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## The Marine Environment

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The marine environment covers over 70% of the surface of the Earth, yet represents special challenges when it comes to scientific inquiry. When compared to terrestrial systems, the marine environment is much less easily accessible and, despite great effort, remains less well known. With the rise of the modern natural sciences, tools and methods have been continually developed to explore marine environments, from the littoral zone and nearshore environment to open waters and the shelf and abyssal seafloor. From tried and true collection equipment, often identical to or based on fishing gear, to new innovations in remotely controlled and autonomous vehicles, exploration of the underwater world is heavily dependent on the tools used.

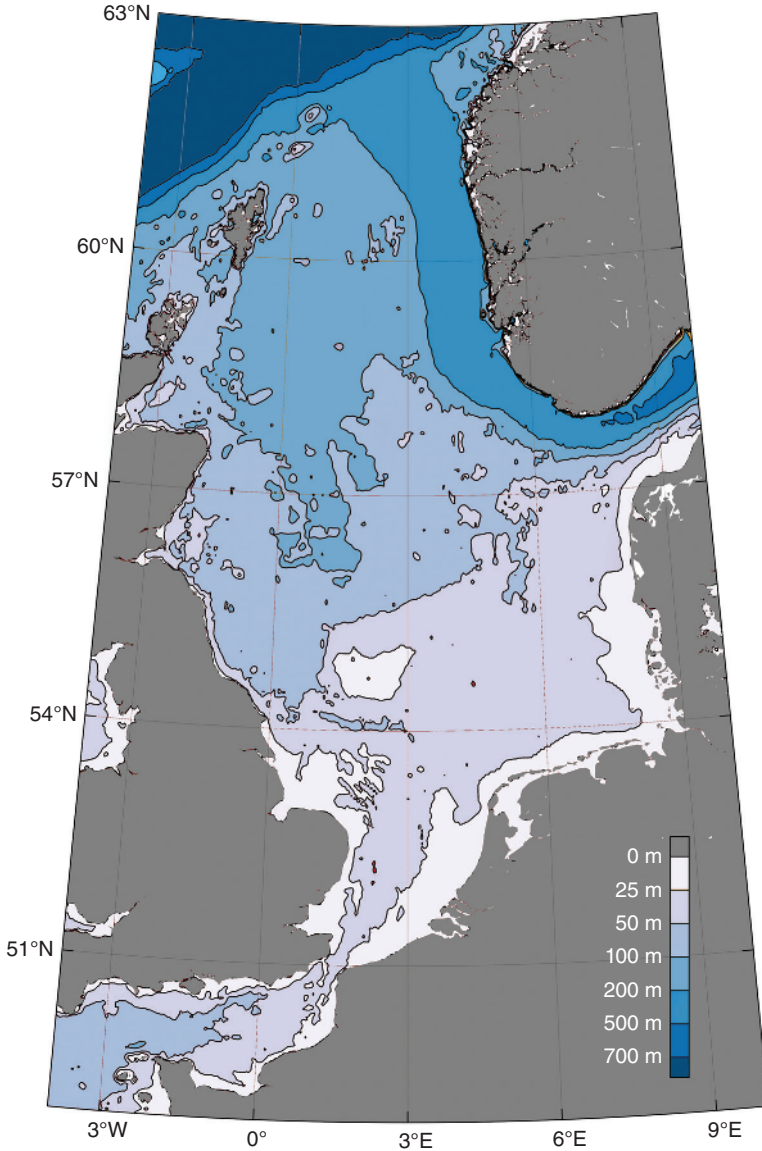
Technological advancement now allows marine field studies to be conducted at all levels: from individuals to populations, to groups of populations, and to entire ecosystems. Habitats from the shallow nearshore to depths of thousands of meters are increasingly accessible; studies of interactions between specific organisms and physical and biological components are possible. The equipment used for sampling is dependent on the research questions asked and the characteristics and depth of the studied organisms and their habitat. Gears range from simple tools that are useful in shallow nearshore areas, such as bottles, secchi discs, and gillnets or beach seines to advanced equipment, such as remotely operated vehicles (ROVs), fishing trawls, and hydroacoustics deployed from large research ships for studies offshore and at greater depths. Even remote observation from space can be performed using satellites.

A characteristic transect from a continental landmass to the deep ocean includes nearshore environments that, depending on local geology, may consist of sandy beaches, cliffs or fjord systems. The continental shelf may stretch out some distance from the continental landmasses, gradually giving way to the continental slope, which descends down to the abyssal plains of the world's major

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oceans. As an example, the western coast of Norway contains an elaborate fjord system with numerous deep basins divided by shallower sills, giving way to the Norwegian Channel and then the shallower continental shelf. To the southwest, the North Sea is a shallow sea on top of a continental shelf only, while to the northwest, the Norwegian Sea descends into a deep-sea basin which also contains the Mid-Arctic Ridge, separating the Eurasian and North American continental plates. Banks, seamounts and submarine canyons are features that add to the topographical complexity of this general system (Figure 1.1).



**Figure 1.1** Topographic chart of the North Sea. *Source:* G. Macaulay, Institute of Marine Research, Norway.

Species composition changes with depth and distance from the coast, both for pelagic species and for organisms associated with the seafloor. Organisms are morphologically, physiologically, and behaviorally adapted to their environment through natural selection. Individuals with favorable genetic traits have increased breeding success than those lacking these traits (genetic adaptation). Some species are able to shift between environments and habitats, for instance benthic species with a pelagic egg and larval phase, or species that shift diurnally between different water depths (diel vertical migration, DVM). Diel vertical migration typically occurs between water masses with different properties in terms of light, temperature, oxygen, and salinity, requiring a physiological response from the organism. In general, effects of abiotic and biotic factors influence morphology, physiology, and behavior and thus how animals adapt to their habitat.

Examples of **abiotic factors** are the optical properties of the water column and include: light and the amount of suspended particles, which are important for visual predation; temperature, which regulates physiology, metabolic processes, and swimming activity; salinity, which affects physiology and osmoregulation; oxygen levels, which regulate respiration and metabolism and can limit reproduction or growth at low levels; and depth, which regulates pressure and affects buoyancy of fish that use swim bladders to obtain neutral buoyancy. Stratification of water masses, which often is seasonally dependent, limits nutrient availability in upper strata (the photic zone, as well as oxygen concentration in the lower strata or in isolated basins. Eutrophication and closeness to urbanized regions will also affect the level of primary production and the depth range where visual feeding is possible.

**Biotic factors** influencing the structure of marine communities and ecosystems include prey availability, predation, competition, and parasitism, and are regulated by direct or indirect access to production from lower trophic levels. Trophic communities in shallow waters benefit from readily available photosynthetic primary production, however, such production may be limited by nutrient availability. Organisms in deeper layers usually depend on energy and biomass from above either through migrating animals, transporting nutrients from surface waters to depths, or through the downward transport of debris, dead organisms, and particulate organic matter (POM). Because lower systems are dependent upon the upper regions, total biomass often decreases with depth. Population and individual growth potential will be further regulated through food access and competition. Access to reproduction (mates and spawning grounds) and reproductive behavior (nest spawning, demersal spawning, or pelagic spawning) will affect recruitment to populations. Presence of suitable nursery environments (e.g., coral reefs and kelp zone habitats) regulates survival of early life stages (larval stages of benthos and juvenile fish). Mortality risk (predator density, visibility, and size) in the habitats also changes with depth and distance from the coast.

Chapter 1 begins with a brief description of zonation in the pelagic and benthic realms, followed by a description of the topographies of coastal and fjord biotopes, the continental shelf and slope, and the deep ocean. These biotopes shape the habitats for bottom associated marine organisms. This is followed by a description of the physical characteristics of the pelagic ecosystem, including circulation of water masses in fjord ecosystems and a description of the light

environment in marine waters. The chapter ends with an overview of temperate organisms (benthos and fish) that inhabit the littoral, sublittoral, continental shelf and slope, deep fjords, and the deep sea.

## 1.1 Marine Habitats

### 1.1.1 The Pelagic and Benthic Realms

The oceans are commonly divided into the pelagic and benthic realms. The pelagic realm refers to the body of water from above the seabed to the surface of the water. The organisms swimming or floating in this water column are termed pelagic and can be roughly divided into nekton, able to control their position in the water masses, and plankton. Traditionally the pelagic realm is subdivided into five zones:

- 1) The epipelagic: from the surface to about 200 meters and where the amount of UV light from the sun still allows photosynthesis.
- 2) The mesopelagic zone: from about 200 to approximately 1000 meters. The twilight zone where the organism still might be able to detect sunlight, but at which depth the energy from UV light is too limited for photosynthesis.
- 3) The bathypelagic zone: from 1000 to about 4000 meters, where no sunlight remains.
- 4) The abyssopelagic zone: from about 4000 to 6000 meters. The average depth of the largest oceans in the world is largely contained in this zone – between the 3300 meters of the Atlantic Ocean to the 4300 meter average depth in the Pacific.
- 5) The hadopelagic zones: between 5000 to 6000 meters. These zones are found in relatively restricted areas like deep trenches to the deepest trench, the Mariana trench, which is about 11000 meters deep.

The benthic realm is defined as the bottom sediment or seabed of the ocean and the organisms in or on it are defined as the benthos. Organisms living in the benthic realm are living in close a relationship with the sediment, often permanently attached to it (epibenthos) or burrowing in it (endobenthos), while others, although they can swim, are never found far away from the seafloor, on which they are totally dependent (hyperbenthos or, in the case of fishes, demersal).

About 80% of the ocean floor consists of soft sediment, which can be designated as marine sediments of particle size ranging from mud to coarse sand (0.05 mm to about 1 mm in diameter). This entails that this soft-bottom substrate type defines the vast majority of habitats, from the high subtidal zone to the deepest part of the abyssal zone. Obviously, the term is very broadly defined, and soft sediments can be divided into a number of subhabitats, which are dependent on latitude, temperature and other local environmental factors, including a wide size range and a high diversity of associated organisms.

Ocean hard bottom areas, while less extensive, represent important habitats distinguished by differences in biota composition and dominating life strategies compared to soft-bottom counterparts. Hard bottom seafloor is often associated with specific topographical features such as for instance submarine canyons, seamounts or mid-ocean ridges, or other areas with stronger currents. It can

provide substrate for large number of immobile organisms, and current activity can form the basis of filter-feeding communities.

