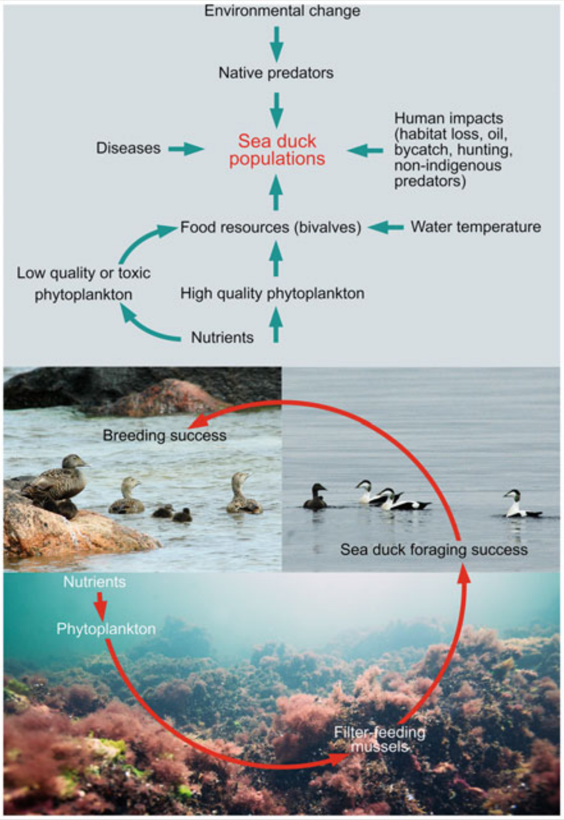
Box Fig. 11.12 The long-tailed duck *Clangula hyemalis*. (**a**) Long-tailed ducks aggregate in large flocks in April and May in the Gulf of Riga and Gulf of Finland before they leave the Baltic Sea for northward migration to their Arctic breeding grounds. (**b**) Long-tailed ducks in winter: four adult males and one female. Photo: © Kjell Larsson

A link between phytoplankton and sea ducks

Sea ducks swallow blue mussels whole, but since it is only the soft parts that is of nutritional value they must consume very large quantities of mussels each day, as well as get rid of large quantities of crushed shells, to maintain their energy balance. Mussels feed by filtering plankton from the water. Because different phytoplankton groups have different energetic and nutritious qualities, the concentrations and species composition of the phytoplankton may affect the growth and condition of the mussels and thus their quality as a food for sea ducks. Large-scale changes at the lower trophic levels in the Baltic Sea may thus affect the population dynamics of sea ducks (Box Fig. 11.13). Sea duck populations may also be affected by large-scale anthropogenic pressures such as habitat destruction, oil spills, bycatch and hunting, as well as by predation and diseases.

Trends in numbers differ between species

The trends in numbers of individuals differ greatly between different waterbird species (Durinck et al. 1994; Skov et al. 2011). Recent surveys of wintering waterbirds in the Baltic Sea indicate that populations of herbivorous waterbirds, for example populations of the mute swan *Cygnus olor*, the mallard *Anas platyrhynchos* and the Eurasian coot *Fulica atra*, are stable or increasing. The trends of fish-eating waterbirds also differ between species. Cormorants and common guillemots have increased in numbers, although the number of breeding cormorants in the Baltic Sea has levelled off in recent years. The trends of fish-eating grebes and divers are more uncertain. A number of surveys have shown that sea duck populations with offshore distribution in winter, especially populations of the long-tailed duck, the common eider and the velvet scoter, have decreased by 50 % or more since the beginning of the 1990s. The rapid declines can most likely be explained by a combination factors including: (1) ecosystem changes affecting the quality and quantity of food resources in the Baltic Sea during the non-breeding season, (2) changing predation pressures in the Baltic region in summer due to the return of the white-tailed eagle *Haliaeetus albicilla* and climate changes affecting the lemming-waterbird-predator relationships in the Arctic, (3) elevated mortality rates because of recurrent oil spills at important wintering sites, and (4) elevated mortality rates because of by-catches of birds in fishing nets and by hunting (Larsson and Tydén 2005; Skov et al. 2011; Bellebaum et al. 2013; Kilpi et al. 2015).



Box Fig. 11.13 Schematic view of how changes at lower trophic levels in the Baltic Sea may affect the population dynamics of sea ducks. Photo: birds © Kjell Larsson, seafloor © Hans Kautsky

