BCS 311: Land and Environments of the Circumpolar World I

Module 7: Freshwater and Marine Ecosystems

Developed by

Stig Skreslet
Faculty of Biosciences and Aquaculture
University of Nordland
Bodø, Norway

Overview

Many environmental conditions are similar in freshwater and marine ecosystems. There are basic differences that have separated aquatic science into two different disciplines called **limnology** and **oceanography**. Limnologists work with the physical and chemical properties of freshwater and freshwater organisms, while oceanographers deal with the marine sciences known as geological, physical, chemical, biological and fisheries oceanography. Researchers tend to be specialists within particular disciplines characterized by the methods they apply to acquire data on the process or object they study. Aquatic ecology is a science that requires broad insight and understanding of a range of specialized knowledge.

Learning Objectives

Upon completion of this module, you should be able to:

1. Distinguish between fresh, brackish and salt waters on the basis of the physical and chemical properties of water.
2. Compare and contrast the circulation of water in lakes, estuaries, coastal waters and open ocean.
3. Describe in general terms ecological similarities and differences between freshwater and marine biological systems.
4. Conceptualize general pathways for the transfer and transformation of energy and matter from autotrophs to higher trophic levels in freshwater and marine ecosystems.
5. Compare and contrast the influence of bottom up and top down controls on ecosystem functions.
6. Describe the impacts of human harvesting activities on aquatic ecosystem structure.

Required Readings (including web sites)

BCS 311 Module 5. Ecological Principles.

CAFF. 2001. Rivers, Lakes and Wetlands. *In:* Arctic Flora and Fauna, Status and Conservation, Akuyeri, pp. 163-182. http://arcticportal.org/arctic-council/working-groups/caff-document-library/arctic-flora-and-fauna/

CAFF. 2001. The Ocean and Seas. *In:* Arctic Flora and Fauna, Status and Conservation, Akuyeri, pp. 183-210. http://arcticportal.org/arctic-council/working-groups/caff-document-library/arctic-flora-and-fauna/

Key Terms and Concepts

- Anadromous
- Benthos
- Bottom Up Control
- Catadromous
- Convergence Front
- Diadromous
- Diurnal Migration
- Estuarine Circulation
- Eutrophication
- Global Thermohaline Circulation
- Halocline
- Halophytes
- Marginal Ice Zone
- Nekton
- Pelagic
- Plankton
- Phototaxis
- Pycnocline
- Sigma-t (density)
- Subarctic Transition Zone
- Sympagic
- Thermocline
- Top Down Control

Learning Material

Introduction

This module examines general concepts of aquatic ecology and applies them in ways relevant to the understanding of aquatic ecosystems in the circumpolar North. The Arctic Ocean is not considered one of the world's oceans. Rather, it is considered part of a mediterranean sea enclosed between the North American and Eurasian continents. Many oceanographers call it the Arctic Mediterranean. It is the recipient of considerable amounts of freshwater from the Arctic regions of two continents that have many common limnological features (Figure 7.1). To understand this module you must know the terms and principles presented in Module 5.

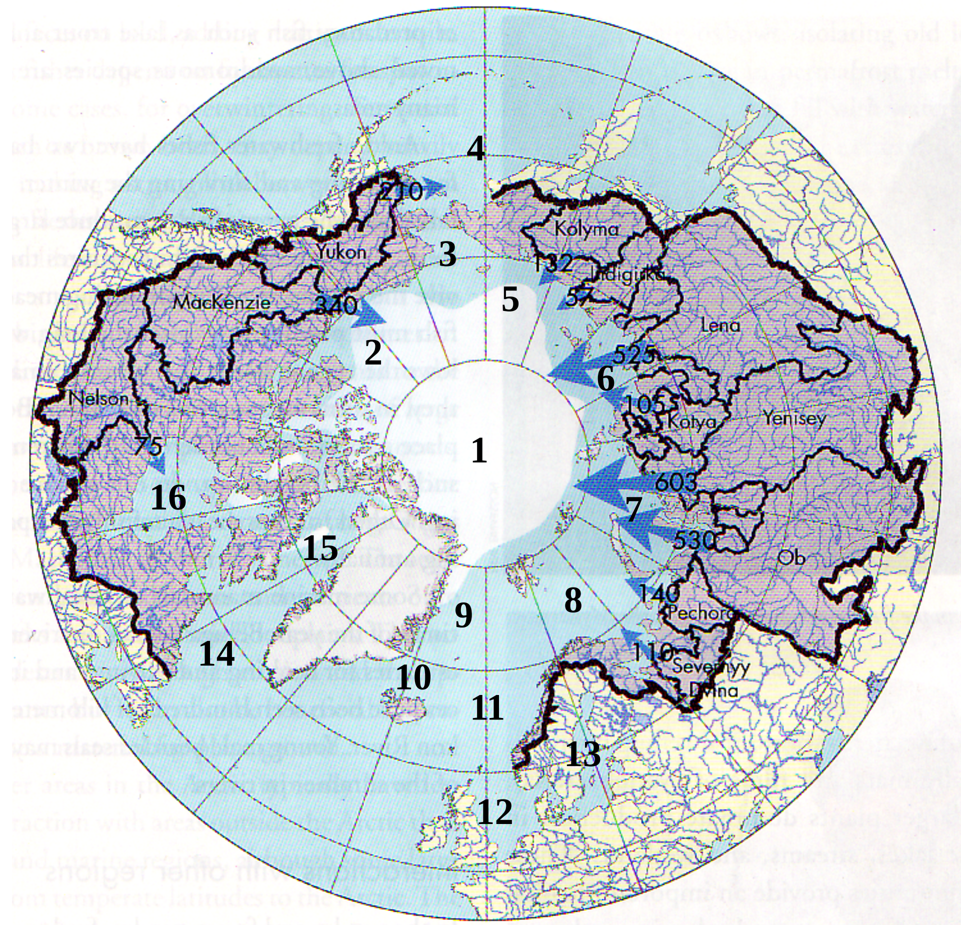

Figure 7.1. The Arctic (Mediterranean) Ocean with continental catchment areas that discharge freshwater into its seas. 1) Arctic Ocean. 2) Beaufort Sea. 3) Chukchi Sea. 4) Bering Sea. 5) East Siberian Sea. 6) Laptev Sea. 7) Kara Sea. 8) Barents Sea. 9) Greenland Sea. 10) Icelandic Sea. 11) Norwegian Sea. 12) North Sea. 13) Baltic Sea. 14) Labrador Sea. 15) Baffin Bay. 16) Hudson Bay. (Map by CAFF)

7.1 Abiotic Components in Aquatic Ecosystems

Physical Properties of Water

The water molecule, H_2O, consists of two hydrogen (H) atoms and one oxygen (O) atom held together by strong chemical bonding caused by the negative charge of the oxygen atom and the positive charge of the hydrogen atom. The hydrogen atoms form an angle of 104.5^o on either side of the oxygen atom (Figure 7.2) giving the molecule a negatively charged side and a positively charged side. This polarity allows water molecules to attract each other. The positive (hydrogen) side of one molecule attracts the negative (oxygen) side of another molecule. Bonding between water molecules is known as hydrogen bonding.