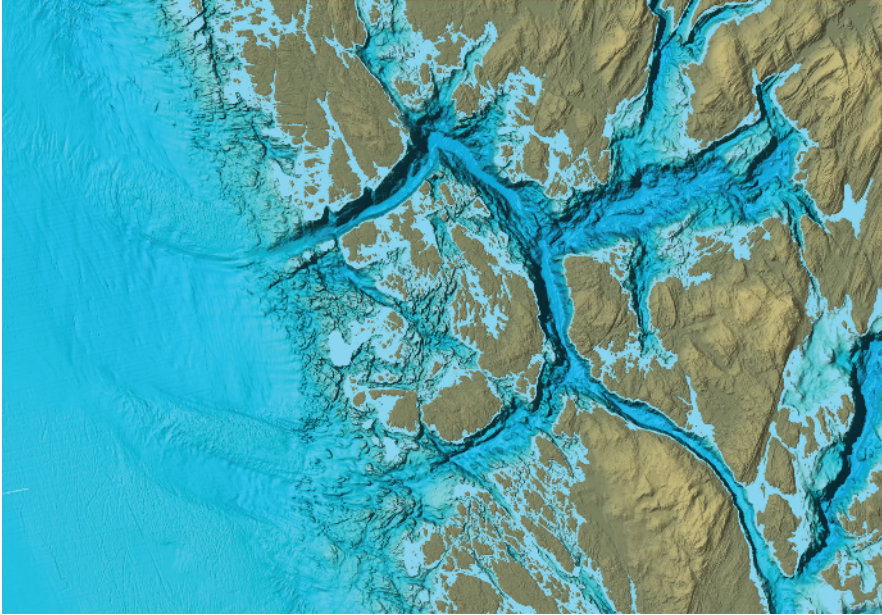
The benthic realm is zoned by depth in a way that generally corresponds to the zones in the pelagic realm:

- 1) The intertidal zone: where land meets the sea. This has no parallel in the pelagic realm.
- 2) The sublittoral zone: defined as the area of the coast that, even at lowest tide, is always submersed to the extent of the continental shelves. The continental shelves extend to approximate depths of 200 meters. This corresponds to the epipelagic zone.
- 3) The bathyal zone: extends from 200 meters to approximately 4000 meters. This also includes the continental slope and corresponds to the mesopelagic and the bathypelagic zone.
- 4) The abyssal and hadal zones includes most of the ocean seafloor from 4000 meters to the deepest trench at 11 000 meters. These zones correspond, respectively, to the abyssopelagic and the hadopelagic zones in the pelagic realm.

## 1.2 The Coastal and Fjord Biotopes

Fjord systems are found in many areas of the world including Alaska, Chile, Greenland, Norway, and New Zealand. They have a complex topography that can include numerous narrow passages, and are often divided into basins divided by shallower sills, which are shallow ridges situated at the mouth of the fjord and are normally old moraines. The outer part of the coast consists of a number of islands and thus the sheltered inland fjords give way to a coastal archipelago with a more wave-exposed and open coast on the outside (Figure 1.2). The topography of the coast of southwestern Norway represents typical characteristics of fjord biotopes, consisting predominantly of rock, with a few areas with sand beaches. The landscape and seascape was formed mainly by the activity of the large ice sheets during the glacial periods. As a result of glacial activity, the coast is divided by a number of large fjords. Many fjords are deeper than adjacent sea areas. For example, the Norwegian Sognefjord reaches a depth of 1308 m, significantly deeper than the offshore continental shelf.

This complex topography creates barriers to the passage of water as well as organisms, meaning that a fjord system can contain several distinct habitats or even ecosystems. Fjords are situated in the cold temperate parts of the world, meaning that they are subjected to strong seasonality, with seasonal differences in light and temperature conditions between winter and summer. Seasonal differences in water temperature are strongest in the surface layers. During winter, increased mixing of surface and deeper water layers creates a uniform water column, while in the summer, increased temperature and freshwater runoff create a distinct surface layer with different water properties than the deeper layer. In periods with high freshwater runoff, such as during the snowmelt period in spring and early summer, a clear salinity gradient from the outer to the inner part of the fjord is often apparent. Surface waters, the uppermost 10–15 m, in the



**Figure 1.2** Part of the coastline of Western Norway, showing the complex bathymetry characteristic of fjords and many other coastal systems. *Source:* Gavin Macaulay, Institute of Marine Research, Norway, with permission from The Norwegian Mapping Authority.

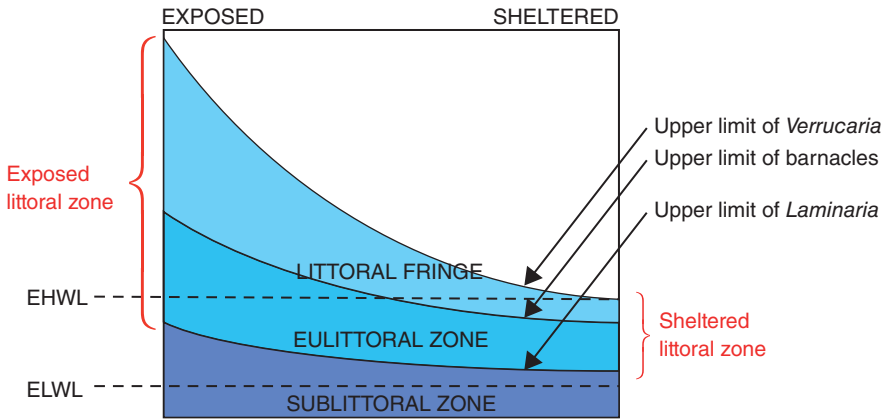
inner parts of the fjord will have the lowest salinity. The bottom waters will often have low to zero oxygen concentrations because of the limitations sills and inlet passages set on water passage in the deeper layers; effects may be seasonal or year round. Nutrient runoff from adjacent land areas will also contribute to decreased oxygen concentrations in deep water.

The high variability in physical factors and barriers to propagation mean that fjord systems are typically home to many different communities and have an overall high biodiversity. In many cases, isolated relict populations of species can survive in fjord basins long after they have disappeared from adjacent sea areas.

### 1.2.1 The Littoral and Sublittoral Habitats

The **littoral zone** is used as a somewhat arbitrary term which normally refers to the intertidal and the very shallowest parts of the sea (*litus, litoris* (Latin) means “shore”). It is most commonly used for marine habitats and covers the **intertidal zone** (the area alternately covered with water or exposed to air during a tidal cycle) and the **splash zone** above the intertidal zone.

The different parts of the littoral zone can be defined by the upper and lower limits of specific zone-forming organisms (Figure 1.3). In temperate areas, the limit between the littoral and the sublittoral zone can be defined by the upper limit of kelp beds. Sometimes the shallowest part below the intertidal zone (the sublittoral zone) is also included in an expanded definition of the littoral zone. The lower extension of the sublittoral zone is arbitrary, but it is common to



**Figure 1.3** The three “universal zones” recognized by Lewis (1961), showing the zones in a gradient from extreme shelter (right) to strong wave-exposure (left). The area between the dotted lines is the intertidal area between extreme high and low water level (EHWL, ELWL). The littoral zone is composed of the splash zone (littoral fringe) and the eulittoral zone, where the limits are set by zone-forming organisms. The littoral zone is defined as the area inhabited by organisms influenced by the tidal cycle and is separated from the sublittoral zone. The width of the littoral zone is strongly extended towards the wave-exposed side due to higher waves and a much wider splash zone. In addition, the limits are shifted upwards on the wave-exposed side due to the more-or-less constant wave action. *Source: Lewis (1961), figure modified.*

separate between an upper zone inhabited by macroalgae (especially kelp) and a lower zone inhabited mostly by invertebrate animals.

The tidal range at a site is not constant, but varies throughout the moon cycle. The tidal ranges are largest at full and new moons since gravitation forces of the moon and the sun work together during these moon phases. Around full and new moons, the tides are called spring tides. When the moon is half full, the tide levels are at their smallest during the moon cycle and are called neap tides. Further, the maximum tidal range at a site is not the same during all spring or neap periods. Tidal levels along coasts are calculated and predicted by using computer models taking, among others, local topography and moon and sun cycles into account. Finally, the local tidal levels are influenced by temporary and unpredictable forces, such as air pressure, and by local weather. Strong wind toward land may, for instance, cause the sea level to rise locally. Such forces may produce variations in water levels even at sites where the local topography results in no amplitude of the tidal wave (amphidromic points).

The height of the tidal range varies between areas. Examples of places where exceptionally large tidal ranges are found are the English Channel and the Bay of Fundy (eastern Canada). Along the Norwegian coast, the range increases northwards, from very small ranges in the Skagerrak area to spring high tide levels of more than 2 m above Chart Datum in Northern Norway. On the southwestern coast of Norway, the middle spring high tide is around 1.5 m above Chart Datum. Chart Datum is the reference level for sea maps; in most areas of Norway, it is at the same level as the Lowest Astronomical Tide level (LAT).

While the littoral zone is more accessible than the majority of the marine environment, fieldwork in this habitat still provides special challenges. When doing fieldwork one needs to take into account the changing level of the tide, not to mention safety precautions when accessing steep shores or exposed localities, where there might be a high degree of dangerous swell.

In the shallowest part of the sublittoral zone, down to around 30 m in clear Atlantic water, where there is sufficient light for net photosynthesis, kelps and other seaweeds will dominate on rocky substratum (referred to as macroalgal communities, kelp beds, kelp forests). Deeper, where light is too low to sustain growth of large seaweeds, the biota will consist of sessile and vagile organisms, for example, sponges, anemones, corals, sea urchins, and mollusks. The sublittoral is linked to the pelagic habitat and receives nutrients and zooplankton produced via advective transport. Spores, gametes, eggs, and larvae produced by the seaweeds and fauna in the sublittoral zone will be transported and dispersed through the pelagic habitat.

In temperate areas, the sublittoral kelp beds have an extraordinarily high primary production, biodiversity, and density of invertebrates (Mann, 2000). Studies of invertebrates associated with different aquatic plants and seaweeds have shown numbers of up to several hundred thousand individuals  $m^{-2}$  per seaweed vegetation (Christie *et al.*, 2009). Since many of the small invertebrates are important as food for larger organisms, the kelp beds form an important habitat for a number of fish species, like labrids and small gadoids, and provide both food and shelter for a number of fishes and large invertebrates. These areas are often important nursery areas for a number of species.

### 1.2.2 The Continental Shelf and Slope

Continental shelves form a narrow fringe around the continents that vary in width, making up around 7% of the ocean's surface and <0.2% of its volume. Continental shelves vary in both width and depth down to 200 m. Environmental and biological characteristics of shelf areas depend on land impact, depth, steepness, seabed texture and topography of the shelf, and the ocean and currents along the slope side. Vertical stability is lower on the shelf compared to the ocean floor. This enhances nutrient availability and thus primary production by algal cells that, in turn, also increases food availability and production at higher trophic levels (Postma and Zijlstra, 1988). The continental shelf gradually gives way to the continental slope, which serves as the transition to the abyssal plains of the deep sea. On the continental slope, submarine canyons created by flows of sediment from the shelf often serve as unique and diverse habitats for benthic organisms.