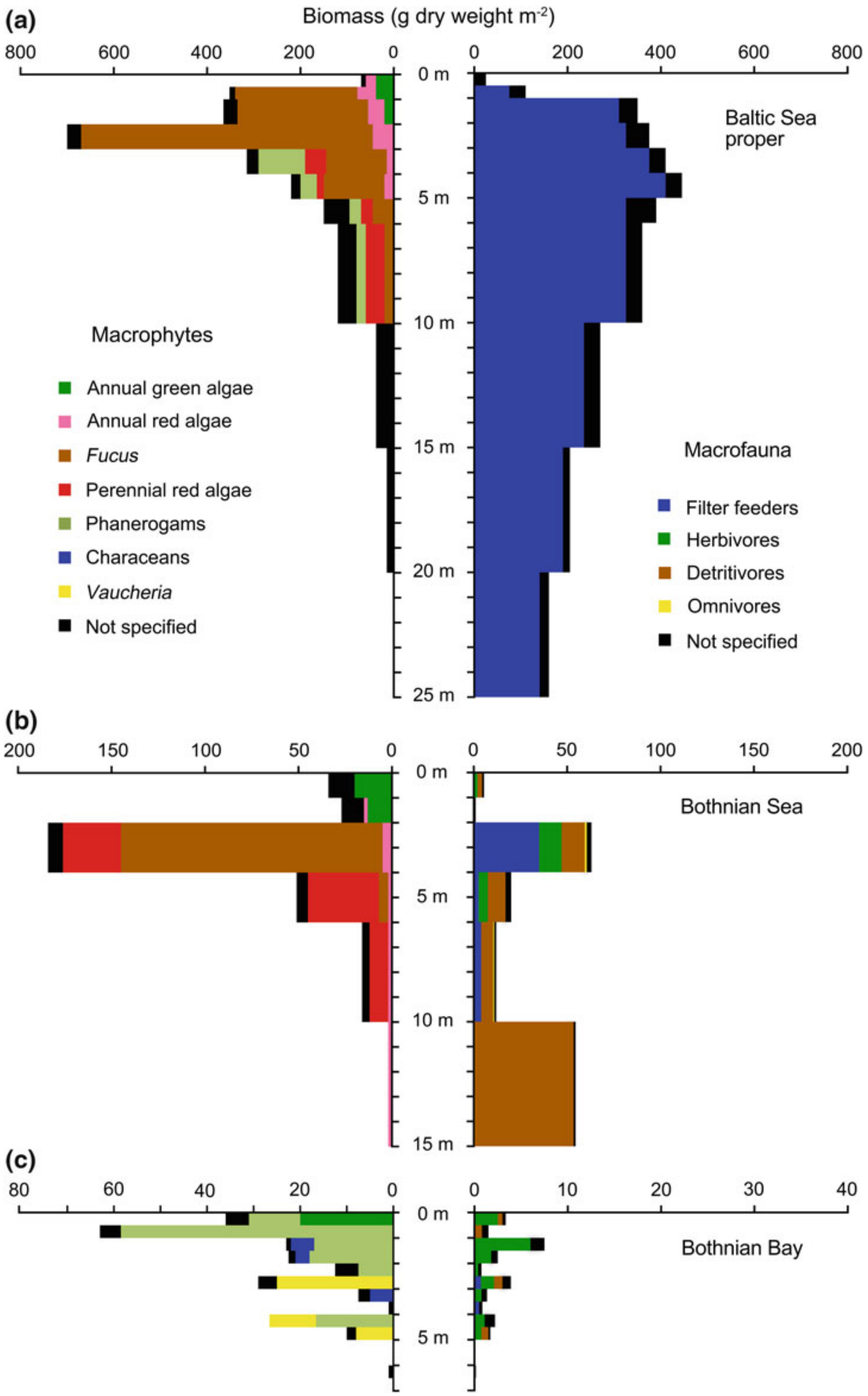


Fig. 11.38 Comparison of the biomass of macrophytes and associated macrofauna in the phytobenthic zone in different parts of the Baltic Sea. (**a**) The Baltic Sea proper at Askö. (**b**) The southern Bothnian Sea at Gräsö. (**c**) The Bothnian Bay at Luleå. The category "Not specified" macrophytes contains mainly filamentous brown algae, both annuals (*e.g. Pylaiella littoralis*) and the perennial *Battersia arctica*. In (**a**) all filter feeders are *Mytilus trossulus*, and all other animals are in the category "Not specified" fauna. In (**c**) the vascular plants are mainly *Isoetes lacustris* at a water depth of 1.0–1.5 m and *Potamogeton perfoliatus* in deeper water, while the herbivores consist mainly of the freshwater snails *Gyraulus acronicus*, *Radix labiata*, *Theodoxus fluviatilis* and *Valvata piscinalis*, the filter feeder is the freshwater clam *Pisidium* sp. and the detritivores are oligochaetes and *Saduria entomon*. Figure modified from Kautsky (1995a)

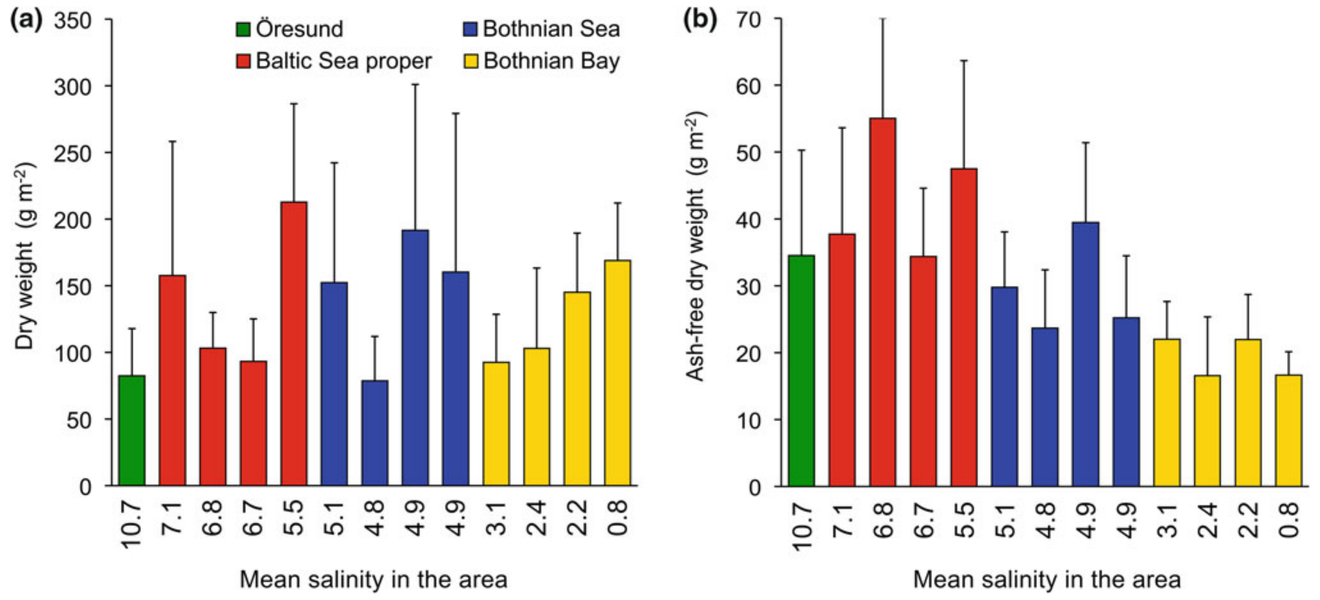


Fig. 11.39 Average biomass of macro- and microphytobenthos in 13 areas along the large-scale Baltic Sea gradient in the upper sublittoral zone at a water depth of 0.2–0.7 m during the benthic spring bloom of diatoms in April-May 1990 and 1991. Within each area, the sampling sites were located along a gradient from the inner to the outer archipelago. Altogether, 135 sampling stations are included. All macroalgae in the samples were filamentous algae, mainly *Pylaiella littoralis*. (**a**) Dry weight of macro- and microphytobenthos. (**b**) Ash-free dry weight of the same samples (without diatom silica frustules and other inorganic materials). Figure modified from Ulanova et al. (2009)

Bothnian Bay (Fig. 11.39). Ash-free dry weight, on the other hand, shows a decreasing trend towards the north, with ~45 g m^{-2} in the Baltic Sea proper, ~30 g m^{-2} in the Bothnian Sea, and ~20 g m^{-2} in the Bothnian Bay (Fig. 11.39). This suggests that, at least in spring, there is an increase in the relative proportion of diatoms towards the north because the silica frustules (as well as other inorganic materials) are not included in the ash-free dry weight.

11.14.3 Biomass and substrate availability

Differences in biomass and composition along the large-scale Baltic Sea gradient are explained not only by salinity and nutrient concentrations but also by substrate availability. For example, a steep coast dominated by hard substrate is inhabited by macroalgae and supports a higher biomass than a gently sloping coast with a rooted vegetation on sand and gravel. Hard substrates are rarer towards the north because of the geological conditions and the flat topography.

The coasts of the Bothnian Bay are characterised by scattered boulders, stones and gravel, intermingled with sand and soft substrates. In the more wave-exposed areas, vast sandflats with no vegetation prevail. Wherever hard substrate occurs in the Bothnian Bay, it is usually covered with a low biomass of filamentous algae and diatoms since no larger marine algae can live in the low salinity. However, in places sheltered from ice scouring, extensive growth of annual freshwater vascular plants and charophytes may occur, and biomass can be as high as in similar habitats in the Bothnian Sea.

11.14.4 Productivity in the phytobenthic zone

Over the year, the primary productivity (biomass production per unit time) in the coastal zone of the Baltic Sea proper is about three times higher in the water column than in the phytobenthic communities (Fig. 11.40a). However, in the Bothnian Sea the primary productivity in the phytobenthic communities is higher than that in the water column in summer, and the yearly primary production is similar in the pelagic and the phytobenthic zone in coastal waters (Fig. 11.40b). Both macrophyte and animal respiration in the phytobenthic zone of the Bothnian Sea are much lower than in the Baltic Sea proper, which is explained by the absence of high *Mytilus trossulus* biomass. In the Baltic Sea proper, *Mytilus trossulus* contributes with 80–90 % of the total animal respiration, but in the Bothnian Sea this is <1 %.