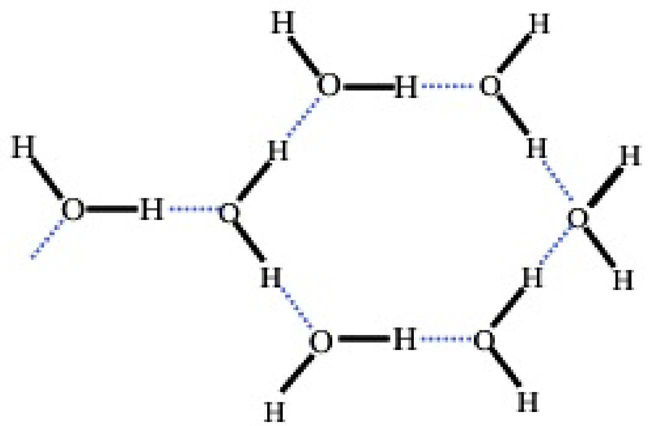

Figure 7.2. A cluster of water molecules held together by weak hydrogen bonds (broken blue lines).

Physical states of matter are represented by solids, liquids and gases. The solid phase of water is represented by snow and ice. The liquid phase of water is represented by freshwater and seawater. The gas phase of water is represented by water vapour, a powerful greenhouse gas (see Module 2). For water to change from one physical state to another, heat energy must be absorbed from or released into the environment. The quantity of heat must be sufficient to affect the strength of the hydrogen bonds between water molecules.

The quantity of heat required to transform snow and ice into liquid water is known as the **latent heat of melting** and consumes 80 calories (375 Joules) of heat per gram of ice. Some hydrogen bonds break when heat is supplied and this causes the ice to melt. Adding more heat increases the number of broken hydrogen bonds until at 4^{o}C freshwater attains its maximum density. When more heat is added water molecules become increasingly excited and the quantity of broken hydrogen bonds increases. The quantity of heat required to transform liquid water into water vapour is known as the **latent heat of vaporization** and consumes 540 calories (2259 Joules) of heat per gram of water. Water becomes less dense as its temperature increases until all hydrogen bonds are broken and the water vaporizes.

Chemical Properties of Water

Seawater is a solution of dissolved minerals consisting of ions with positive or negative electrical charges. The most common ions in seawater are illustrated in Table 7.1.

Table 7.1. The most common chemical constituents in seawater constituting 99.28% of the total amount of dissolved solids at any salinity.

Ion	Chemical Symbol	Percentage by Weight
Chloride	Cl^-	55.04
Sodium	Na^+	30.61
Sulphate	SO_4^{2-}	7.68
Magnesium	Mg^{2+}	3.69
Calcium	Ca^{2+}	1.16
Potassium	K^+	1.10

The electrical charges of ions make them adhere to water molecules and interfere with hydrogen bonding. The density of seawater increases steadily as its temperature decreases below 0^{o}C without freezing. Ions dissolved in seawater create the effect known as **freezing point depression** such that seawater freezes at -1.9^{o}C at its maximum density.

Seawater that freezes will build perfect hexagonal ice crystals squeezing the dissolved minerals into pockets of highly concentrated brine**.** The dense brine is eventually lost by drainage through tiny channels in the sea ice into the seawater below. This is why multi-year sea ice can be melted and used for drinking water.

Droplets of seawater and salt particles suspended in the air during vigorous storms are called **aerosols** and have important consequences when they are washed out by rain or snow over a coastal landscape. Saline precipitation contributes to the chemical weathering of rocks releasing minerals such as sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe) and phosphorus (P) into lakes and rivers. These dissolved minerals are eventually returned to the ocean by surface runoff from land. The quantity of marine aerosols decreases with altitude and distance from the coast and is seldom noticeable in inland watercourses. There may be considerable differences in the chemical quality of coastal and inland freshwater systems (Figure 7.3).

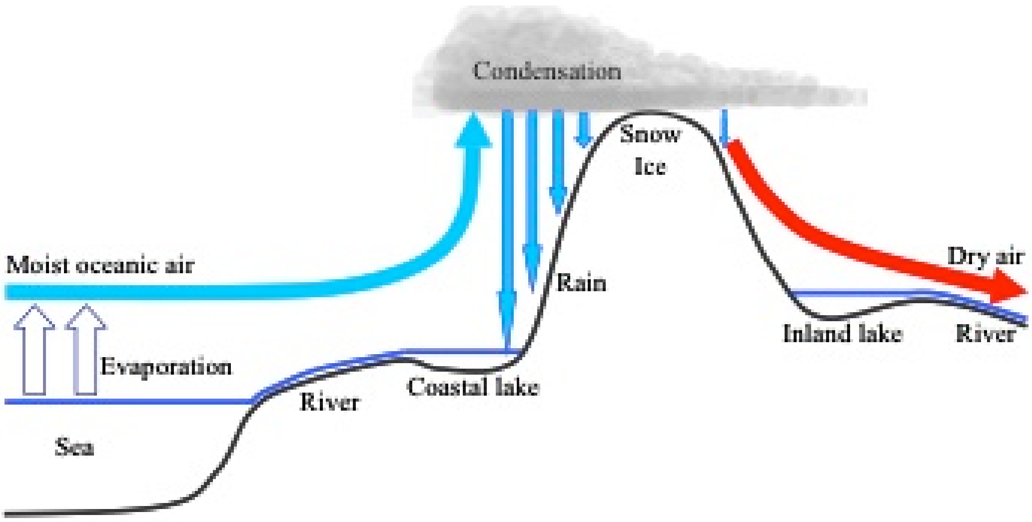

Figure 7.3. Marine aerosols are transferred from the ocean over land where precipitation delivers these saline materials to lakes and rivers. The precipitation illustrated in this figure on the windward side of a mountain barrier is generated by **orographic uplift**. Note the flow of dry air on the leeward side of the mountain barrier creating a **rain shadow** effect. Chemical weathering of rocks is facilitated by the deposition of these saline materials in precipitation, releasing dissolved minerals into lakes and rivers to be returned to the oceans in surface runoff from the land.