**Upwelling ecosystems** are shelf areas that are particularly productive due to continuous wind-induced upwelling of nutrient-rich deep water, often lying over seabeds rich in fine sediments. The nutrient-rich waters then stimulate growth and production of plankton, which has a cascading effect on higher trophic levels. The best known upwelling ecosystems are the Benguela Upwelling System (on the west coast of Namibia and South Africa), California Current



System, Canary Current System, Humboldt Current System, and the Somali Upwelling System (See Mann and Lazier, 2006 for details).

**The North Sea** is an example of a relatively large continental shelf, also considered a semi-enclosed sea (Figure 1.1). The North Sea contains many shallow bank areas in the south and more channels, deep holes, and slope areas in the north. In the southeast, the North Sea is bordered by the European continent. Here it is shallow and has large areas of mud, most of which are in the estuarine area called the Wadden Sea. In the northeast, the shelf area drops into a deep trench, the Norwegian Trench, and is bordered by the Scandinavian peninsula. To the west and north, the North Sea is bordered by the British Isles, with the English Channel connecting it to the Atlantic, and the deeper Norwegian Sea (see Zijlstra, 1988 for further details).

### 1.2.3 The Deep Ocean

The seafloor of the world's major oceans is created by the action of divergent continental plates. Because of the relatively high weight of the basalt-rich rocks of the seafloor crust when compared to granite-rich rocks of continental landmasses, the depth of the major ocean basins is usually around 4000–5000 m. The deep sea can be defined in a few different ways, but because changes in temperature are much less pronounced at depths below 1500–2000 m, depths in this range are often used to distinguish the deep sea from shallower areas. Thus the deep sea comprises part of the bathyal or bathypelagic zone (1000–4000 m), the abyssal or abyssopelagic zone (4000–6000 m), and the hadal zone (>6000 m). Hadal depths are usually common for special geological features such as back-arc basins, created by the break-up of tectonic plates due to nearby subduction zones.

The deep-sea seabed is uniform in physical characteristics over large areas, typically has low amounts of available energy and nutrients, but is home to a surprisingly high diversity of benthic organisms. Special features, such as mid-ocean ridges, volcanic islands, and seamounts, are found in the deep-sea environment and represent distinct ecosystems. As a special case, hydrothermal vent systems along mid-ocean ridges support rich communities based on chemoautotrophic bacteria living on enriched vent fluid.

The deep sea is characterized by several gradients in abiotic factors, such as pressure, light (lacking in the aphotic zones), temperature, and dissolved oxygen. Most importantly, the availability of nutrients rapidly diminishes with distance from photosynthetic primary production at the ocean surface. Early views considered the deep sea as mostly devoid of life or characterized by more primordial organisms.

Surveys of life in the deep sea have shown that while biomass is lower, there is an extraordinary diversity of organisms, with a maximum at the mid to lower bathyal zone (Rex and Etter, 2010). While there are several hypotheses regarding this surprising diversity, the comparative lack of experimental data means that these are somewhat tentative. The environmental stability hypothesis is based on the relative unchanging conditions of the deep sea, while the intermediate disturbance hypothesis explains diversity in terms of the “right” amount of

disturbance present. The sheer size of the deep sea may facilitate speciation. Food particle diversity is greater at depths >1500m, which may lead to further specialization and, for benthic organisms, the small size of benthic detritivores means that there is further room for exploitation of microvariations in benthic topography.

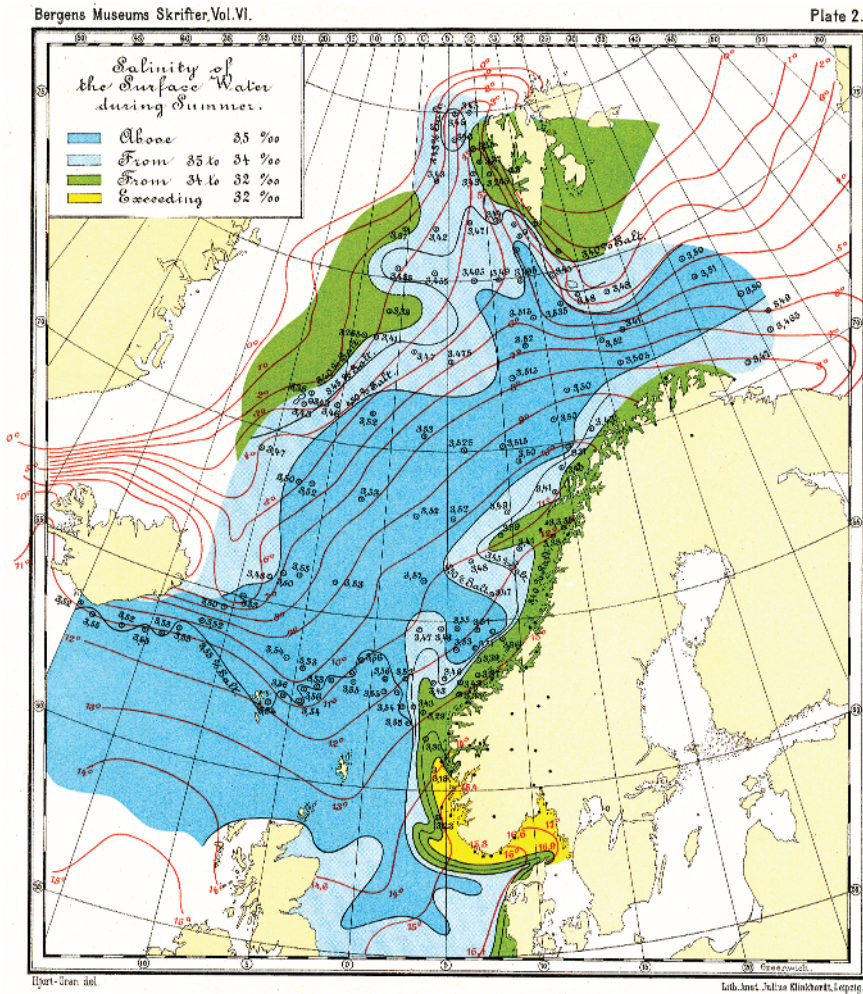
### 1.3 Physical Characteristics of the Pelagic System

*Dag L. Aksnes, University of Bergen and Lars Asplin, Institute of Marine Research, Norway*

Here, we make a brief account of some of the physical variables that structure the pelagic ecosystem. Our emphasis is on the difference between oceanic and coastal locations that are affected by freshwater supply. For example, the Norwegian coast is surrounded by Norwegian Coastal Water (NCW). NCW is characterized by lower salinity (Figure 1.4, yellow and green shading) than the oceanic water, denoted North Atlantic Water (NAW, salinity > 35 ppt). Strong gradients are observed in the environmental variables when moving offshore from the coast toward the ocean (Sætre, 2007). Here, this is illustrated by an idealized transect from inshore to offshore Norway (Figure 1.5, Figure 1.6 and Figure 1.7). The lower salinity (<34.5 ppt) of NCW is caused by large freshwater drainage from the Baltic Sea, the southern North Sea, and local drainage along the Norwegian coast. Due to the rotation of the earth (e.g., the Coriolis Effect and Ekman drift), NCW is like a giant “river”, pressing against the coast on its northward movement toward the Barents Sea. This current is named the Norwegian Coastal Current (NCC). West of the NCC we have the North Atlantic Current (NAC), which is a northern branch of the Gulf Stream, carrying saline (>35 ppt) NAW into the Norwegian Sea.

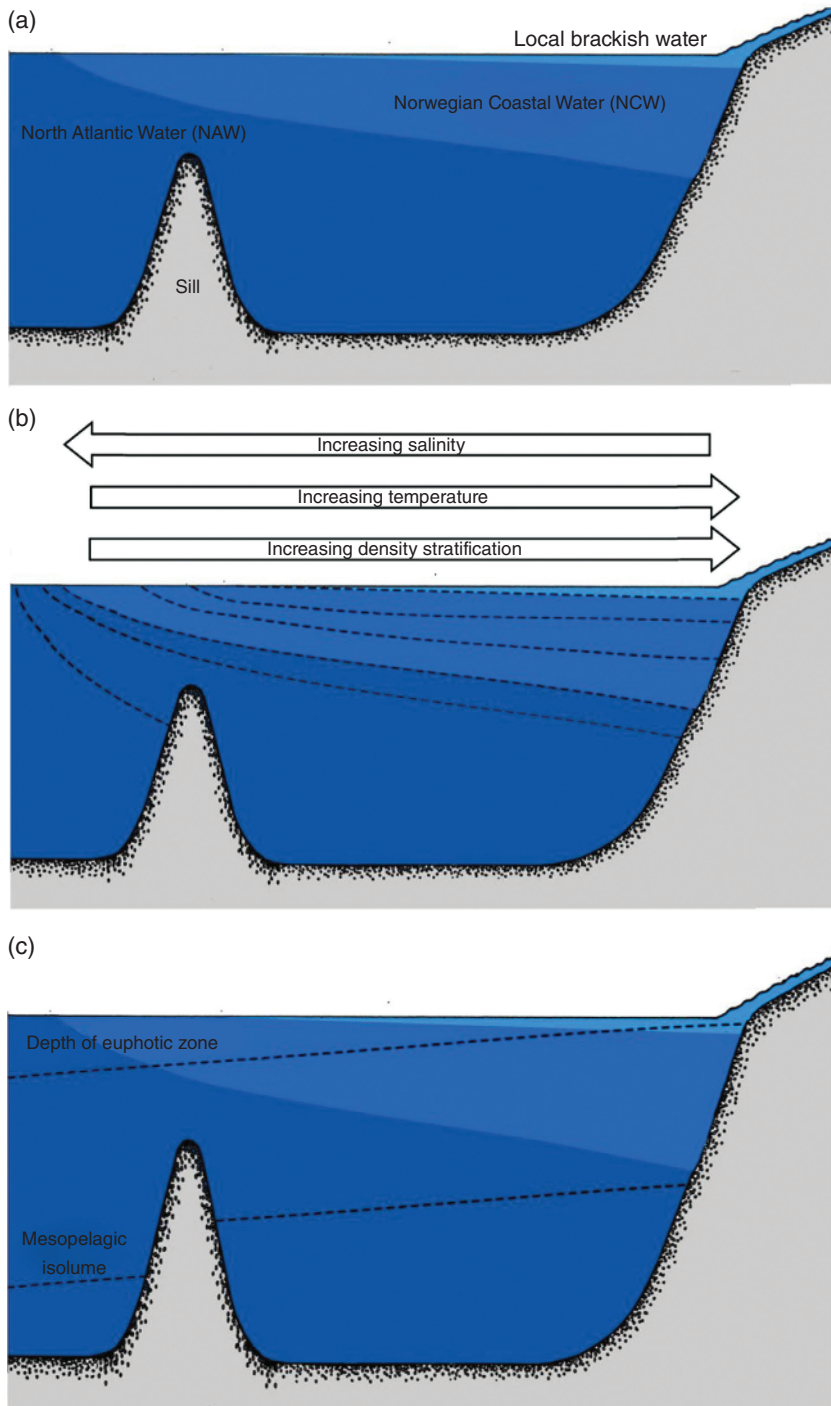
We now consider an imaginary cruise line from the innermost part of a coastal location (e.g., a fjord), through the coastal water and out into the open ocean (Figure 1.5a). At the head of the fjord, a river drains into the sea; this gives rise to a relatively local, thin, brackish layer. This is because freshwater is less dense (i.e. weighs less) than saline water. Moving outwards toward the ocean, the brackish water is gradually mixed into the underlying NCW and the brackish layer will soon disappear. Also further out, the NCW is mixed with the underlying NAW and transported northwards along with the NCC. Thus, at some point along the transect, the NCW disappears and is replaced by NAW.