11.14.5 Energy flows in the phytobenthic zone

A holistic approach to understanding the ecosystem functioning is to model the energy flow between different

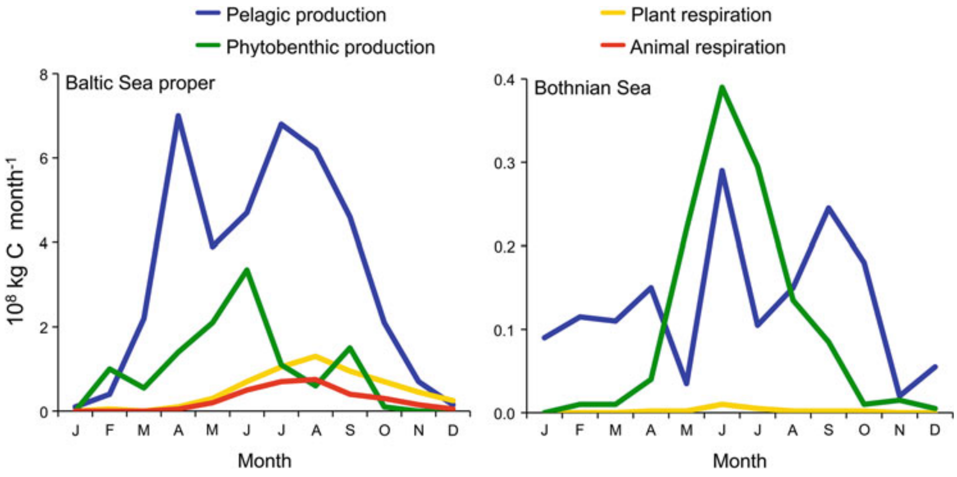


Fig. 11.40 Comparison of the net primary productivity by the macro- and microphytobenthos at a water depth of 0–30 m calculated for the coastal zones of the whole Baltic Sea proper and the whole Bothnian Sea. In the Bothnian Sea animal respiration is negligible. Note the different scales on the y-axes (twenty times lower in the Bothnian Sea). Figure based on data in Kautsky (1995b)

ecosystem compartments (Jansson 1978; Kautsky and Kautsky 1995). Such models can help us to determine whether a studied mechanism (*e.g.* the possibility for *Idotea* spp. to graze down the *Fucus* vegetation) is realistic or not. Simple energy-flow measurements based on biomass and food demand and the food preference of single species can depict mismatches, missing parts and efficiency of the ecosystem. By answering questions such as “can the measured primary production support all the organisms found?” and “are there alternative energy sources?” different aspects of ecosystem functioning can be disclosed and also make it possible to predict changes when conditions are altered, *e.g.* through eutrophication, climate change or overfishing.

The pelagic and phytobenthic energy flows differ between the Bothnian Bay, Bothnian Sea and Baltic Sea proper (Fig. 11.41). The standing stock of benthic and pelagic primary producers is about four times higher in the Bothnian Sea than in the Bothnian Bay. In the Baltic Sea proper, the pelagic standing stock is again about four times higher than in the Bothnian Sea, but the pelagic primary production has increased more than ten-fold (from ~2,240 to ~39,300 10^5 kg C year^{-1}). The phytobenthic biomass and primary production in the Baltic Sea proper are about ten times and almost eight times those in the Bothnian Sea, respectively.

Of the total annual benthic and pelagic primary production in the coastal zone of the Baltic Sea (with the border to open water set at the 25 m depth isoline), the phytobenthos production is estimated to contribute 12 % to the total coastal production in the Baltic Sea proper, 23 % in the Bothnian Sea and 50 % in the Bothnian Bay (Kautsky and Kautsky 1995). According to these estimates, the phytobenthic zone accounts for a significant part of the total primary production and carbon turnover in the coastal areas of the Baltic Sea. Also, benthic-pelagic coupling seems to be strong.

11.15 Anthropogenic impacts

11.15.1 Sensitivity to disturbances

Since attached organisms cannot escape when environmental conditions become detrimental (unless they die), they reflect what actually happens at a specific site and are therefore excellent indicators of environmental change. The long water residence time of the Baltic Sea, with ~85 million people living in its drainage area, makes the Baltic Sea one of the most polluted and eutrophicated seas in the world. Much is done to reduce the anthropogenic impacts (*cf.* Sects. 17.8 and 18.5), and deterioration as well as recovery of the environment in the Baltic Sea are closely monitored.

In general, the low-salinity phytobenthic communities in the Baltic Sea are more sensitive to disturbance than their marine counterparts since many species are already stressed by low salinity. In addition, many macrophytes lose the ability to reproduce sexually when they approach their salinity limit, and for this reason re-establishment after a disturbance may be more difficult than under fully marine conditions. When one of the habitat-forming key species, *e.g. Fucus vesiculosus*, *Zostera marina* or *Mytilus trossulus*, disappears from an area, this has a major negative effect on the pelagic system as well. For example, the phytobenthic communities act as herring spawning habitats (*cf.* Fig. 4.28) and the *Mytilus* beds recirculate nutrients.

A macrophyte vegetation also reduces water movement, both within and adjacent to the vegetation itself, resulting in increased sedimentation and reduced turbidity in the water. Reduced turbidity increases light availability for macrophytes, increasing their growth. Additionally, macrophytes affect the distribution, composition and grain size of sediments and reduce erosion. Therefore, phytobenthic