Precipitation is naturally rich in dissolved carbon dioxide (CO_2) making rainwater acidic. Limestone ($CaCO_3$), a common sedimentary rock exposed at the Earth's surface, is easily eroded by acidic water to produce dissolved calcium (Ca^{2+}) and carbonate (CO_3^{2-}). Lake water holding abundant dissolved calcium, known as "hard" water, helps organisms regulate the salt balance of their bodies. Dissolved carbonate reacts with water molecules to maintain freshwater at a neutral pH that allows for high biodiversity in limestone lakes.

Humic matter consists of organic molecules left over when decomposers have finished consuming detritus. Dissolved humic matter is especially abundant in peat bogs turning the water brown and acidic and excluding many species that reduce the bog biota's biodiversity.

Dissolved iron produced by the chemical weathering of rock minerals is an important constituent in the respiratory processes in all cells. Dissolved iron is kept in solution in freshwater, but combines with humic matter in seawater to form aggregates that sink to the sea floor. That is why oceanic areas far from continents have little autotrophic production but bloom vigorously if iron is added in scientific experiments and when they receive dust carried by winds from continental deserts (e.g. Harmattan winds that blow westward across the Sahara desert of northern Africa and over the Gulf of Guinea).

Precipitation may contain nitrate (NO_3^-) produced by lightning in the atmosphere but contains no phosphate (PO_4^{3-}), a major nutrient present in many cell components. Aquatic producers do not consume all available nitrate which generates a surplus delivered by rivers into the sea. Terrestrial plant communities conserve phosphate by storing it in soil preventing phosphate from being leached into groundwater, which flows into rivers. River water is poor in dissolved phosphate, which is a limiting factor for the growth of freshwater plants and algae. Phosphate is conserved in aquatic environments when organic matter accumulates in bottom sediments of freshwater lakes and bogs. Deep-sea basins are also immense storage tanks for phosphate-rich seawater. Phosphate is released into water by decomposers and used by aquatic producers. In ocean basins dissolved phosphate is brought to the sea surface by turbulent mixing and in this environment it represents a surplus nutrient compared to nitrate. Nitrate is more limiting to the growth of marine algae than phosphate. However, the N:P ratio changes with the salinity gradient from river mouths to open ocean making phosphate limiting near the river and nitrogen limiting towards open sea. Phosphate input from households to lakes, rivers and nearshore marine environments causes **eutrophication**, meaning the growth of aquatic plants and algae exceeds natural production.

Learning Activity 1

Perform a short literature search to discover examples of eutrophication of aquatic habitats, commonly identified by prolific algae blooms and fish kills, in the circumpolar North. Is eutrophication more likely to occur in habitats situated within or close to urban as opposed to rural landscapes?

Classification of Water According to Salinity

Dissolved minerals in river discharge have contributed to the salinity of oceans since time immemorial. Volcanic eruptions on land and on the sea floor have contributed other chemicals such as chlorine (Cl) and sulfur (S) resulting in the salinity we experience today. Normal seawater has a salt content that is 3.5 percent of the weight of seawater, meaning 1 kg of seawater will yield 35 g of salt if all the water evaporates. The salt content of seawater is expressed as a quantity measured in **practical salinity units**, **psu**, which is equivalent to the salinity unit expressed as parts per thousand ($S^0/_{00}$) presented in older scientific texts.

The salinity of seawater usually varies within the range of 30 – 40 psu. The value of 30 psu is often used to distinguish oceanic water from coastal water containing river water. The term **brackish water** is widely used to describe a mixture of seawater and freshwater with salinity in the 0.5 – 30 psu range which normally occurs in marine surface waters near river outlets and where sea ice melts. The salinity of freshwater is lower than 0.5 psu.

7.2 Water Circulation

Freshwater

Much of the freshwater that drains from Arctic landscapes is meltwater that flows over frozen ground into small streams that merge into rivers. As topsoil thaws the water seeps into it and contributes to groundwater reservoirs accumulated in porous sediments (Figure 7.4). Where permafrost occurs meltwater accumulates in shallow groundwater reservoirs within the active layer that contribute to the development of wetlands (Figure 7.4). Groundwater flow supplies water to ponds, lakes and streams (Figure 7.4). Ponds are small freshwater basins and frequently have no inlet or outlet other than occasional diffuse surface floods and seepage of groundwater into and out of its basin. Some ponds are highly seasonal, only existing when river floods raise the groundwater level and feed water into depressions in the surrounding landscape. Lakes have surface areas larger than two hectares (20,000 m^2) and are typically drained by a distinct outlet stream. Man-made dams store water in artificial reservoirs for various uses, notably hydroelectric power generation.

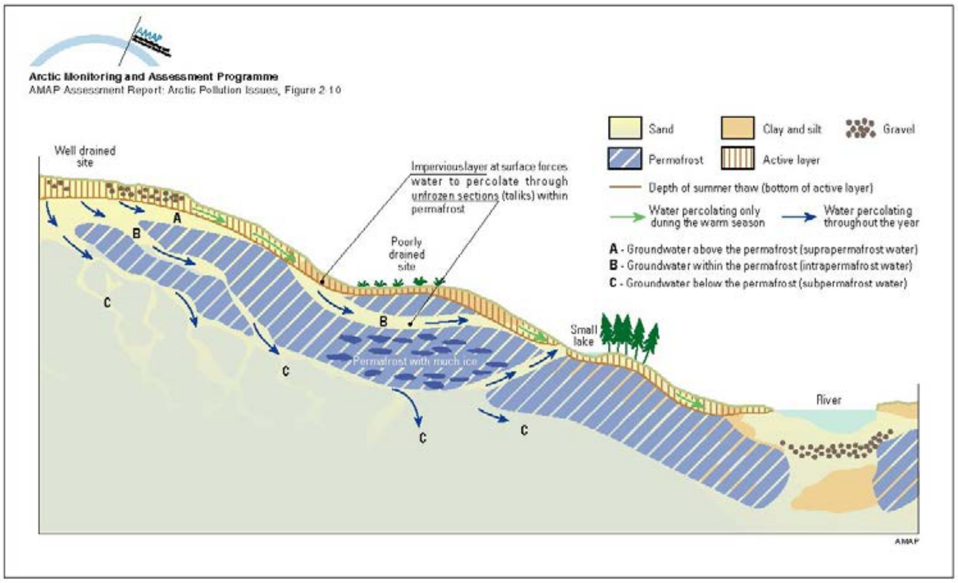

Figure 7.4. Precipitation received at the ground surface may flow across the landscape as runoff or infiltrate the soil to contribute to the groundwater reservoir. Surface runoff and the movement of groundwater (base flow) regulate the level of free water surfaces in streams, lakes, ponds and wetlands.