A water column, which is characterized by increasing density with depth, is said to be density stratified. This is an important concept in oceanography. A stratified water column requires more energy from wind, waves, and tides, for example, to be vertically mixed. Although the density of seawater is controlled by both temperature and salinity, salinity has the strongest effect on density stratification in areas with large freshwater influence, such as where NCW is present. In the open ocean, where vertical salinity gradients are small, density stratification is mainly controlled by the vertical gradient in temperature.

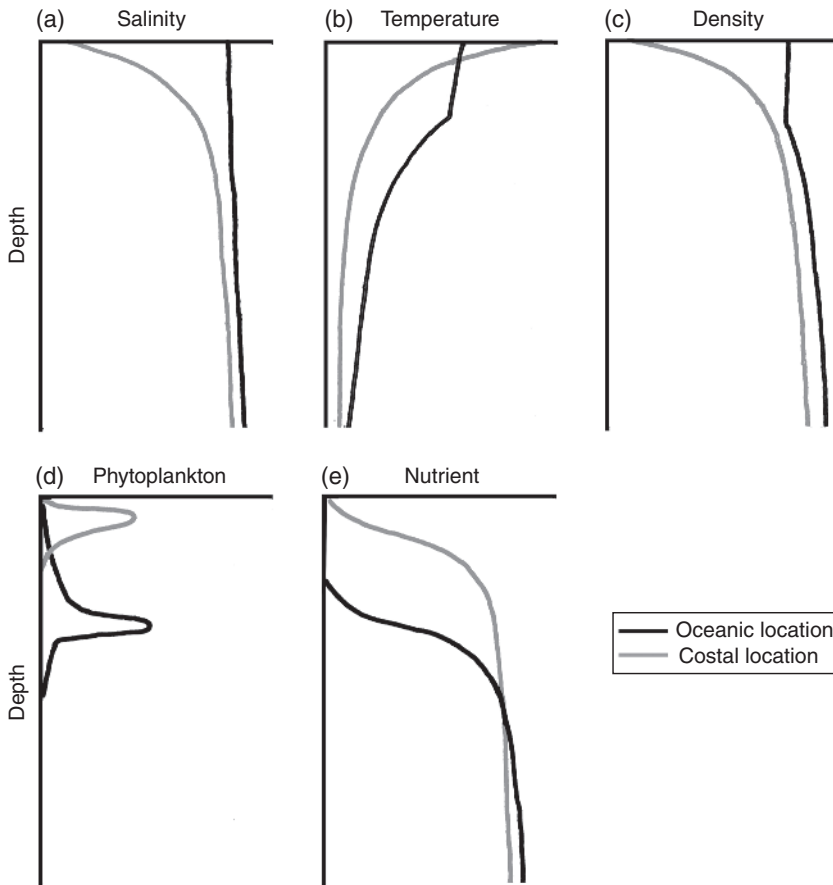


**Figure 1.4** An early map illustrating the Norwegian Coastal Water (yellow and green) between the Norwegian coastline and the oceanic North Atlantic Water (blue) (Hjort and Gran, 1899). Source: University of Bergen Library, Norway.

We now consider an idealized “steady state” summer situation where the weather has been calm for a period of time (Figure 1.5b, 1.5c, and Figure 1.6). The strong density stratification at the coastal location results in a higher surface temperature than at the oceanic location (Figure 1.5b and 1.6b). At both locations, sun radiation is quickly absorbed and converted to heat in the upper few meters. Due to the weaker density stratification (small vertical gradient in salinity) at the oceanic location (Figure 1.6c), vertical mixing will be higher than at the coastal location. This mixing will result in a larger net transport of heat downwards and consequently leads to a lower surface temperature than at the coastal location.

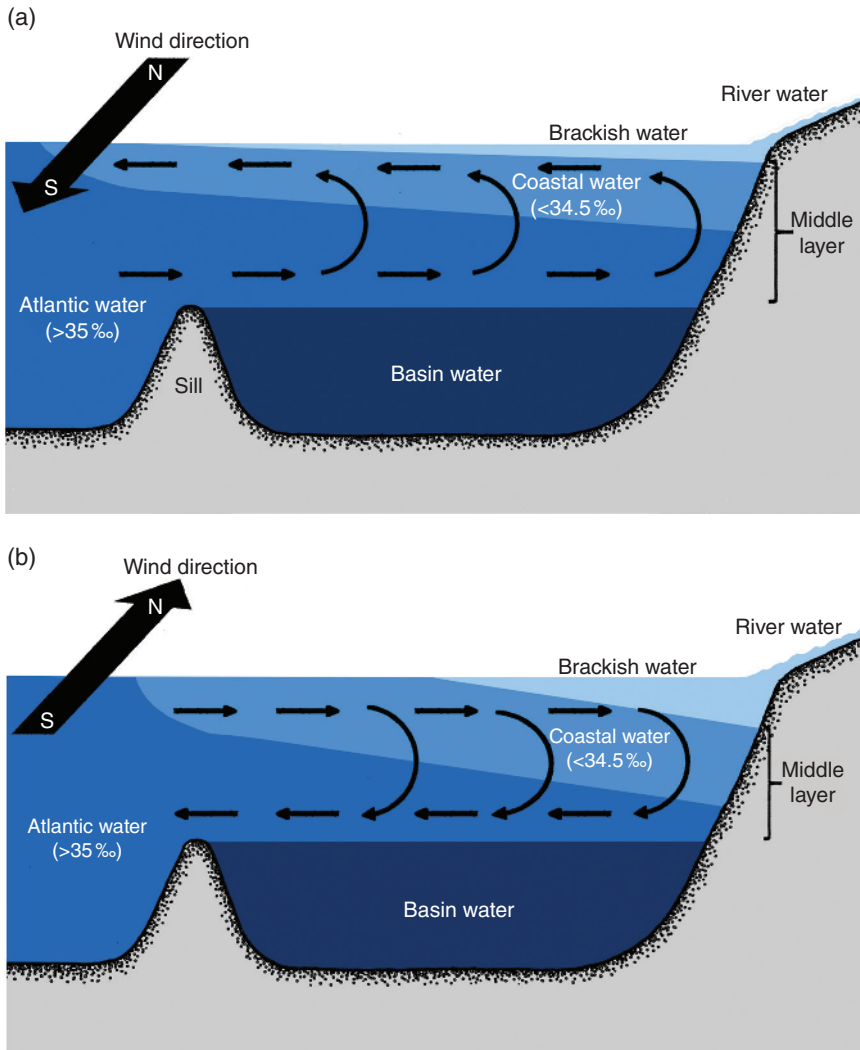


**Figure 1.5** A transect from the head of a fjord (right) to an oceanic location (left) showing (a) the three main water masses: local brackish water, Norwegian Coastal Water (NCW), and North Atlantic Water (NAW). A summer situation is indicated in (b). The arrows indicate the gradients in salinity, temperature, and density stratification; broken lines indicate isoclines for the three variables. Fresher water contains higher concentrations of CDOM with terrestrial origin causing isolumes, like the euphotic depth, to shoal toward locations more affected by freshwater. Depth of euphotic zone and Mesopelagic isolume is indicated in (c).  
 Source: Artwork by R. Jakobsen.



**Figure 1.6** Difference in vertical distributions of (a) salinity, (b) temperature, (c) density, (d) phytoplankton, and (e) nutrients at a coastal (grey) and an oceanic location (black) in an idealized steady state summer situation. *Source:* Artwork by R. Jakobsen.

Freshwater affects light penetration. This is because freshwater drainage from land contains a high concentration of dissolved organic matter (DOM). These substances are referred to as chromophoric or colored dissolved organic matter (CDOM). A large fraction of the CDOM, which is mainly of terrestrial origin (e.g. humic substances), is resistant to microbial degradation and has long residence times in the ocean. CDOM is a strong light absorber and therefore increases the attenuation of sunlight on its way through the water column. The CDOM light attenuation tends to be proportional to the fraction of the freshwater and consequently relates inversely to salinity (Stedmon and Markager, 2003). Thus NCW attenuates light more than NAW (Aksnes, 2015). This means that the depth of the euphotic zone, which corresponds to around  $1\text{--}10\ \mu\text{mol quanta m}^{-2}\ \text{s}^{-1}$ , is shallower in coastal than in oceanic water (Figure 1.5c). Such shoaling of isolumes (Figure 1.5c) not only has consequences for the vertical distribution of photosynthetic organisms like phytoplankton (Figure 1.6d) and benthic algae, but also of inorganic nutrients (Omand and Mahadevan, 2015, Figure 1.6e) as



**Figure 1.7** Effects of coastal winds on circulation patterns of coastal areas and fjords. Northerly and southerly winds cause (a) upwelling and (b) downwelling with opposite circulation patterns in the intermediate layer (the water layer between the brackish water and the sill depth) of a fjord. *Source:* Artwork by R. Jakobsen.

well as of organisms that make use of light in vision and orientation. For example, a mesopelagic organism searching for a light comfort zone of the order  $10^{-5}$   $\mu\text{mol}$  quanta  $\text{m}^{-2} \text{s}^{-1}$  will generally find this zone several hundred meters shallower in a murky coastal than a clear oceanic location (Røstad, Kaartvedt, and Aksnes, 2016). Similarly, we would expect that the amplitude of diel vertical migrations would be less pronounced in murky coastal than in clear oceanic water.