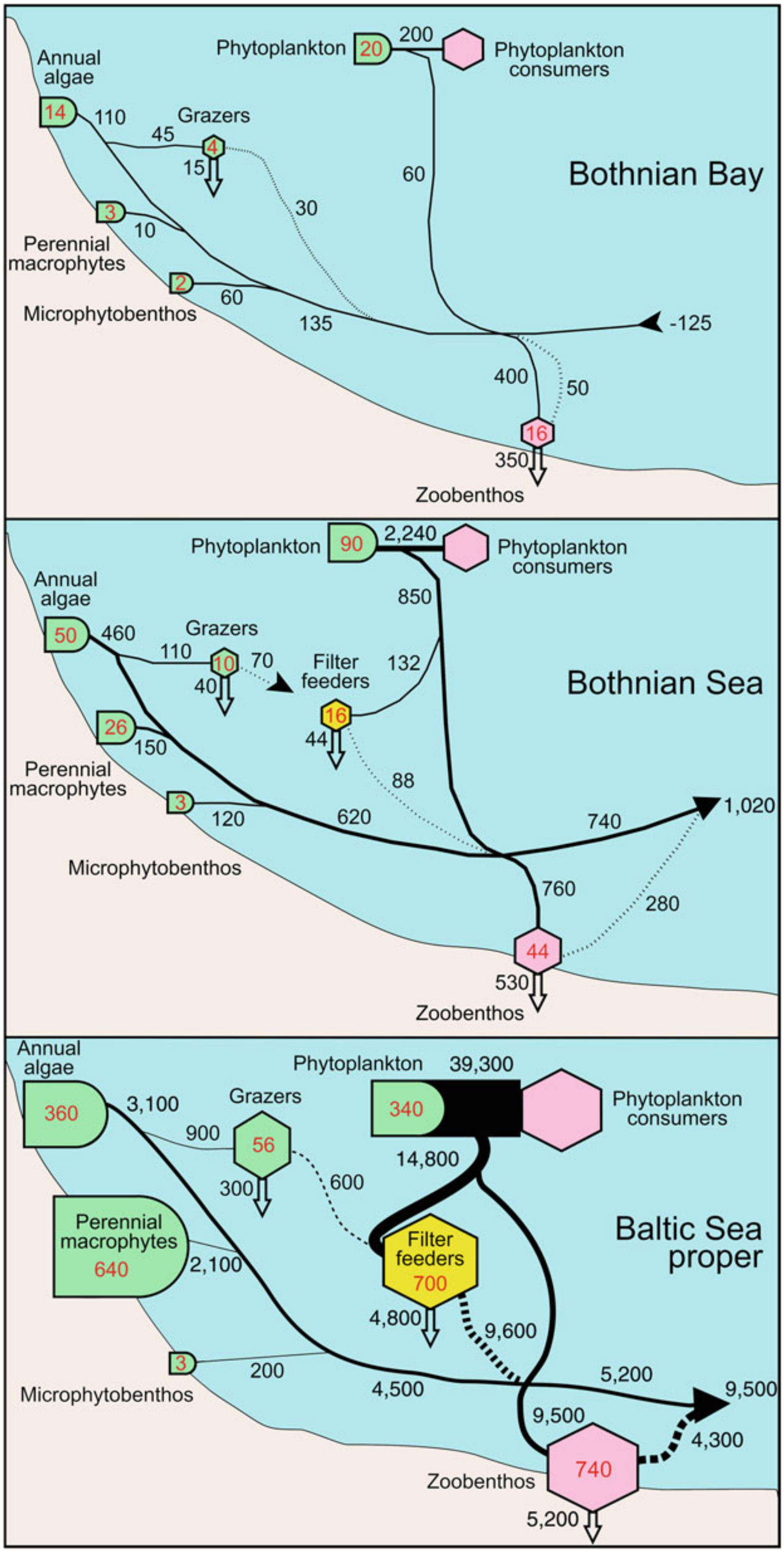


Fig. 11.41 Standing stocks and flows of carbon through the Baltic Sea coastal ecosystem in the three largest subbasins, the Bothnian Bay, the Bothnian Sea and the Baltic Sea proper. Bullet-shaped symbols are primary producers and hexagons are consumers. Phytoplankton consumers include both zooplankton and the microbial loop. The zoobenthos consists mainly of detritivores. Numbers in red show standing stocks in 10^5 kg C, and numbers in black show flows of carbon in 10^5 kg C year^{-1}. Solid lines show primary produced matter and dotted lines show secondary production and faeces. Open arrows pointing down from storages (the boxes) indicate respiration. Filled black arrows indicate export to the open waters and deeper benthos or, as in Bothnian Bay, the need of import of energy input from the open water and deeper benthos. Figure modified from Kautsky and Kautsky (1995)

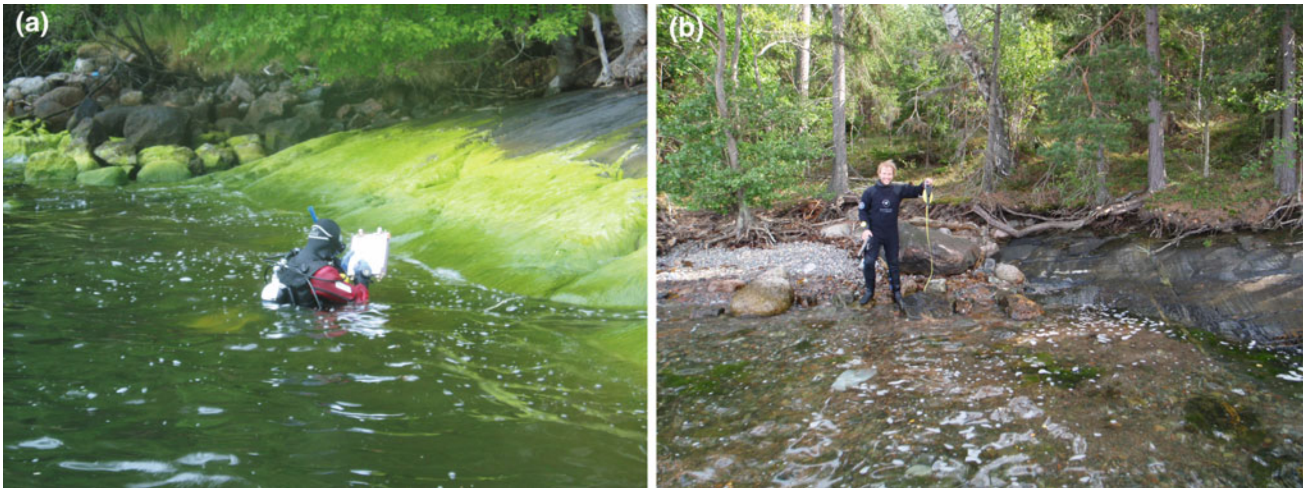


Fig. 11.42 Impacts of ferry traffic on coastal habitats in the Baltic Sea. (**a**) *Cladophora glomerata* grows higher up on the bedrock than normal because of the regular occurrence of large waves. (**b**) smaller-grained substrates are swept away by the large waves, causing severe erosion. Photo: (**a**) © Michael Borgiel, (**b**) © Hans Kautsky

communities provide important ecosystem services, including the improvement of water quality and the stabilisation of sediments. The major threats to the phytobenthic zone of the Baltic Sea are habitat destruction, eutrophication and hazardous substances.

11.15.2 Impacts of habitat destruction

Direct physical damage to the littoral zone impoverishes the phytobenthic communities through fractionation of populations and destruction of recruitment areas for algae, plants and animals. Such damage results from *e.g.* dredging, locating marinas in sheltered bays, increasing harbour facilities by land reclamation, destruction of salt marshes, building offshore constructions such as windmill farms and installing pipelines. Stone-fishing (harvesting stones from the seafloor) decreases the available hard substrate for the settlement of algae. Sand extraction reduces the amount of the substrate, but also induces instability of the seafloor which may cause coastal landslides. Sand extraction and pipelines may create holes in the seafloor, that fill with decaying organic material followed by bacterial decomposition and hypoxia.

Waves induced by ship traffic not only cause coastal erosion (Fig. 11.42b), but also change the structure and composition of phytobenthic communities. Especially the high-speed ferries that create “artificial tides” of up to 1.8 m when they displace a water volume of the size of a small lake, affect the vegetation along their routes in the archipelagos of the Baltic Sea (Östman and Rönnberg 1991; Kurennoy et al. 2009). The regular strong water circulation induced by the ship traffic may have a local positive effect on perennial macroalgae by keeping the seafloor free from sediments and drift algae (Roos et al. 2003; Eriksson et al. 2004). Algal diversity is not affected, but *Cladophora glomerata* grows higher up on the bedrock than normal because of the regular occurrence of large waves (Fig. 11.42a). However, at sheltered sites and in inlets along ferry routes, perennial algae decline as a result of increased turbidity and sedimentation, which seems to favour *e.g. Myriophyllum spicatum* and *Ceratophyllum demersum* (species typical of turbid, nutrient-rich muddy habitats) and to disfavour exposure-sensitive mud-thriving species such as *Chara tomentosa* and *Najas marina* (Roos et al. 2003; Eriksson et al. 2004).

11.15.3 Impacts of eutrophication

In the phytobenthic zone, eutrophication is often manifested as an increased growth of filamentous algae, which may occur as mats covering the perennial vegetation or as free-floating algal mats at the water surface (Fig. 11.43a, b). The decomposition of these algae may cause hypoxia at the seafloor (Fig. 11.43c). Increased abundances of opportunistic algal species, especially along the eastern coast of the Baltic Sea proper, as well as the occurrence of algal mats consisting of filamentous algae such as *Cladophora glomerata*, *Pylaiella littoralis* and *Ectocarpus siliculosus* in the outer Archipelago Sea (Finland), may be caused by eutrophication (Vahteri et al. 2000; Korpinen et al. 2007). Eutrophication is also manifested as increased growth of phytoplankton; as a result, less light can penetrate through the water column to the phytobenthic communities (Sandén and Håkansson 1996).