Source: Linell, K.A. and J.C.F. Tedrow, 1981. Soil and permafrost surveys in the Arctic. Clarendon Press, Oxford, 279p. Cartographer/Designer Graphical production: Philippe Rekacewicz and Emmanuelle Bournay (GRID-Arendal). Appears in [AMAP Assessment Report: Arctic Pollution Issues] published in 1998.

Gravity causes water with a high density to accumulate at the bottom of a basin while lighter water floats on top. At northern latitudes the bottom temperature of a deep lake is usually 4°C because at this temperature freshwater is at its maximum density. The bottom water may become anoxic and even contain hydrogen sulfide (H_2S) if allowed to remain isolated from air in response to the depletion of oxygen by biota.

Solar heating during summer decreases the density of surface water and winds may establish a mixed upper layer with homogeneous temperature through turbulent mixing. Less dense water floats on top of a cooler layer, which establishes a two-layered stratification. The layers are separated by a **thermocline,** the temperature gradient between the upper and lower layer (Figure 7.5).

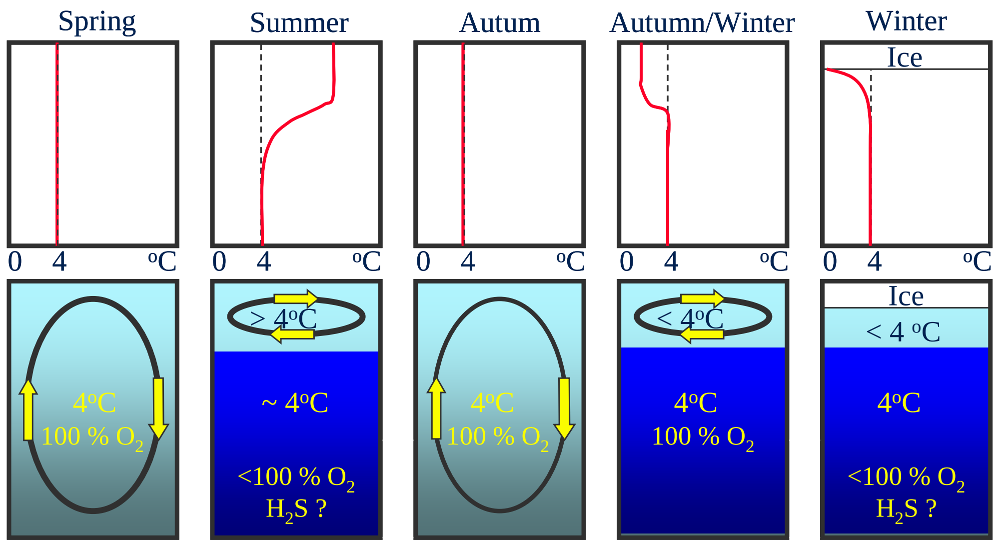

Figure 7.5. Seasonal variation in mixing and stratification of northern lakes. Red curves are typical temperature profiles.

During autumn when solar radiation decreases lake surfaces lose more heat energy than solar radiation can replace. Cooling increases the density of the wind-mixed layer, until the temperature has dropped to 4^{o}C and the density is the same from the surface to the bottom of the lake. This period known as **autumn overturn** is when the whole water body circulates. Water saturated with oxygen is mixed with bottom water and removes hydrogen sulfide if present. As surface cooling continues below 4^{o}C water with lower density forms a new upper layer eventually forming an ice cover at 0^{o}C. Considering the length of time Arctic lakes are isolated from the atmosphere by ice some lakes may become anoxic at the bottom. When the ice breaks and the surface water is heated to 4^{o}C the water column becomes aerated, establishing conditions for **spring overturn**.

Estuaries

An **estuary** is a partly enclosed coastal body of water with one or more rivers flowing into it, and with a free connection to the open sea. River discharge into the sea generates friction and turbulence in the **halocline**, the transition zone between freshwater and seawater, where mixing results in a layer of brackish water that flows away from the river outlet while more salt is added from below (Figure 7.6). The surface flow causes a loss of brackish water that is replaced by a **compensation current** transporting seawater flowing in the opposite direction underneath the brackish layer: this is called **estuarine circulation**.

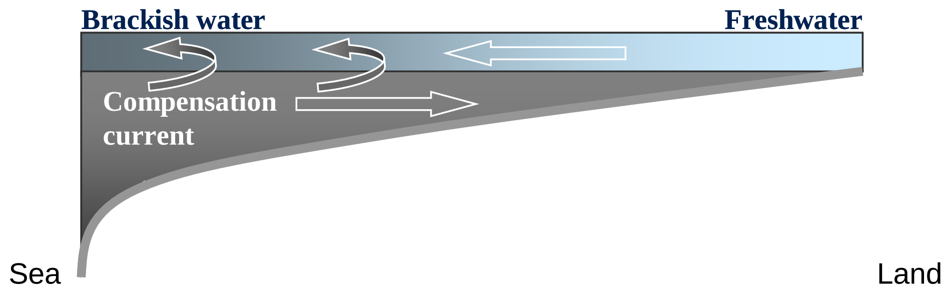

Figure 7.6. Estuarine circulation driven by river discharge of freshwater that mixes with saline water imported by the compensation current.

Fjords are estuaries by definition and are characterized by their glacial origin (see Module 4). Typical fjords are U-shaped troughs excavated by glaciers and subsequently flooded by post-glacial sea-level rise. Fjords in Greenland, the Canadian Arctic Archipelago and Alaska are commonly associated with active glaciers flowing through coastal mountains. Many fjords have a shallow **sill** at the entrance that separates a deeper basin from deep ocean waters outside (Figure 7.7) and some have a series of deep basins subdivided by several sills. They may be formed by either glacial moraines or hard, resistant bedrock. Open fjords have no sills, but may extend as troughs eroded through rocks and sediments that compose the continental shelf outside the fjord.