It should be noted that a number of processes not considered here affect the patterns discussed above, for example, coastal upwelling, downwelling, storm events, and mesoscale eddies will all affect these patterns (Sætre, 2007). We make

one remark concerning episodic downwelling and upwelling events that occur along the coast as a function of wind patterns. With persistent wind from the north along the coast, the NCW tends to drift toward the ocean due to Ekman drift (outward directed arrows in Figure 1.7a). This loss of coastal water is compensated by deeper water that moves in the opposite direction (inward and upward arrows in Figure 1.7a) a process termed upwelling. With wind from the south, the situation is reversed (Figure 1.7b). The NCW now presses against the coast and causes a downwelling situation. Thus the wind situation at the coast has a large effect on the circulation patterns and the advection of, for example, zooplankton in coastal areas and fjords (Aksnes *et al.*, 1989). The water transport into (and out of) a fjord in the intermediate layer typically amounts to thousands of m<sup>3</sup> per second, while the estuarine circulation (not illustrated in Figure 1.7) that is associated with local river discharges is an order of magnitude lower.

While the deep ocean is generally well oxygenated due to the global thermohaline circulation, this is often not the case in coastal locations, for example, the deep basins of the Baltic Sea and the Black Sea are permanently anoxic. This is because shallow sills hamper the exchange of the basin water with outer, oxygen-rich water. When the basin water has a long residence time it becomes stagnant; oxygen is consumed more rapidly than it is supplied, resulting in anoxia. Several fjords are similarly characterized by low concentrations of dissolved oxygen and even anoxia. Generally, this occurs when the sill is shallow so that the basin water of the fjord has no direct contact with the outer oceanic water. At times, for example, with long periods of northerly wind and upwelling of dense deep water along the coast, dense surface water might intrude into the fjord above the sill depth and then sink into the basin due to its greater weight. Such renewals of the basin water will lead to a temporary increase in the oxygen concentration.

### 1.3.1 The Light Environment

*Dag L. Aksnes, University of Bergen*

The variation in light intensity during a 24 h day–night cycle or over a 1000 m water column typically spans 10 orders of magnitude. Such huge temporal and spatial variations are seldom seen for other environmental variables. Thus it is no surprise that organisms respond to changes in light such as in diel vertical migration. Measuring the light environment is less trivial than measuring salinity, temperature, and oxygen for example. Some knowledge of optical quantities and light transmission are required to know what different instruments measure.

#### 1.3.1.1 Inherent Optical Properties: Scattering and Absorption Coefficients

The common definition of light is the electromagnetic radiation that can be sensed by the human eye. Visible light spans approximately from 390 to 700 nm. It is sometimes convenient to sum the energy (photons) in this band, but since the photons of different wavelengths are **absorbed** and **scattered** differently, this is not always appropriate. As the photons travel through water, some are **absorbed** (*a*), that is, converted to heat, and some are **scattered** (*b*), which means that the direction of the photon is changed. These two **inherent** optical properties

of the water have units per meter ( $\text{m}^{-1}$ ) and determine how fast light is attenuated in water. An absorption coefficient of, for example,  $0.3\text{m}^{-1}$  for a particular wavelength means that 74% ( $e^{-0.3} \times 100\%$ ) of the photons of this wavelength “survive” per meter travelled distance and 26% are absorbed, that is, are converted to heat. Similarly, a scattering coefficient of  $0.3\text{m}^{-1}$  means that 26% of the photons change direction and that 74% of the photons of the wavelength in question pass through one meter in a straight line.

### 1.3.1.2 Visibility, Sighting Distance, and the Beam Attenuation Coefficient

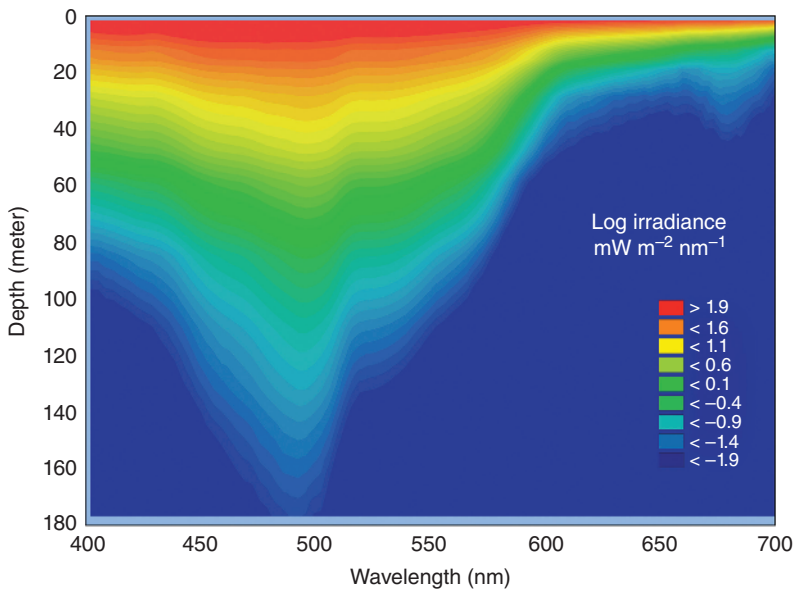
Light is attenuated more in water than in the atmosphere because water absorbs more photons than air. In addition to absorption, light is also scattered more in water than in air (unless it is very foggy). A light beam (photons moving in the same direction) is destroyed as it moves through water because the photons are scattered in different directions. Visibility is based on image transmission, that is, a light beam that preserves the image through space/water. Scattering (in addition to absorption) therefore destroys the image of an object along the path of sight. That is why the underwater sighting distance is short in water (often a few cm in particle rich water, but more than 50 m in very clear water) compared to the atmosphere.

It is important to recognize that there are two different light attenuation coefficients. Most ecological textbooks refer to the “attenuation of light” between the surface and a specific depth (such as the compensation depth or the euphotic depth). We return to this in Section 1.3.1.3, but now consider the attenuation relevant for transfer of images, that is, light beams. The **beam attenuation** coefficient, given the symbol  $c$  with unit  $\text{m}^{-1}$ , tells us how rapidly a light beam, and consequently an image, is destroyed. Since the image of a copepod, for example, is carried through the water by photons travelling in straight lines from the copepod to the eye of the fish, the beam attenuation coefficient determines the maximal **sighting distance** in water. The beam attenuation is simply the sum of absorption ( $a$ ) and scattering ( $b$ ), that is,  $c = a + b$ . A high  $c$  means poor **visibility** and a short sighting distance. The maximal sighting distance depends also on the contrast of the object and the sensitivity of the visual system of the viewer. Remember also that  $a$ ,  $b$ , and  $c$  are all wavelength specific and so are sighting distances, contrasts, and visual sensitivity. Particularly in shallow water with a large span in the wavelengths of incoming sunlight, the wavelength composition is important for vision. As the downwelling sunlight becomes more monochromatic at larger depths (i.e. only photons of a narrow wavelength band around 480 nm have survived), the situation becomes somewhat simpler (see Figure 1.8).

### 1.3.1.3 Light Penetration and the Attenuation Coefficient of Diffuse Light

Clear water (i.e. a low  $c$ ) is not sufficient to see an object. Obviously, without light, nothing can be seen. If sunlight is utilized in vision, the sunlight intensity at depth must be sufficient. The **attenuation coefficient of diffuse light**, or more precisely the **attenuation coefficient of downwelling irradiance** ( $K$ , also with the unit  $\text{m}^{-1}$ ) determines how large a fraction of the surface light penetrates down to a particular depth. Like the beam attenuation coefficient,  $K$  is also a function of  $a$  and  $b$ , but  $K$  is generally much lower than  $c$ . This is because sunlight photons at a particular depth might not have travelled in a straight line, but





**Figure 1.8** Measurements of downwelling irradiance with a spectroradiometer in the Norwegian Sea. Note that most of the light that remains at large depth narrows to around 480 nm. *Source:* D.L. Aksnes.

might have changed direction a number of times before they reached the depth in question. A flat sensor facing upward is used to measure downwelling irradiance. Thus all photons from above, regardless of their hitting angle, are counted. If the same sensor faces downward, the upwelling irradiance is measured (photons that have been scattered upwards). We now understand why the attenuation coefficient of downwelling irradiance,  $K$ , is useful to characterize the amount of sunlight that is available for vision or photosynthesis at a particular depth, while the beam attenuation,  $c$ , is useful to characterize the visibility between the object and the viewer. Again, it should be noted that  $K$ , like  $c$ , varies with the wavelength. Furthermore,  $K$  is said to be an **apparent optical property** of water because it depends not only on the properties of the water (i.e. inherent to the water), but also on the angle of the incoming sunlight (the angular distribution of light). For example, if the sun is at its zenith, the photons have on average a shorter distance to travel to a particular depth than if the sun is just above the horizon. This means that  $K$  for a particular water column is lower at midday than during dawn and dusk.

#### 1.3.1.4 Photosynthetically Active Radiation (PAR)

Photosynthetically Active Radiation (PAR) is the summed energy in the wavelength band 400 to 700 nm. This quantity is often referred to in textbooks and used in ecological studies. PAR measurements are popular because they provide just one number for the light intensity (i.e. wavelength distribution is ignored) and robust sensors are commercially available. Note, however, that the rationale for the PAR definition is photosynthesis and not vision. PAR is a good predictor for the photosynthetic rate, but there are some caveats in using  $K$ 's which are based

on PAR measurements. In addition to its dependence on the angular distribution of light (see 1.3.1.3), PAR derived  $K$ 's are also affected by the wavelength composition of light and this composition changes with depth (see Figure 1.8).

## 1.4 Temperate Marine Communities – Environment and Organisms

### 1.4.1 Littoral Organisms

#### 1.4.1.1 Species, Zonation, and Communities

The littoral zone does not form a uniform biotope within an area. The substrate in the littoral zone may vary from solid rock to muddy substratum. The degree of wave exposure will vary from perfectly calm and sheltered estuaries to extremely wave-exposed sites on the open coasts, subjected to heavy swell most of the time. The degree of inclination may also vary substantially along the coast. Close to rivers, the surface water will be less saline, and in enclosed and sheltered bays, the sea surface temperature will be higher than in open, wave-exposed areas. These and other physical factors influence species distribution and community composition along the shore.