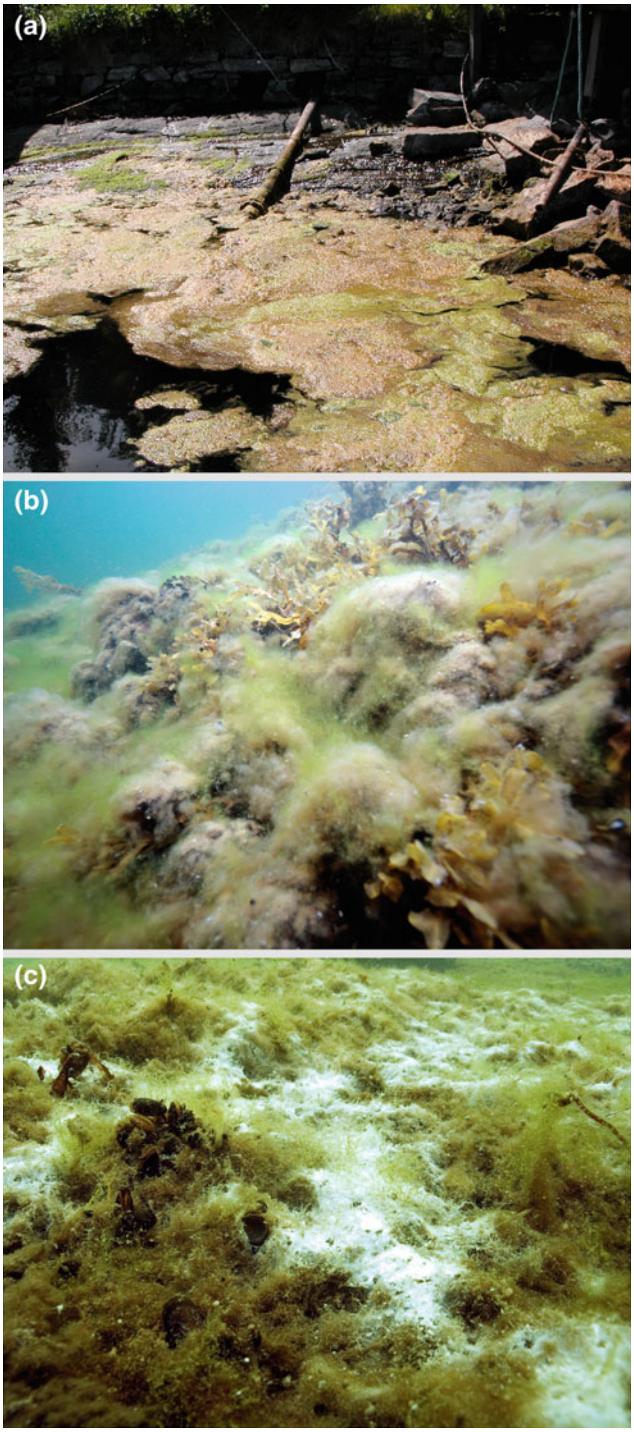


Fig. 11.43 Signs of eutrophication. (**a**) A floating algal mat at a sheltered site influenced by excess nutrients. (**b**) Overgrowth of perennial algae by filamentous algae. (**c**) White sulphur bacteria (*Beggiatoa*) at the seafloor indicate hypoxia. Photo: (**a**) © Pauline Snoeijs-Leijonmalm, (**b**, **c**) © Hans Kautsky

The significance of eutrophication and substrate type for the distribution of phytobenthic communities is clearly observed in an example from the Gulf of Riga (Fig. 11.44). The station just north of the city of Riga and the two stations closest to the city of Pärnu were strongly influenced by city effluents, and biomass was low due to the absence of perennial algae, notably *Fucus vesiculosus* and *Furcellaria lumbricalis*. The biomass was also very low at two unpolluted stations, but here the reason was the lack of hard substrate. The station just north of Riga, where the Daugava river enters the Gulf of Riga, was totally dominated by *Cladophora glomerata* and omnivores (*Gammarus* spp.). The relative amount of green algae represented in the samples decreased with increasing distance from the cities and may be an indicator of eutrophication.

The western and eastern coasts of the Gulf of Riga furthest away from the cities, as well as the northern coast of the island of Saaremaa, support luxuriant phytobenthic communities of composition and biomass comparable to those found elsewhere in less eutrophied areas of the Baltic Sea proper. In comparison to the macrophyte biomass, the animal biomass was much lower and more evenly distributed in the Gulf of Riga with the filter feeders *Amphibalanus improvisus* (Fig. 11.18b, c) and *Mytilus trossulus* (Fig. 11.32). Moreover, at salinity <4 in the reach of the Daugava river, the non-indigenous freshwater species *Dreissena polymorpha* (*cf.* Box 5.4) and the detritivore *Macoma balthica* (*cf.* Box 13.5) were dominant.

11.15.4 Impacts of hazardous substances

Contrary to the nutrients nitrogen and phosphorus, which cause eutrophication, hazardous substances are detrimental or directly toxic to organisms. The same hazardous substance can be more toxic to one group of species than to another. For example, chlorine, which previously was used for bleaching in pulp mills, affects mainly brown algae. Thus, hazardous substances can change the competitive balance within a phytobenthic community and alter its species composition and structure.

Especially in the 1960s–1980s, pulp mills along the coasts of the northern Baltic Sea were severe and complex pollution sources causing increased turbidity (decreased light penetration), increased levels of hazardous substances and eutrophication in the coastal environment. In the direct vicinity of pulp mill effluents, the biomass and species richness of the phytobenthic communities were low, with green filamentous algae and filter-feeding animals dominating (Fig. 11.45). With improving conditions further away from the effluents, species richness increased and reached a maximum at an intermediate distance from the pollution source. Here the species were relatively evenly distributed among the functional groups. In the least polluted areas farther away from the pollution source, species richness and evenness among functional groups was lower than in the intermediate area. This pattern is well in