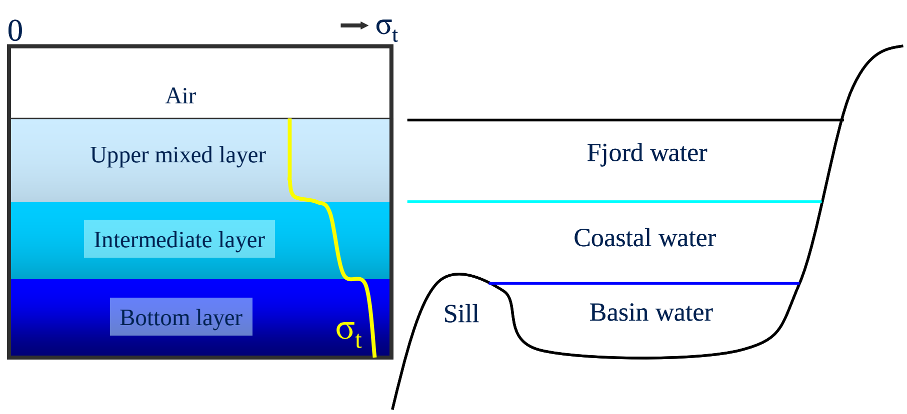

Figure 7.7. General model for stratification of marine water bodies (left), exemplified by a typical fjord (right). The yellow curve shows two pycnoclines indicating interfaces where the density of seawater (σ_t) changes rapidly with depth.

During summer a typical fjord has a three-layered water column with the heaviest water at the bottom and the lightest water at the surface (Figure 7.7). The **density (σ_t)** of seawater is calculated by measuring salinity and temperature. Density increases with increasing salinity and decreasing temperature. A salinity change of 1 psu corresponds to roughly 10^{o}C change in temperature meaning thermal stratification is only significant when a water layer with uniform salinity accumulates solar heat at the surface. The density gradient between two uniform layers with different densities is known as a **pycnocline**.

Learning Activity 2

Explore the influence of salinity on water density. Use the information related to density (sigma-t) in the Glossary of Terms to assist you in calculating the sigma-t value of the following water masses: Polar Water (density = 1.02600 g/cm^3); Atlantic Water (density = 1.02790 g/cm^3) and Arctic Bottom Water (density = 1.02809 g/cm^3).

The summer stratification of Arctic fjords is mainly due to meltwater input either from river discharge or melting glaciers and sea ice. Estuarine circulation occurs in the upper fjord water. Turbulent mixing forced by river flow, wind stress and tidal currents makes surface salinity increase with distance from the freshwater source. The intermediate layer exchanges water with shelf waters outside the fjord, back and forth across the sill, due to tidal currents and changes in atmospheric pressure. The basin water is a saline bottom layer that would become anoxic if allowed to remain undisturbed. Basin water is affected by tidal movements in the layer above and mixes with less saline water that gradually lowers the basin water density and facilitates oxygenation.

Stratification may be very different during winter because the freshwater supply is minimal and cooling increases the density of surface water. The conditions favour deep mixing by winds and tidal forcing establishing an upper mixed layer that may be several hundred meters deep. Shallower fjords with even shallower sills may be thoroughly mixed to the bottom of their basins and become very cold. Deeper fjords may have basin water that responds only slowly to external forcing, but cannot completely resist tidal mixing that decreases its salinity and density. Basin water will sooner or later be exchanged when heavier water sinks into the basin and lifts the old basin water to levels where it may leave the fjord. The new basin water may be saltier coastal shelf water that intrudes over the sill. Fjords in the High Arctic may produce their own basin water. Local sea ice formation releases brine and makes the water underneath heavy enough to sink to the bottom. This is why High Arctic basins may hold deep water with sub-zero temperatures and extraordinarily high salinities (i.e., > 36 psu). Latitude, sea surface area, sill and basin depths, local tidal range and microclimate are variables that combine to generate a range of Arctic fjord environments with individual blends of common and unique characteristics.

Open Seas

The flow of brackish water in an estuary in the northern hemisphere is deflected towards the right of its direction of motion inside the estuary and forms a tongue-like plume that may be distinguished from surrounding surface waters by its lower salinity when it flows into more open ocean waters. The deflection to the right is due to the **Coriolis force** generated by the spinning of the Earth around its axis. The identity of a plume from a single estuary is quickly lost when coasts are indented with many fjords and rivers. Different plumes merge due to tidal mixing and form a coastal current that flows to the right along the coast.

The outer margin of a coastal current meets and exchanges water with shelf water in a dynamic mixing zone known as a **convergence front**. The mixed water flows away from the front at the surface while the more saline water from outside sinks below the front. The surface level of a coastal current is slightly elevated compared to the shelf water outside causing gravity to force a fast jet current running along its outer margin (Figure 7.8). Tidal currents interact with the jet and generate counterclockwise (cyclonic) and clockwise (anti-cyclonic) eddies where water rises and sinks respectively adding inorganic nutrients vital to primary production in the upper mixed layer. Frontal jets are associated with sloping bottom topography and are stable oceanographic features important to the transportation of fish larvae and other zooplankton between different habitats. Jets that run along continental margins are generated by the convergence front between shelf water and oceanic water of the deep sea, and are frequently called **shelf break jets**.