The species composition and type of community found at a particular littoral locality is influenced by both abiotic and biotic factors. The most important abiotic factors are **substratum type** (rocky vs. soft) and **degree of exposure to waves** (sheltered vs. exposed). Biotic factors like **competition** for substrate and sunlight, **trophic interactions** (predation), and **anthropogenic disturbance** (recreational use or pollution) are further important in shaping the littoral community.

Macroalgae and sessile animals require firm substratum and are consequently excluded from littoral areas composed of sand or mud. In such habitats, animals that may live buried or dig through the substratum will dominate. Strong waves create a harsh physical environment in the intertidal and upper sublittoral zone of strongly wave-exposed areas, and has a big impact on the biota in such places. The intertidal zone tends to be dominated by either small, sessile animals and either small and turf forming or long and flexible macroalgae (Figure 1.9). In the North Atlantic, sessile animals like the barnacle *Semibalanus balanoides* and the blue mussel *Mytilus edulis* commonly dominate. In addition, long and flexible kelps, like *Alaria esculenta* and *Laminaria digitata*, dominate in the lower intertidal zone.

Sheltered rocky shores of the temperate North Atlantic are typically dominated by large brown macroalgae (Figure 1.10). Along most of the Norwegian coast, the following intertidal zonation pattern is characteristic for sheltered sites:

- 1) In the uppermost part of the littoral zone, we typically find encrusting lichens and, a bit lower, tufts of the brown alga *Pelvetia canaliculata*.
- 2) In the mid–upper intertidal zone, a common dominating brown alga is *Fucus spiralis*, with *Fucus vesiculosus* occurring lower. *F. spiralis* is typically found at somewhat more sheltered localities, while *F. vesiculosus* may dominate in more wave-exposed areas. A narrow zone of the barnacle *Semibalanus balanoides* can be found above or between the *Fucus* zones.



**Figure 1.9** The intertidal community at a locality with high degree of wave exposure. The shore is dominated by barnacles and small, turf-forming algae. *Source:* K. Sjøtun.



**Figure 1.10** The intertidal community at a sheltered locality with low degree of wave exposure. The shore is dominated by large brown algae. *Source:* K. Sjøtun.

- 3) In the mid–lower intertidal zone, the most common dominating species is the brown alga *Ascophyllum nodosum*. The amount of *Ascophyllum* is related to degree of wave exposure and inclination of the locality.
- 4) Below *A. nodosum* there will normally be a zone of *Fucus serratus*.
- 5) In the sublittoral zone, temperate kelps dominate, with *Saccharina latissima* being most common in sheltered sites and *Laminaria* in more wave-exposed sites.

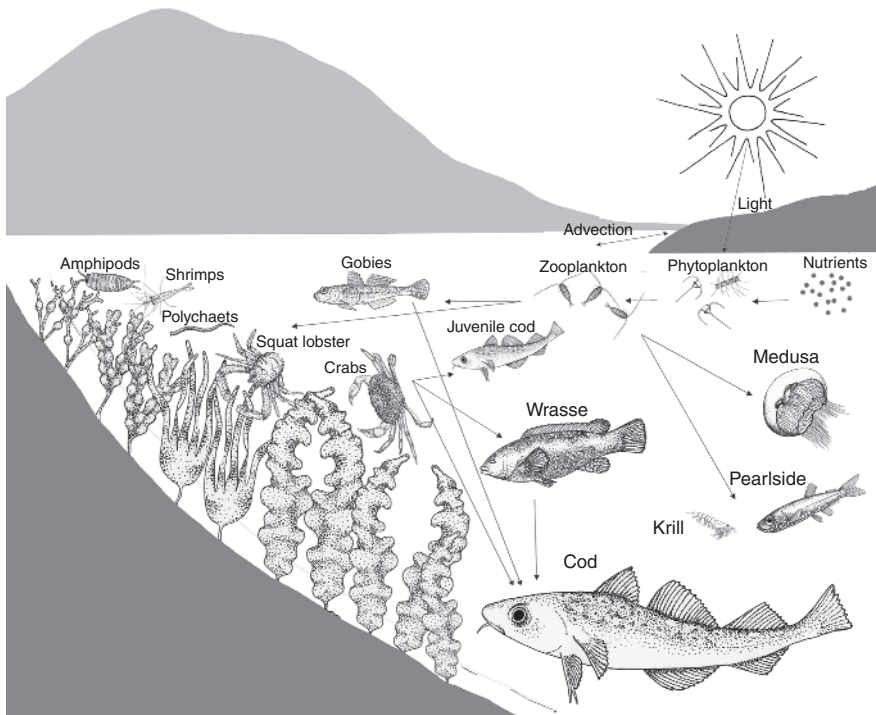
The horizontal bands formed by some dominating organisms are especially conspicuous in sheltered sites. These bands or zones are mainly shaped by a combination of differential tolerance to physical stress by the organisms and competition between them. Within the littoral zone, the ebb and flow of the tide creates a gradient in the amount of time the organisms are exposed to air versus the amount of time they are submerged under water. Organisms growing in the lowermost part of the intertidal zone will spend only a relatively short time exposed to air, while the organisms in the upper part must tolerate being out of seawater for many hours per tidal cycle. In this way, the tidal cycle creates a **gradient of physical stress** to the marine organisms inhabiting this zone, which is a major feature of this habitat. The organisms we find in the intertidal zone are specialized so that they tolerate this environment and most of them only live in the intertidal biotope. Relatively few organisms have adapted to the stressful conditions of the intertidal; normally species richness decreases toward the upper part of the intertidal level, where the period of air exposure is highest.

Typically, many dominating organisms in the littoral zone inhabit different niches and are specialized toward different levels of air exposure. The **physiological tolerance levels** toward, for example, desiccation, temperature, and salinity determine at which vertical level a species can survive. This, in combination with **competition between habitat forming species**, produces characteristic patterns of **vertical zonation**, where different algae and animals typically form dominating and distinct bands at fixed vertical levels along the shore.

Soft-bottom littoral communities differ significantly from their hard substratum counterparts. Beaches and other soft-bottom littoral zones usually have a very shallow inclination. Lack of suitable substrate means that large macroalgae or encrusting organisms are normally not found. Instead, we find a variety of burrowing animals, such as different species of polychaetes, crabs, and bivalves. While briefly mentioned here, intertidal soft-bottom communities will not be treated further.

### 1.4.2 Sublittoral Organisms

The sublittoral zone is highly productive and houses a rich flora and fauna. In the North Atlantic, large extensions of kelp, mainly of the genera *Laminaria* and *Saccharina*, serve as sources for primary production in the nearshore areas and as substrate for sessile benthic organisms and for epiphytes of algae. In addition, kelps, together with other large habitat-forming seaweeds in the coastal zone, form a three-dimensional shelter for numerous small invertebrates, with



**Figure 1.11** A typical sublittoral habitat illustrating trophic relations and links to the physical environment. *Source:* Artwork by R. Jakobsen.

gastropods and amphipods being most abundant. Many nest-building fish species reproduce here and utilize seaweeds as substrate for their nests. Examples are members of the families Gobiidae (gobies) and Labridae (wrasse), where the males build nests for the females to deposit their eggs. The males care for the eggs until hatching. These fish typically stay in the sublittoral during their entire life cycle. Juveniles of other species settle in the sublittoral before moving deeper with age. Examples from temperate areas of the North Atlantic include coastal populations of species from the family Gadidae (codfish). Gadoids have pelagic reproduction and pelagic eggs and larvae. The sublittoral provides shelter and feeding opportunities for the post-settlement stages. As juveniles grow larger, their feeding and shelter needs change and they migrate to deeper waters. An example of a temperate sublittoral habitat in a North Atlantic fjord and links to the pelagic and outer coast is shown in Figure 1.11.

### 1.4.3 Demersal and Benthic Organisms

#### 1.4.3.1 Bottom-associated Organisms

Organisms associated with the seabed can be defined in a variety of ways depending on which characteristics are deemed most important in a particular setting.

The following is a list of some commonly used terminology describing bottom associated fauna:

- **Demersal:** Animals associated with the water column close to the seabed (the demersal zone). Mostly used in connection with fish.
- **Epibenthos:** Animals living on or immediately above the seafloor. Some are attached to the substrate, others are mobile. Examples are sponges, corals, and sea stars.
- **Endobenthos = Infauna:** The animal life within sediment.
- **Hyperbenthos:** Small-sized bottom-dependent animals that have good swimming ability and perform seasonal or daily vertical migrations above the seabed, with varying amplitude, intensity, and regularity.
- **Hypoplankton:** Forms of marine life whose swimming ability lies somewhere between that of the plankton and the nekton; includes some mysids, amphipods, and cumacids.
- **Macrofauna:** Animals visible to the naked eye.
- **Meiofauna:** Small benthic animals ranging in size between macrofauna and microfauna. Often defined as animals not retained by a 1 mm mesh size; includes interstitial fauna (animals living in between sediment particles).
- **Microfauna:** Microscopic animals such as protozoa (unicellular animals) and small nematodes.
- **Nektobenthos:** Those forms of marine life that swim just above the ocean bottom and occasionally rest on it.
- **Nekton:** Mobile animals that can swim against currents, Examples are fish, cephalopods, large crustaceans, and even whales.

#### 1.4.3.2 Continental Shelf and Slope Benthos

The continental shelf and slope is a vast habitat containing a range of sub-habitats associated with differences in substrate composition and other abiotic factors. A large part of the continental shelf and slope seafloor is composed of soft-bottom sediments. While variable in qualities, it is nevertheless possible to extract a few generalities that characterize most soft-bottom sediments, namely that they are dominated by invertebrates more than 0.5 mm in length and that these belong to a few characteristic phyla:

- 1) Polychaeta: mostly suspension-feeding, deposit-feeding, or predatory;
- 2) Crustaceans: mostly scavengers, suspension-feeders, grazers, and predators;
- 3) Echinoderms: suspension-feeders, grazers, and predators;
- 4) Cnidarians: suspension-feeders and/or predators;
- 5) Mollusks: all feeding modes.

Latitude also appears to have a structuring effect on the soft sediment communities. In polar regions, which constitute about 25% of the world's open ocean areas and 25% of the world's continental shelf areas, communities are predominantly:

- 1) Suspension feeders: dominated by sponges, clams, polychaetes, and soft corals;
- 2) Deposit feeders/grazers: mainly sea stars, sea urchins, polychaetes, and isopods;
- 3) Predators: fish, amphipods, pycnogonids, sea stars, amphipods, and polychaetes.

Meanwhile, the temperate zone, which includes 35% of world's open ocean areas and about 45% of world's continental shelf areas, the soft sediment communities consist of:

- 1) Suspension feeders: dominated by clams and polychaetes;
- 2) Deposit feeders: mainly clams and sea cucumbers;
- 3) Predators: crabs, amphipods, gastropods, and polychaetes.