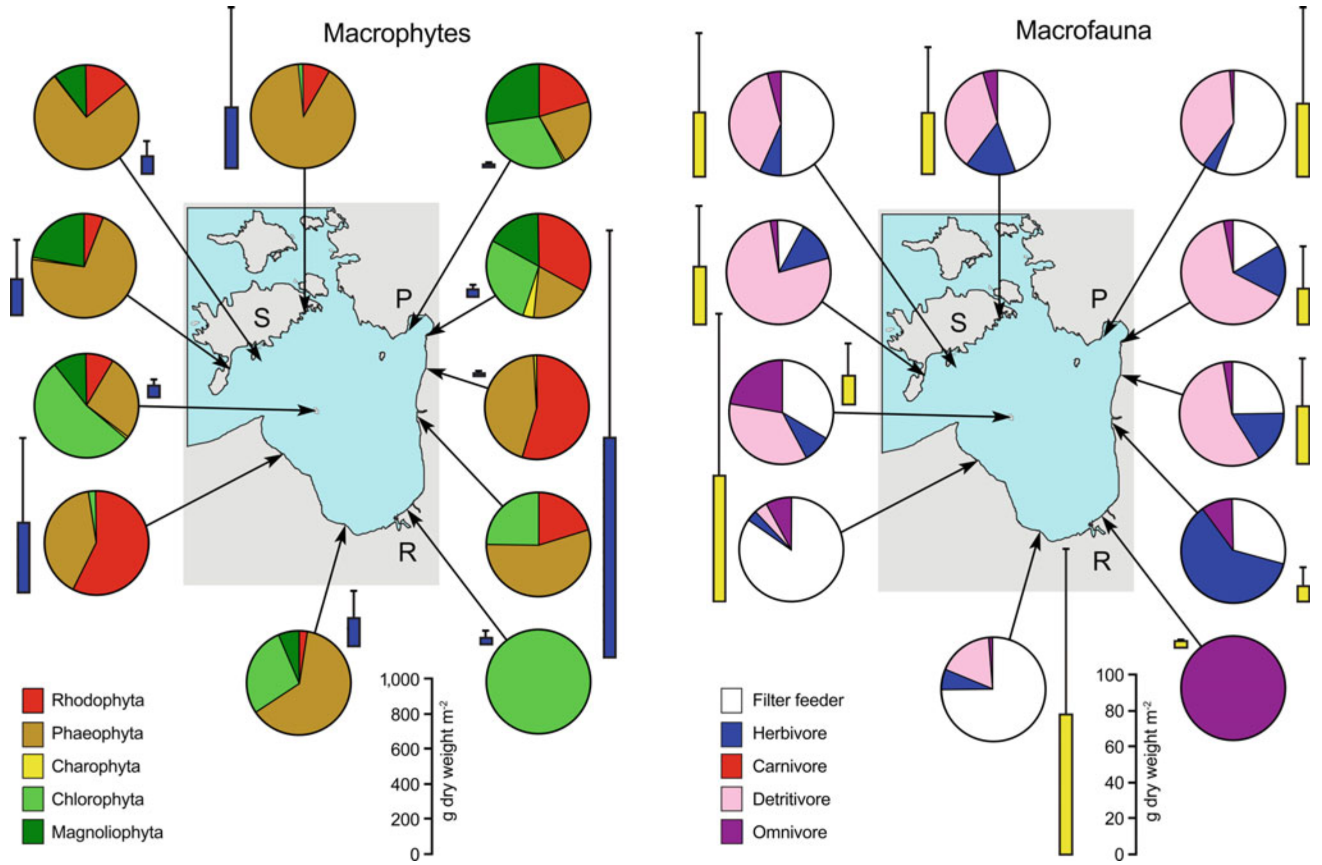


Fig. 11.44 The composition of macrophytes and associated macrofauna in the phytobenthic zone of 11 diving transects in the Gulf of Riga in 1995–1996. (**a**) Macrophytes subdivided into taxonomic groups, in % of the average biomass in each transect. (**b**) Animals subdivided into feeding groups, in % of the average biomass in each transect. The vertical bars show the average biomass in each transect. P = the city of Pärnu (Estonia), R = the city of Riga (Latvia), where the Daugava river enters the Gulf of Riga, S = the island of Saaremaa. Figure modified from Kautsky et al. (1999)

accordance with the "intermediate disturbance hypothesis" (*cf.* Box 4.16).

11.15.5 Climate change in the Baltic Sea Area

Regional climate scenarios for the brackish Baltic Sea Area predict, besides an increase in the sea surface temperature, a decrease in salinity with a changed water budget (*cf.* Fig. 2.12), including increased terrestrial runoff due to precipitation (HELCOM 2013b). Signs of the on-going climate change have already been observed in the temperature record. Historical data on the maximum summer surface-water temperature in the Baltic Sea show an increase of ~1.3 °C between 1861–1900 and 1985–2005 (Mackenzie and Schiedek 2007).

The changing environment created by climate change will alter the composition of the phytobenthic communities in the Baltic Sea Area. Critical questions to be answered are how communities will reorganise at a higher temperature and lower salinity and what the consequences of these community changes will be for ecosystem functioning. It is not possible to project recorded changes along the large-scale Baltic Sea gradient directly on climate scenarios because along this gradient the temperature and salinity decrease in concert while with climate change the temperature will increase but the salinity is expected to decrease.

11.15.6 Experiences from artificially raised water temperature

Studies in cooling-water discharges from nuclear power plants into the Baltic Sea, *i.e.* artificially heated natural environments, have identified the following changes that occur in the phytobenthic communities at higher water temperature and the absence of a winter ice cover: extension of the growing season, increased primary production, species shifts towards a higher proportion of opportunistic species, and increased temporal β-diversity (species turnover) (Snoeijs and Prentice 1989; Snoeijs 1989; Ilus 2009; Hillebrand et al. 2010).

Reduction in body size has been proposed as a universal response of organisms to both warming and decreased salinity. For example, the average cell volume was found to decrease linearly with ~2.2 % per °C in species-rich diatom communities and with ~2.5 % per °C within protistan species (Atkinson et al. 2003; Svensson et al. 2014). These observations confirm the "temperature-size rule" (Atkinson 1994; Foster et al. 2013).

While such linear relationships may be found in large pooled data sets, the conditions in the field (including factors other than temperature) are higly variable on a temporal scale. For diatoms in the phytobenthic zone of the Baltic Sea it was suggested that climate change in this century may polarise seasonality by creating two new ecological niches, one with elevated temperature at high nutrient concentrations in the cold season (increasing cell size) and the other one with elevated temperature at low nutrient concentrations in the warm season (decreasing cell size) (Svensson et al. 2014). Thus, higher temperature in summer and lower salinity by a changed water budget in the Baltic Sea are expected to decrease the average cell size of the microphytobenthos, which is likely to affect the transfer of energy to higher trophic levels.

11.15.7 Impacts of climate change

Species shifts in phytobenthic communities at elevated temperature include *e.g.* increases in the green filamentous algae *Cladophora glomerata* and *Ulva intestinalis* and decreases in perennial algae, *e.g. Fucus radicans* and *Fucus vesiculosus* disappear (Snoeijs and Prentice 1989). Parallel changes occur in the fauna, *e.g.* snails that can reproduce all year round (*Potamopyrgus antipodarum* and *Theodoxus fluviatilis*) increase in abundance at the expense of snails that hatch only during early summer (*Bithynia tentaculata* and *Radix labiata*) (Snoeijs 1989). Noteworthy is also the increase in non-indigenous species in cooling-water discharge areas, which may cause changes in food web interactions (*cf.* Box 5.9).

The projected decrease in salinity in the Baltic Sea as a result of climate change will clearly affect the key species *Fucus vesiculosus*, *Fucus radicans* and *Mytilus trossulus* at their northern limit of distribution, which may move 400 km to the south, from the Norra Kvarken area to the Södra Kvarken area (Strandmark et al. 2015). In this case, marine algae will be replaced by freshwater species in the Bothnian Sea, the large algal belts will disappear, and consequently the diversity of associated invertebrates will decrease.

Similarly affected will be the marine vascular plant *Zostera marina*, which has its northern salinity limit in the Stockholm archipelago and the southwestern coast of Finland (Boström et al. 2002). If salinity decreases it will probably be found only on the southern coasts of the Baltic Sea, which would have fundamental consequences for many associated species, including the coastal fish species that use seagrass meadows as hatching and nursery habitats. Altogether, climate change may reverse the recent improvements in the phytobenthic zone that have been achieved through the eutrophication decrease (oligotrophication) (Fig. 11.35).

11.15.8 Impacts of acidification

The global increase in the partial pressure of atmospheric CO_2 decreases the pH of marine surface waters worldwide, a process known as "ocean acidification". The pH decreases because CO_2 reacts with water to form hydrogen carbonate (bicarbonate) and hydrogen ions (*cf.* Sect. 1.3.6). The pH shift changes the equilibrium between hydrogen carbonate and carbonate, thereby depleting the available carbonate pool, which increases the solubility of $CaCO_3$ (*cf.* Sect. 1.3.7).

The ocean surface-water pH is expected to have dropped by an average 0.5 pH units at the end of the present century (Caldeira and Wickett 2003; Raven et al. 2005). For the Baltic Sea it has been estimated that this process will result in a reduction by 0.2–0.4 pH units by the year 2100 (Havenhand 2012). Coastal pH is more variable and difficult to predict than that of the open sea through complicated local effects of *e.g.* runoff (Andersson et al. 2005). The pH also varies on diurnal and seasonal scales, depending on photosynthetic carbon uptake, especially in shallow sheltered bays (Saderne et al. 2013).