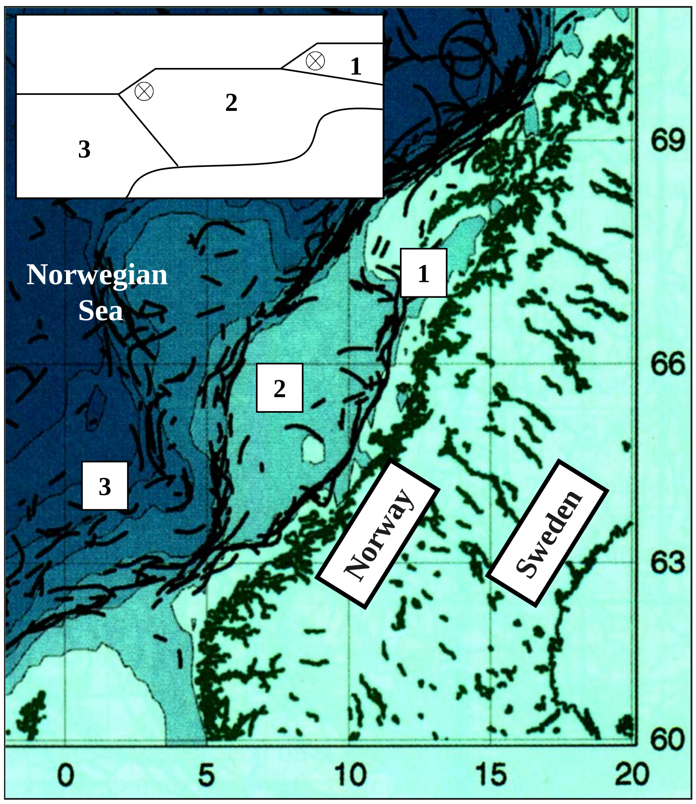

Figure 7.8. Jet currents along the Norwegian fjord coast. Map shows the trajectories of Argo buoys (in black) drifting faster than 40 cm/s (from Poulin *et al*., 1996). Circled crosses in the inserted sketch identify jet currents running northwards. One jet occurs in the convergence front between 1) the Norwegian Coastal Current (NCC) and 2) the Mid-Norwegian shelf water. The continental shelf break jet occurs where the shelf water converges with Atlantic water (3). It merges with the NCC jet where the continental shelf is narrow.

Freshwater discharged into the Arctic Ocean from large rivers in Eurasia and North America generates brackish plumes of polar water that flow eastward over the continental shelves due to the Coriolis effect (Figure 7.9). Some polar water flows between Greenland and Canada into the Labrador Sea or may circulate to the Beaufort Gyre where it is retained and forms masses of multi-year ice. Most surface water and drift ice is transported by the Trans-Polar Drift past the North Pole and through Fram Strait between Greenland and Svalbard where transport becomes the East Greenland Current bound for the Labrador Sea.

Seawater lost by surface currents from the Arctic Ocean is compensated by the North Atlantic Drift, a current of warmer and more saline water flowing northward from the Atlantic Ocean, which is forced to sink north of Svalbard and forms an intermediate layer in the Arctic Ocean at a depth of 200 – 900 m (Figure 7.9). The Coriolis effect deflects the current eastward forming Atlantic slope water along the Siberian continental shelf as far as the East Siberian Sea. Below, to a maximum depth of about 4,200 m, rests Arctic Bottom water, a mixture of Atlantic water and cold brine formed during the freezing of sea ice at the surface that circulates slowly counterclockwise within the Arctic Ocean basin. Arctic Bottom water fills the deep basins of the Greenland and Norwegian Seas at depths of 1000 m to more than 3000 m.

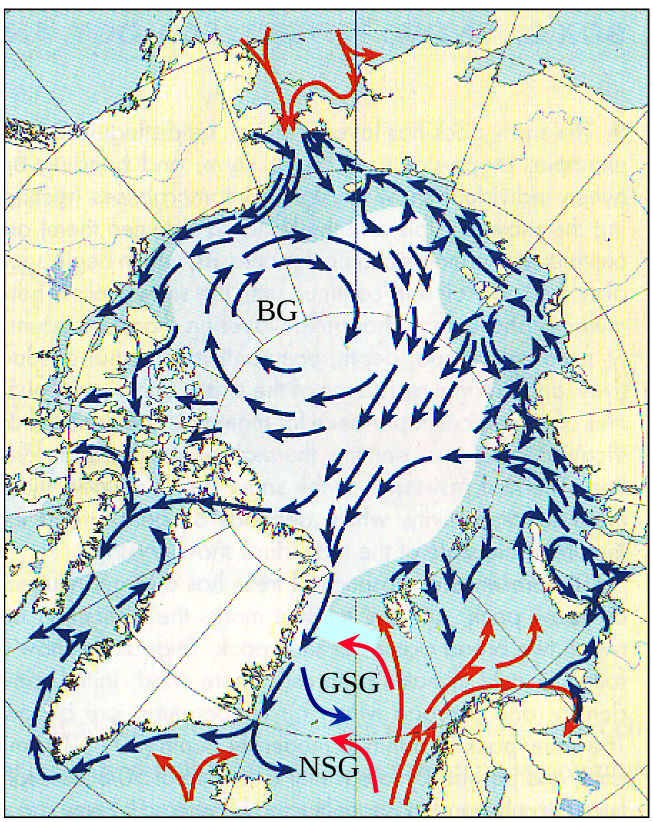

Figure 7.9. Surface currents in the Arctic Ocean (modified from the Norwegian Institute of Marine Research). Red arrows indicate the inflow of warm, saline oceanic water. Blue arrows indicate the flows of cold, low salinity Polar water. The light blue area around the North Pole represents the extent of multi-year sea ice during summer. BG: Beaufort Gyre. GSG: Greenland Sea Gyre. NSG: Norwegian Sea Gyre. Coastal currents are not shown.

Of particular interest is the Greenland Sea Gyre where cooling surface water sinks to a depth of about 600 m giving rise to the **Global Thermohaline Circulation** (Figure 7.10). Deep water from the Greenland Sea flows southward in the Norwegian Sea and sinks to the bottom of the North Atlantic Basin, flowing then into the Southern Ocean and circulating around Antarctica before entering the Indian and Pacific Oceans where it is brought to the surface by vertical mixing. Surface currents return the water to the southern Atlantic Ocean where it is transported across the Equator and into the Gulf of Mexico where it becomes the Gulf Stream. The Gulf Stream supplies warm and salt water across the Atlantic and into the Norwegian Sea closing the cycle as the Atlantic water submerges into the Arctic Ocean.