#### 1.4.3.3 Benthic Fish of the Continental Shelf and Slope

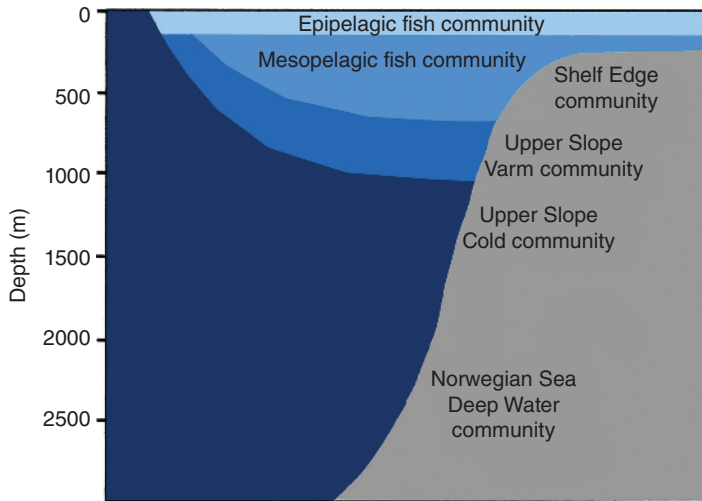
Continental shelf areas are very productive areas where most fisheries occur. This is also the reason why both fundamental and applied research have a long history in continental shelf areas; basic research questions, such as “Why do fish stocks fluctuate?”, started in the nineteenth century. The North Sea ecosystem and other continental shelf ecosystems of the world are described in Postma and Zijlstra (1988), while details of the Norwegian Sea Ecosystem can be found in Skjoldal (2004). An overview of all species can be found in Wheeler (1969), Moen and Svensen (2004), and Heessen, Daan, and Ellis (2015), but see also the web page at the University of Bergen and Institute of Marine Research, Norway.

In **shallow, nearshore coastal areas**, small species of the families Gobiidae (gobies) and Labridae (wrasses) are common and very abundant, particularly during the summer season when they reproduce. On the west coast of Norway, the most numerous small fish species is the two-spot goby (*Gobiusculus flavescens*; Fosså, 1991) and five labrid species; rock cook (*Centrolabrus exoletus*), goldsinny (*Ctenolabrus rupestris*), ballan wrasse (*Labrus bergylta*), cuckoo wrasse (*Labrus bimaculatus*), and corkwing (*Symphodus melops*) (Salvanes and Nordeide, 1993). In addition, juvenile cod (*Gadus morhua*), pollack (*Pollachius pollachius*), and saithe (*Pollachius virens*) have their nursery area here, while the small gadoid species, poor-cod (*Trisopterus minutus*), are also abundant (Salvanes and Nordeide, 1993).

**The fish fauna of the North Sea** and surrounding coastal areas is rich and consists of at least 160–170 species (see Heessen, Daan, and Ellis, 2015). Those that are fished upon are best known and belong to the families Gadidae, Ammodytidae, and Pleuronectidae, which include cod (*Gadus morhua*), Norway pout (*Trisopterus esmarkii*), whiting (*Merlangus merlangus*), saithe (*Pollachius virens*), sand-eel (*Ammodytes* spp.), and plaice (*Pleuronectes platessa*). Rays and skates (Rajiformes) are also common on the shallow banks of the North Sea.

**The benthic shelf-edge and slope fishes.** On the continental shelf and slope of the eastern Norwegian Sea, a total of sixty fish species have been described. Biomass and diversity decrease with depth (Bjelland and Holst, 2004). The fish communities are divided into four categories, characterized by environmental variables and depth (Bergstad, Bjelland, and Gordon, 1999; Bjelland and Holst, 2004; Figure 1.12):

- 1) The deep-water species consist mainly of eelpouts and snailfish (*Lycodes frigidus*, *Paraliparis bathybius*, and *Rhodichthys regina*).
- 2) Common “upper-slope cold species” are rays (*Raja hyperborea* and *R. clavata*), the two eelpout species (*Lycodes pallidus* and *L. flagellicaudata*), and the gadid Arctic rockling (*Onogadus argentatus*).



**Figure 1.12** Classification of fish communities by depth using the Norwegian Sea shelf slope summer situation as an example. *Source:* Redrawn from Bjelland and Holst (2004). *Artwork by:* R. Jakobsen.

- 3) The most common “upper-slope warm species” include four eelpout species (*Lycodes esmarkii*, *L. eudopleurostictus*, *L. seminudus*, and *Lycenchelys muraena*), Greenland halibut (*Reinhardtius hippoglossoides*), roughhead grenadier (*Macrourus berglax*), and the bullhead (US: sculpin; *Cottunculus microps*).
- 4) The most important “shelf-edge species” include redfishes (*Sebastes* spp.), ling (*Molva molva*), tusk (*Brosme brosme*), and monkfish (*Lophius piscatores*).

#### 1.4.3.4 Deep Bottom Fish of Fjords and the Norwegian Deep

In Masfjord at depths >400 m, the dominating bottom fish species are roundnose grenadier (*Coryphaenoides rupestris*); three chondrichthyan species: black-mouthed dogfish (*Galeus melastomus*), velvet belly (*Etmopterus spinax*), and rabbit fish (*Chimaera monstrosa*); blue ling (*Molva dipterygia*); tusk (*Brosme brosme*); sølvtorsk (*Gadus argenteus*); witch (*Glyptocephalus cynoglossus*); European hake (*Merluccius merluccius*); and the hagfish (*Myxine glutinosa*). Saithe was also observed on the seabed from an ROV. Most of these deep bottom associated fjord species are also found in the Norwegian deeps and along the continental slope (see Bergstad, 1990a, b for details). However, the deep-water benthic fish community is more diverse outside of Masfjord (Bergstad, 1990a).

### 1.4.4 Pelagic Organisms

#### 1.4.4.1 Plankton and Micronekton

Tone Falkenhaus, Institute of Marine Research, Norway

**Plankton** is a diverse group of organisms that spend either part or all their life drifting in the water column. Although many of these organisms are capable of



**Table 1.1** Plankton size classes.

Group	Size	Examples
Femtoplankton	<0.2 μm	Viruses
Picoplankton	0.2–2 μm	Bacteria
Nanoplankton	2–20 μm	Dinoflagellates
Microplankton	20–200 μm	Diatoms, eggs and larvae of crustaceans
Mesoplankton	0.2–20 mm	Copepods, fish larvae, chaetognaths
Macroplankton	2–20 cm	Euphausiids, amphipods, jellyfish
Megaplankton	>20 cm	Large jellyfish, salps

locomotion, they generally have low swimming ability and are unable to move against currents. This separates plankton from nekton, which includes organisms that can control their movement in the water (such as fish). Plankton are generally smaller than nekton, however, some planktonic organisms can be quite large (jellyfish up to a meter or more) (Table 1.1). **Micronekton** is the name for an intermediate group between plankton and nekton; usually they are smaller pelagic organisms and caught in moderately sized trawls with mesh sizes of 4–5 mm. Micronekton, consisting mainly of decapod crustaceans, smaller cephalopods, and small fishes, are described below under “mesopelagic organisms”.

Many zooplankton and micronekton undertake **diel vertical migrations** (DVM) over the course of every 24-hour period, moving into the upper waters at night and descending into the darker depths during the day. This behavior is considered an adaptation for feeding in food-rich surface waters at night and avoiding visual predators during the day. The DVM of zooplankton may span several hundred meters and is considered the largest (in terms of biomass) and most regular migratory movement on the planet.

It is possible to classify members of the plankton in multiple ways. One way is according to how they obtain energy: **phytoplankton** are plant-like autotrophs that perform photosynthesis, while **zooplankton** are animals that consume other organisms.

Size is another way to categorize plankton, which includes organisms from micrometers (viruses) to several meters (large jellyfish). Usually the following divisions are used, which reflects the mesh size needed to filter them out of the water:

Plankton may also be categorized according to how much of the life cycle is spent in the plankton. **Holoplankton** are planktonic their entire lives (e.g. phytoplankton, copepods, ctenophores, chaetognaths). **Meroplankton** spend only a part of their life cycle as plankton. This group includes organisms with planktonic larvae that eventually change into a bottom-living (worms, mollusks, crustaceans, corals, echinoderms) or free-swimming life stage (fishes).

**Phytoplankton**, also called micro-algae, are single-celled, photoautotrophic microorganisms. Phytoplankton account for half of the photosynthesis on earth and play an important role in the removal of CO<sub>2</sub> from the atmosphere.

Phytoplankton are the basis for the vast majority of oceanic food webs. Since phytoplankton are dependent on sunlight for photosynthesis, they are restricted to the photic zone in the upper 50–100 m of the water column. Growth also depends upon mineral nutrients, which is supplied from deeper layers or land. Given enough sunlight, CO<sub>2</sub>, and nutrients, populations of phytoplankton can reproduce explosively, doubling their numbers in just one day. There are about 4000 described species of marine phytoplankton. In terms of numbers, there are four important groups of phytoplankton:

- **Diatoms** have an outer shell comprised of silica and are the ecologically most important group in arctic and boreal ecosystems, usually dominating the phytoplankton spring bloom.
- **Dinoflagellates** are more common in the summer and autumn period. Some species within this group are known to produce toxins that can be harmful for humans through accumulation in shellfish.
- **Coccolithophores** have outer shells comprised of calcium carbonate and thrive in warm, nutrient poor waters. Blooms of the coccolithophore species *Emiliania huxleyi* usually occur during summer in coastal waters and fjords, which gives the ocean a chalky color, visible from space.
- **Cyanobacteria** (sometimes erroneously called blue-green algae) are a group of bacteria that are able to perform photosynthesis. Blooms of toxin producing cyanobacteria have become an increasing problem in polluted estuarine and brackish waters, such as the Baltic Sea.

**Zooplankton** are consumers that eat other plankton and thus provide an important link between primary producers (phytoplankton) and higher trophic levels. Some are herbivorous, filtering phytoplankton out of the surrounding water, whilst others are carnivorous predators on smaller zooplankton. Zooplankton are found in all oceans, from the surface to the deepest trenches. Every major phylum of the animal kingdom is represented in the zooplankton, either as adults or as larvae. The following taxonomic groups are commonly found in plankton samples.