Acidification changes the rates of some important biological processes, *e.g.* it stimulates photosynthetic carbon uptake and counteracts calcification. Artificially elevated CO_2 concentrations in Baltic Sea water were shown to increase the photosynthetic carbon uptake of *Chara aspera*, *Chara horrida* and *Chara tomentosa* (Pajusalu et al. 2015), as well as that of *Furcellaria lumbricalis* and *Ulva intestinalis*, but not of *Fucus vesiculosus* (Pajusalu et al. 2013). This suggests that the natural content of CO_2 in the water of the Baltic Sea may limit the primary production of macrophytes today.

The observed positive effect of acidification on photosynthetic activity seems to be stronger in species with fast growth rates, such as *Ulva intestinalis*, than in species with low growth rates, such as *Fucus vesiculosus* (Fig. 11.46), which would lead to the conclusion that the predicted acidification in the Baltic Sea may cause shifts in the species composition of macrophyte communities towards a larger proportion of opportunistic filamentous algae. However, the majority of algae possess carbon-concentrating mechanisms which enable them to take up hydrogen carbonate as well as CO_2 (Raven et al. 2012), and it is uncertain how an 0.2–0.4 pH unit reduction, in combination with changes in other environmental drivers, would affect a macrophyte vegetation in the field.

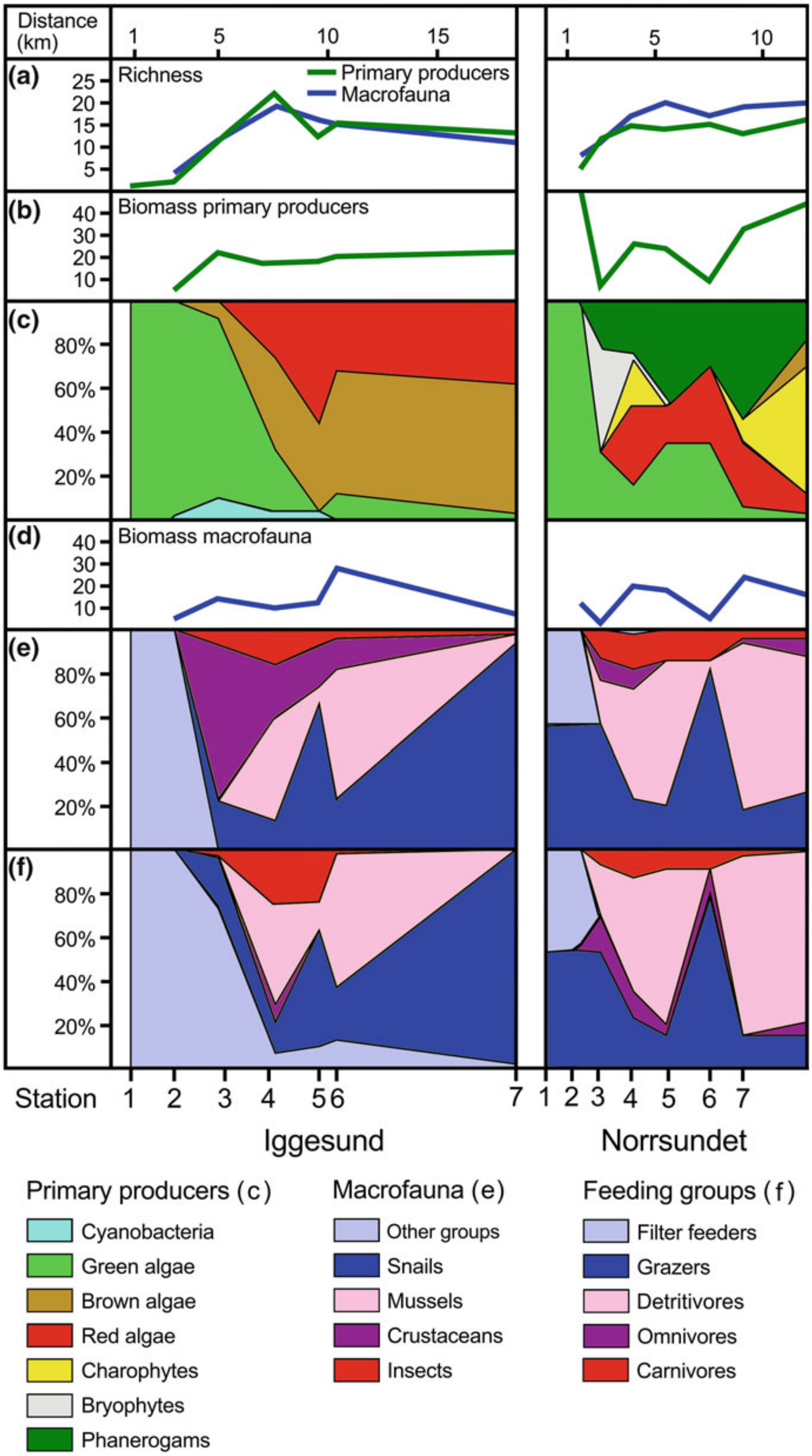


Fig. 11.45 Distribution of primary producers (macrophytes and cyanobacteria) and associated macrofauna in the phytobenthic zone along pollution gradients outside two pulp mills in the Bothnian Sea (Iggesund and Norrsundet) in the 1980s. (**a**) Species richness of primary producers and macrofauna. (**b**) mean biomass of primary producers. (**c**) % of total biomass of macrophytes + cyanobacteria. (**d**) = mean biomass of the macrofauna. (**e**) % of total biomass of the macrofauna. (**f**) % of total biomass of macrofaunal feeding groups. Numbers 1–7 indicate the sampling stations at each pulp mill, and the distance denotes the distance between the pulp mill outlet and the sampling station. Figure modified from Kautsky (1992)

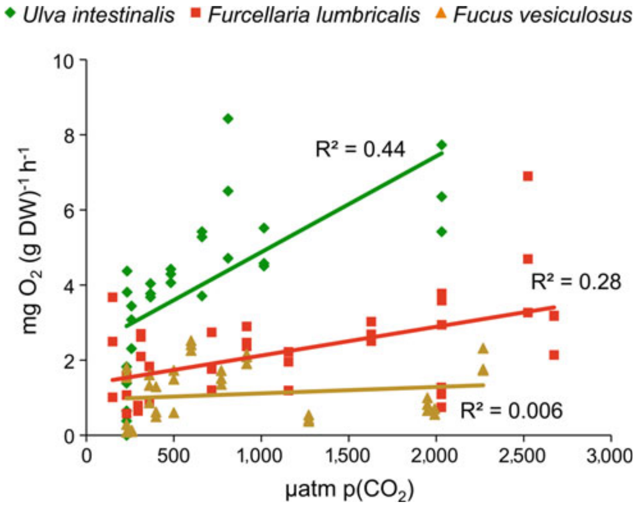


Fig. 11.46 Net primary production rates (expressed as oxygen evolution) of the three macroalgal species *Ulva intestinalis*, *Fucus vesiculosus*, and *Furcellaria lumbricalis* at different CO_2 concentrations in short-term incubation experiments. Figure modified from Pajusalu et al. (2013)

11.16 Long-term trends

11.16.1 Long-term trends in the *Fucus* belt

The external nutrient inputs into the Baltic Sea as a whole have dramatically increased since ~1950, having peaked in the 1980s and significantly decreased after that (*cf.* Box 2.2). These changes in nutrient inputs caused changes in the *Fucus vesiculosus* vegetation. The classical work in the Södra Kvarken area by Mats Wærn in the 1940s provides a baseline for the depth distribution of *Fucus vesiculosus* in unpolluted water (Wærn 1952). In 1943/44, the maximum development of the *Fucus* belt was found at a 5–6 m water depth and the lower depth limit of *Fucus vesiculosus* was 11.5 m. In 1984, the maximum development occurred at a 3–4 m water depth, and the lower depth limit was 8.5 m, in the same diving transects (Kautsky et al. 1986).