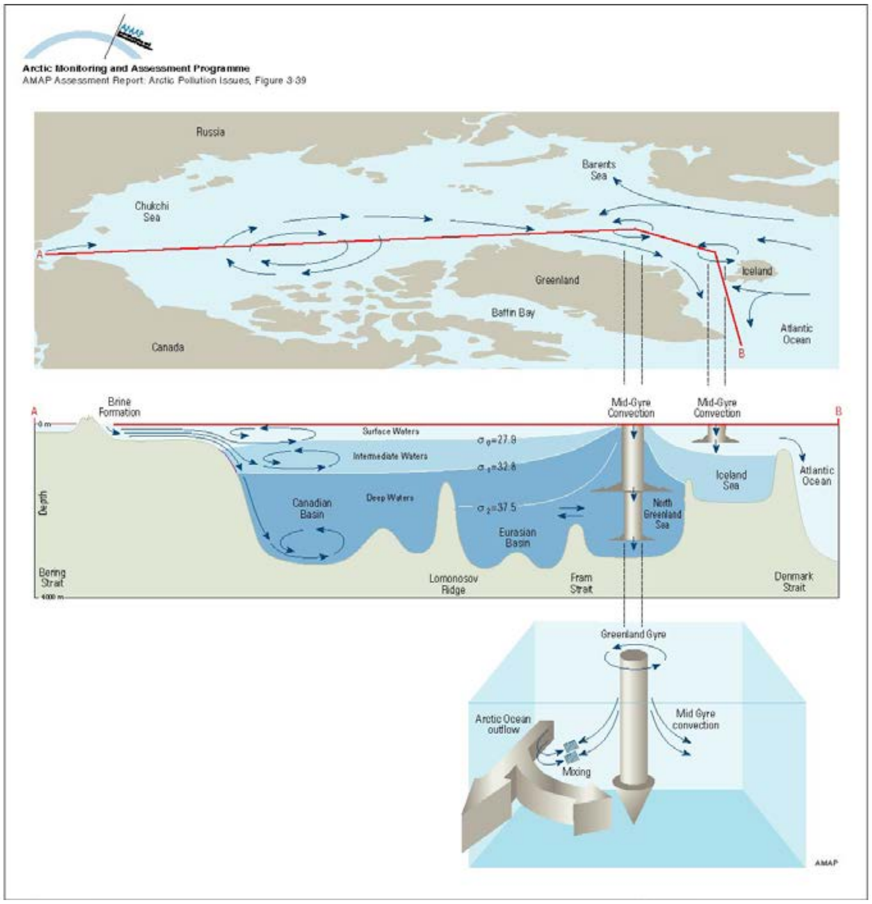

Figure 7.10. The Global Thermohaline Circulation is forced by the sinking of Greenland Sea Deep Water and involves all of the world oceans. Notice the uneven bottom topography of submarine ridges and basins of the Arctic Ocean, especially the shallow Bering Sea that blocks deep circulation to the Pacific Ocean.

Source: After Aagaard, K., J.H. Swift and E.C. Carmack, 1985. Thermohaline circulation in the Arctic Mediterranean seas. J. Geophys. Res. 90: 4833-4846. Cartographer/Designer Graphical production: Philippe Rekacewicz and Emmanuelle Bournay (GRID-Arendal). Appears in [AMAP Assessment Report: Arctic Pollution Issues] published in 1998.

7.3 Biotic Components of Aquatic Ecosystems

Common Terms and Conditions

Aquatic life forms are known as **benthic** when they live on or within bottom sediments and **pelagic** when they can move freely in water masses above the bottom. **Benthos** is a collective term for all benthic organisms. Life forms associated with floating sea ice are known as **sympagic** animals. **Plankton** is a term for all pelagic organisms that cannot resist transportation by currents and includes everything from bacteria to jellyfish more than 1 m in diameter. **Nekton** are pelagic animals capable of horizontal migration between chosen habitats within their population system. Planktonic and nektonic organisms perform vertical migrations to stay at a preferred light intensity. The behavior is called **phototaxis** and causes the animals to move towards the surface at night and down again during the day, which is known as diurnal migration. Nekton are **planktivorous** when feeding on plankton and **piscivorous** when feeding on fish.

A similarity in lakes and the sea is that solar radiation penetration in water is limited. Aquatic plants and algae grow in the **euphotic zone** where there is sufficient light for photosynthesis. Vertical penetration of solar radiation in water varies with the amount of suspended particles. Surfaces of glacial lakes appear whitish because high concentrations of suspended sediments reflect most of the light. Virtually no energy remains for photosynthesis below the surface. Clear alpine lakes and oceanic water let all light penetrate deeper, but yellow and red light are rapidly absorbed by water. Blue light has more energy and penetrates much deeper. Some blue light reflected by water molecules radiates back to the surface causing clear water to appear blue. Clear water allows photosynthesis to occur in the upper 50 m depth range and sometimes deeper. Many consumers that feed on producers within the euphotic zone migrate vertically at night from depths where they hide in darkness during day. This is also the case with predators that hunt herbivores.

Pelagic Components

Phytoplankton is the flora of planktonic micro-algae that grows in the sea, lakes and rivers (Figure 7.11). Some, e.g., planktonic diatoms, are whirled about in the upper mixed layer of lakes and oceans. Micro-algae cannot multiply if they are mixed below their compensation depth causing photosynthesis to be lower than respiration. Some micro-algae only multiply if the mixed layer remains fertilized by plant nutrients and population growth stops when the least abundant nutrient becomes a limiting factor. Other micro-algae can regulate their buoyancy and float in a pycnocline where they optimize their growth in relation to light from above and nutrients from below. Flagellates move by flagella and can position themselves at optimal depths.

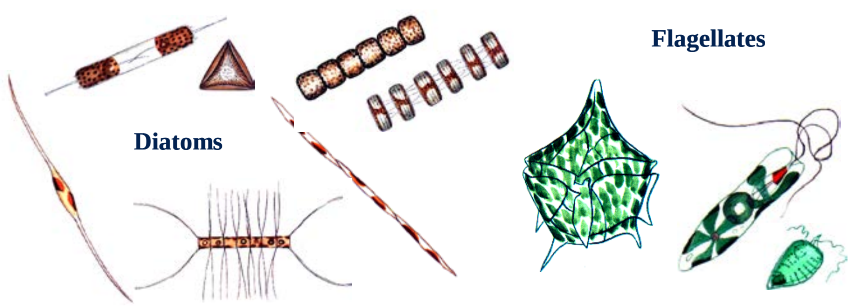

Figure 7.11. Two main groups of phytoplankton. All are unicellular, but some diatoms form long chains that remain unbroken in calm water. Flagellates have whip-like flagellae for locomotion.

Sympagic biota belong to the pelagic biome of the polar sea ice, although its producers have much in common with benthic micro-algae. Some ice algae may inhabit freshwater ponds on the ice or tiny channels inside the ice, while marine species stick together in long threads and thick mats attached to the underside of the ice. Some join the phytoplankton and continue production in ice-free water when their sympagic habitat melts.