The **Copepods** are small crustaceans of great ecological importance. The most abundant copepod species in the North Atlantic, *Calanus finmarchicus*, feeds on phytoplankton and, in turn, is an important food source for fish larvae and pelagic fish (herring and mackerel). During spring, this species builds up fat reserves (omega-3 fatty acids), which it draws upon during the winter when it hibernates 2000 meters below the sea surface. **Euphausiids** are relatively large shrimp-like crustaceans that are more commonly known as krill. The Nordic krill (*Meganyctiphanes norvegica*) reaches a length of 45 mm and is widespread in the North Atlantic. Krill are often found in large swarms particularly in the polar seas, providing food for whales, fish, and birds. **Amphipods** are another important type of planktonic crustacean. They have large well-developed eyes at the front of their head to actively seek-out their prey. Some species of amphipods live in association with gelatinous organisms such as jellyfish and salps. **Chaetognaths**, or “arrow worms” belong to a separate phylum, comprising about 120 species. Their name comes from their long, transparent bodies, with side and tail fins. All species are carnivorous with grasping hooks and rows of strong

teeth that make them efficient predators on copepods and other small crustaceans. Holoplanktonic **gastropods** (mollusks) swim with their modified foot, which has evolved into two wing-like lobes. The “sea butterflies” (*Limacina* spp.) have calcified shells and feed mainly on phytoplankton. The “sea angel” (*Clione limacina*) has no outer shell and is a specialized predator on *Limacina*.

**Appendicularians** and **Salps** are holoplanktonic animals with nerve cords and are thus closely related to the vertebrates. They are filter feeders, consuming small food particles, such as phytoplankton and detritus. Appendicularians produce a mucus house with a complicated arrangement of filters to extract particles from the water. The most common species belong to the genera *Oikopleura* and *Fritillaria*. Salps live singly or in colonies and can form massive aggregations of millions of individuals that may play a significant role in marine ecosystems.

**Jellyfish** are gelatinous animals that belong to the phylum Cnidaria, which are characterized by the possession of nematocysts (stinging cells). Jellyfish are the largest example of plankton and can grow as large as 2 meters wide, with tentacles up to 37 meters. Jellyfish have only primitive organs and nervous systems, and no hard body parts. They are, however, effective predators that catch plankton and larval fish with stinging cells on their tentacles. Common species among **jellyfish** are the moon jellyfish (*Aurelia aurita*), the lion’s mane jellyfish (*Cyanea capillata*), and the blue stinging jellyfish (*Cyanea lamarckii*). The colonial **siphonophores** are composed of many specialized individuals which may stretch out up to 50 meters in length like giant fishing nets.

The **comb jellies** resemble the cnidarian jellyfish with their gelatinous bodies, but are members of an unrelated phylum (Ctenophora). The comb jellies use eight rows of ciliary plates for propulsion. These “comb rows” often radiate beautiful color reflections. Ctenophores lack the stinging nematocysts and capture their prey with sticky tentacles (*Pleurobrachia pileus*) or mucous-covered oral lobes (*Bolinopsis infundibulum*).

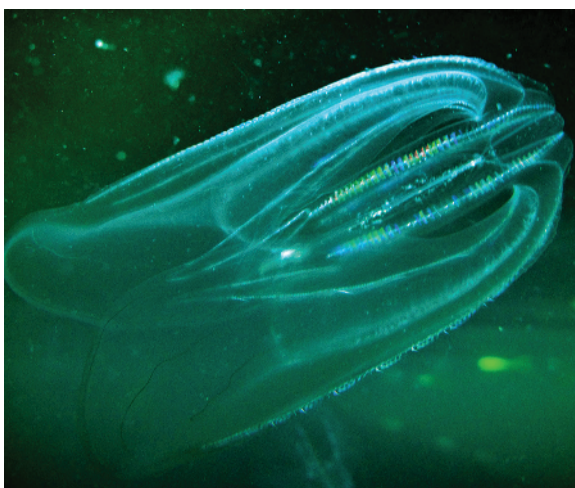
Jellyfish and comb jellies are ancient animals that have existed in the seas for at least 500 million years. When marine ecosystems become disturbed, jellyfish can proliferate. Human impacts, such as climate change, increased nutrient levels, overfishing, and increased coastal construction, have been cited as contributing to increased frequency of jellyfish blooms. Once an ecosystem has become dominated by jellies, it may become difficult for fish stocks to reestablish themselves, because jellies are predators on fish eggs and larvae.

One example of a large species that recently has increased in deep Norwegian fjords is the deep-water helmet jelly *Periphylla periphylla* (Figure 1.13). It is believed that the increase is due to changes in environmental variables such as salinity, light, and/or variables that could be associated with changes in climate. The preferred depth range of *P. periphylla* is 350–450 m.

Invasive populations of alien jellies can expand rapidly because they often face no predators in the new habitat. Examples include the introduction of the comb jelly *Mnemiopsis leidyi* (Figure 1.14) to the Black Sea in the early 1980s, where it had a catastrophic effect on the entire ecosystem. This alien species has also been introduced via the ballast water of ships to the North Sea and Skagerrak, where it occurs in dense blooms in coastal waters during late summer.



**Figure 1.13** The helmet jelly *Periphylla periphylla*.  
Source: E. Svendsen, Norway.

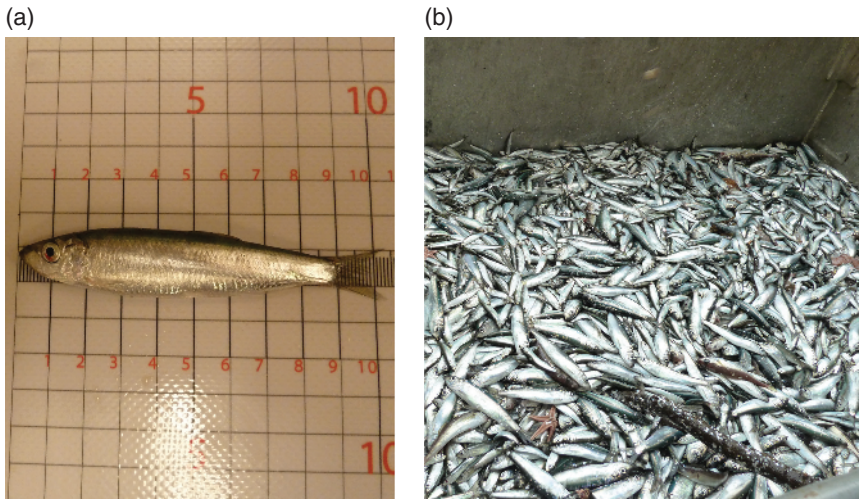


**Figure 1.14** The alien ctenophore *Mnemiopsis leidyi* was first observed in the North Sea in 2005. Source: Ø. Paulsen, Institute of Marine Research, Norway.

#### 1.4.4.2 Pelagic Fish

Fish species in the pelagic water masses differ somewhat with distance from the coast, but there are common species in both the open ocean and the fjords. Within the pelagic zone, there is a limit to which depth it is practical to sample. In the open ocean, this is usually restricted to maximum 1000 m depth.

Several **epipelagic fish** species that occur from the surface to 200 m depth are common for fjords and the coast, over the continental shelf, and in the open ocean. These include herring (*Clupea harengus*), mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou*). Sprat (*Sprattus sprattus*) is abundant in fjords and over the continental shelf (Zijlstra, 1988) (Figure 1.15). Greater argentine (*Argentina silus*), horse mackerel (*Trachurus trachurus*), and the benthopelagic spiny dogfish (*Squalus acanthias*), lump sucker (*Cyclopterus lumpus*), and pollack (*Pollachius pollachius*) also occur sporadically within fjords.

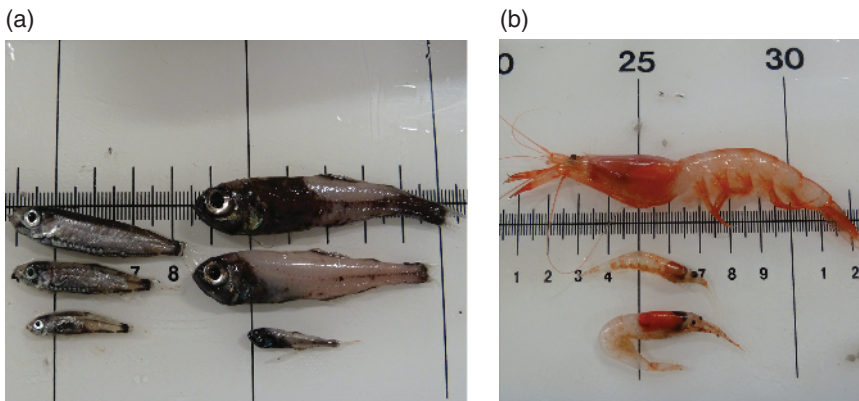


**Figure 1.15** (a) A typical pelagic fish is the sprat (*Sprattus sprattus*). (b) Pictured are some specimens of the local Lustrafjord population caught in the Fjøsne Bay, September 2016. Source: A.G.V. Salvanes.

#### 1.4.4.3 Mesopelagic Organisms

The most numerous fish in the pelagic habitat belong to so-called mesopelagic species (Salvanes and Kristoffersen, 2001). Mesopelagic species are typically found between 150 and 1000 meters deep, often concentrated in one to several deep scattering layers (Sound Scattering Layers; SSLs). Species in these layers undergo diel vertical migration (DVM) to surface waters at night to feed, and stay deep at day time (Marshall, 1971; Salvanes, 2004).

The most common mesopelagic organisms in European deep coastal waters and fjords are pearlside (*Maurolicus muelleri*), northern lanternfish (*Benthosema glaciale*), the shrimps (*Pasiphaea* spp. and *Sergestes* spp.) and krill (*Meganyctiphanes norvegica*) (Figure 1.16). In the open ocean, the



**Figure 1.16** Typical mesopelagic organisms from fjord areas. Pictured are specimens caught in Masfjord. (a) Left; *Maurolicus muelleri* and right; *Benthosema glaciale*. (b) Top; *Pasiphaea* spp., middle; *Meganyctiphanes norvegica*, and bottom; *Sergestes* spp. Source: A.G.V. Salvanes.

stomatoid fish *Cyclotone* spp. and *Notolepis rissoi* can be very abundant in deep mesopelagic samples. Further information on deep-water species are available in Marshall (1971) and Bergstad (1990a).

#### 1.4.4.4 Deep-pelagic Fish

The bathypelagic zone is below the mesopelagic zone and deeper than 1000 m. The most numerous fish belong to the *Cyclotone* genus (e.g., bristlemouths). Other numerous species include gulper eels, bobtail snipe eels, a few species of macrourids, and brotulids (Marshall, 1971). For further details see Marshall (1971), Merrett and Haedrich (1997), or Randall and Farrell (1997).

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