Both in 1943/44 and 1984 the decrease in *Fucus vesiculosus* coverage with water depth towards its lower depth limit could be approximately fitted to an exponentially decreasing light attenuation curve. These results indicate that the decreased water transparency in 1984 was due to a 40–50 % increases in summer chlorophyll *a* and nutrient concentrations in the offshore surface water of the Baltic Sea since the 1940s. Since the 1980s, *Fucus vesiculosus* has been expanding its depth distribution towards greater water depth, and in 2006 at almost all stations revisited the bladderwrack went as deep down as in the 1940s (Fig. 11.47), which suggests that the light conditions in the water column have improved. Also, in the Askö area of the Baltic Sea proper, the lower depth limit of *Fucus vesiculosus* has increased, from ~6 m in the 1970s to ~9 m in the 2010s, in the same diving transects.

11.16.2 Long-term trends in *Zostera* meadows

In a longer time perspective, the areas covered by the common eelgrass *Zostera marina* have decreased in the Skagerrak, Kattegat, Belt Seas and Baltic Sea proper (Boström et al. 2014). In the early 1930s, a fungal infection, the "wasting disease", caused by the slime mold *Labyrinthula zosterae*, eradicated a large proportion of the populations in the Kattegat, Belt Sea and the southern Baltic Sea, similarly to many other areas in the northern hemisphere (Rasmussen 1977). This event highlighted the importance of *Zostera marina* in protecting seashores from erosion and as a habitat for fish recruitment (Pihl et al. 2006).

Only in the 1950s and 1960s did the *Zostera marina* populations in the Baltic Sea Area start to recover after the fungal infection; however, since the 1980s declines in eelgrass depth limits and areal cover have been documented again, particularly in regions experiencing high anthropogenic pressure. Although the distribution may vary inter-annually by ~5 %, a large-scale long-term decline has been confirmed (Baden et al. 2003; Nyqvist et al. 2009). For example, the areal extent of eelgrass along the Swedish Skagerrak coast has declined by 60 % since the mid-1980s. In well-investigated areas such as the Puck Bay (Poland), the disappearance of *Zostera marina* was clearly related to

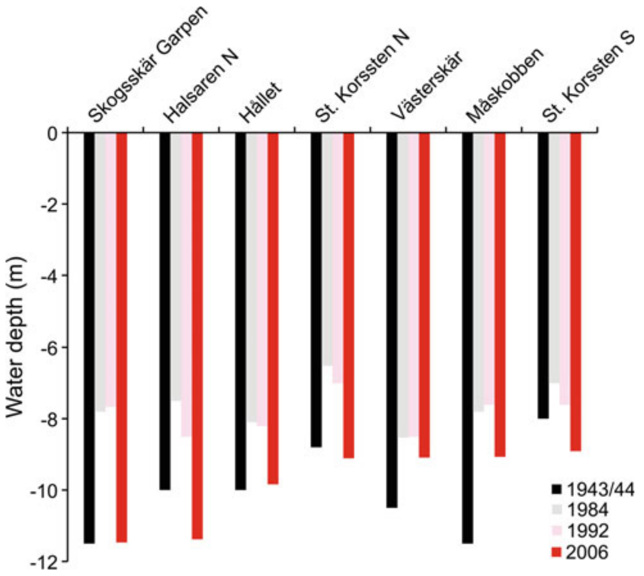


Fig. 11.47 The lower depth limit of *Fucus vesiculosus* at seven diving transects in the Södra Kvarken area. All transects were visited four times. Figure based on data for 1943/44 in Wærn (1952), for 1984 in Kautsky et al. (1986) and and additional unpublished data for 1992 and 2006 from the Swedish monitoring programme for phytobenthos

heavy eutrophication of the bay. Since the 1990s conditions have been improving, but the *Zostera marina* vegetation of the Puck Bay recovers slowly.

The failure of eelgrass to re-establish itself in affected areas, despite nutrient reductions and improved water quality, signals complex recovery trajectories and calls for large conservation efforts to protect the existing meadows (Boström et al. 2014). Even if the aboveground biomass in a *Zostera* meadow may be low in certain years with adverse growing conditions, new shoots will emerge in the next growing season if the rhizomes remain. However, once *Zostera marina* plants have disappeared, including their rhizomes that stabilise the substrate, it is difficult for new plants to re-establish healthy communities because of substrate instability. Close to the limit of its salinity tolerance in the Baltic Sea, where *Zostera marina* mainly grows vegetatively (Reusch et al. 1999), it may take a very long time (10–50 years or more) before the species re-establishes because vegetative (clonal) growth is slow (only 10–20 cm per year).

11.16.3 Long-term trends in *Mytilus*

In some areas of the Baltic Sea, a decreasing trend in the *Mytilus trossulus* biomass has been observed since the 1990s. This may be caused by decreased food availability (plankton) due to the eutrophication decrease in coastal waters. For example, in the Askö area in the Baltic Sea proper, the phytoplankton spring bloom has been almost halved between the years 1980 and 2012, and since the early 1990s *Mytilus* has decreased as well (Fig. 11.35). These changes are especially obvious in the inner parts of the archipelago, but there are also signs of a decrease in the outer archipelago. Detritivores should also decrease with a eutrophication decrease, and since the turn of the century they actually have decreased in the Askö area (Fig. 11.35).

Considerable fluctuations in the densities and biomass of *Mytilus trossulus* recorded at different locations in the Baltic Sea are difficult to explain by variation in environmental conditions such as salinity or nutrient concentrations (Westerbom and Jattu 2006). A virus disease or periodic oxygen deficiency may have been involved, especially in areas with large eutrophication problems. A decline of the *Mytilus trossulus* population in the Askö area in 1994, which also was observed in most parts of the Baltic Sea proper, was most probably due to unusually high temperatures down to the thermocline (at a ~20 m water depth) for a long period in summer and a simultaneous low pelagic primary production (Axén 1999). Due to the lack of food, the mussels probably respired themselves to death.

Finally, especially in the southern and eastern Baltic Sea proper, non-indigenous species may increase the predation pressure on *Mytilus trossulus* to an extent resulting in a drastic population decline. For example, *Mytilus trossulus* seems to be a favourite food item for the Chinese mitten crab *Eriocheir sinensis* (*cf.* Box 5.8) and the round goby *Neogobius melanostomus* (*cf.* Box 5.6), two non-indigenous species that are currently spreading in the Baltic Sea (Karlson et al. 2007; Wójcik et al. 2015).

Review questions

1. How does the vegetation reflect the type of substrate in an archipelago of the Baltic Sea? How does this relate to water movement?
2. How can morphology groups of macroalgae be used in ecology?
3. How would you distinguish between *Calothrix scopulorum* and *Verrucaria maura* macroscopically and microscopically?
4. Describe how the algal zonation on hard substrates differs between the Kattegat, Baltic Sea proper, Bothnian Sea and Bothnian Bay. How are these differences explained?
5. Which key species of the Baltic Sea ecosystem live in the phytobenthic zone? Why are they key species?

Discussion questions

1. Why are biotic interactions less important in the phytobenthic zone of the Baltic Sea than in the phytobenthic zone of Atlantic coasts?
2. Why is the phytobenthos important for the fish stocks of the Baltic Sea?
3. Why is the sequence “algae – *Amphibalanus improvisus* – *Mytilus trossulus* – *Cordylophora caspia* and *Einhornia crustulenta*” (and not in another order) in the microzonation shown in Fig. 11.15b?
4. What is the best way to study phytobenthic communities?
5. What is the best way to protect phytobenthic communities?

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