Zooplankton are the fauna of planktonic animals in freshwater and marine ecosystems (Figure 7.12). First order consumers that feed on phytoplankton are mainly small crustaceans. Cladocerans constitute a large group of species that dominate in lakes and a few marine species are important in coastal waters. A group of copepods dominate the consumption of marine phytoplankton and contains some important freshwater species. Some mysid shrimps are nearshore phytoplankton consumers that move up and down estuaries with the tide. One species lives in brackish habitats along Arctic coasts and are present as an Arctic relict in lakes. Many other mysids are important detritus feeders in deep marine basins.

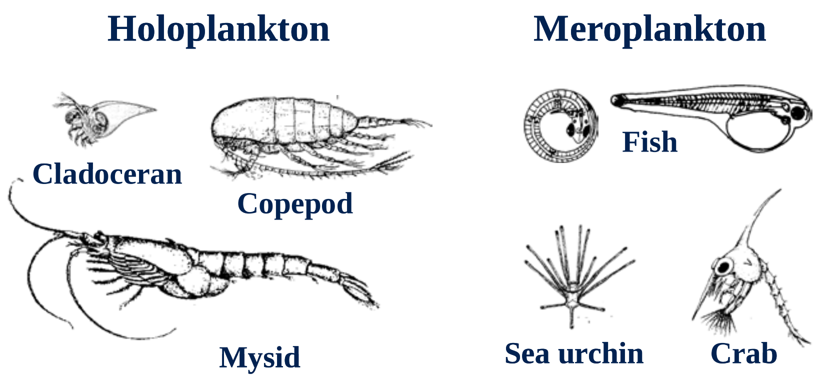

Figure 7.12. Zooplankton consists of animals spending all their life cycle as plankton and other animals that spend only parts of their life cycle as plankton, mostly as eggs and larvae.

Most fish that reproduce in Arctic seawater cannot live in freshwater. Many freshwater fish can live in brackish water at salinities up to about 7 psu. This is the case in the most brackish parts of the Baltic Sea and many large river deltas in Arctic seas. Many freshwater fish form pelagic schools that feed on plankton in lakes and estuaries. Salmon migrate into the sea and turn into a nektonic predator on plankton and smaller nekton.

Nekton range from small plankton-feeding fish to large fish-eating seals and whales. The **epipelagic zone** extending from the ocean surface to a depth of 200 m is the feeding habitat of fish like herring and capelin, and is roughly equivalent with the upper mixed layer of ice-free Arctic waters during winter. Nektonic fish and squid and large predatory plankton inhabit the darker mesopelagic zone between 200 and 1000 m. These organisms make fast diurnal migrations feeding in the epipelagic zone at night and migrating down to hide in darkness during the day. The **bathypelagic zone,** below 1000 m depth, contains Arctic deepwater characterized by sub-zero temperatures. Bathypelagic animals only see **bioluminescence,** which is light produced to detect or trick prey, confuse predators or attract mates. Bioluminescent algae and animals are also frequently observed at night near the ocean surface.

Benthic Components

Algae and vascular plants are the benthic primary producers in the upper part of the euphotic zone. A slimy film of motile diatoms that occupy hard and soft bottoms near the water surface and the spray zone of waves also perform some photosynthesis. These motile diatoms are food for a variety of invertebrates like snails and other first order consumers. Deeper benthic biota depend on detritus falling from the euphotic zone.

Marshes of vascular plants dominate shallow freshwater bottom habitats sheltered from waves and running water in which fine-grained sediments and organic particles are deposited and form a soft mud. Roots and vascular systems of plants allow the uptake of nutrients released from decomposers living in the sediment. Much of the organic material in freshwater sediments originates from land, e.g., leaves falling at the end of their growth season. Mosses gradually extend their occupation of marsh fringes and prepare new ground for vascular plants, creating bogs that extend into lakes. Ponds may completely fill with peat over time and turn into a terrestrial biota with grasses, herbs and trees.

Coastal salt marshes develop in estuaries where low salinity allows some plants to grow in fine-grained sediments deposited by rivers. Such **halophytes** may tolerate high ambient salinity by shedding salts from their leaves. Plants produce seeds that may be consumed by birds and rodents performing a major ecological function by shaping habitats for other organisms. Epiphytic macro- and micro-algae grow on their stems and diatoms grow on the mud surface creating food for snails, worms and crustaceans. Leaves and stems of plants wither during autumn, fall down and form floating mats of wrack that may accumulate near the high-tide level. This organic detritus may form nesting places for birds or establish ponds of fresh or brackish water where insects reproduce and spend their juvenile life as larvae and pupae and are preyed upon by insectivorous birds and shrews. Marine phytoplankton transported by tides into salt marshes may be fed upon by bivalves and mysid shrimps and imported zooplankton may fall prey to small fish and other predators. Although the biodiversity of salt-marshes is low because of the harsh abiotic environment, their productivity is high making them important habitats for wildlife.

The only truly marine vascular plants belong to the genus *Zostera* that form **sea-grass** beds in shallow water, mostly in estuaries. These plants disappeared from Arctic Norway due to a disease that hit Europe early in the 20th century and are still rare. The sea-grass now seems to be declining in Hudson Bay (Canada), which may deprive many populations of animals of an important habitat.

Macro-algae are multicellular producers attached to a firm bottom substrate, other macro-algae or shell-bearing animals. They may be distinguished by their photosynthetic pigments into green, red and brown algae, which also indicate preferred habitats. Green algae prefer sheltered and permanently wet habitats with abundant light and nutrients. Red algae utilize blue light that penetrates deeply through water making many red algae prefer deep habitats or the shade of other algae. Brown algae are large and robust, resist wave action and many tolerate drying at low tide.

Macro-algae living in freshwater are mostly green, but some red and brown species occur. However, much of the production in lakes is by aquatic plants. Mosses have much in common with macro-algae, having no roots or vascular system. Mosses also absorb nutrients directly from water and some species are well adapted to form dense vegetation in Arctic lakes. Many mosses live in damp places on land.

Macro-algae are important producers along subarctic coasts. Seaweeds can form dense mats in intertidal and subtidal habitats to about 20 m depth and kelps can grow into subtidal forests to the same depth depending on the latitude and transparency of the seawater. Various species are adapted to particular environmental conditions, some tolerating longer periods of air exposure, frost and drought. This accounts for the depth zonation of benthic algae growing in belts parallel to the shoreline.

Kelp forests and seaweed belts are important habitats for many animals that seek a physically stable environment or hiding place from predators. Intertidal animals avoid solar heating during summer and heat loss during winter by staying under seaweeds at low tide. During high tide many consumers feed on the thin film of benthic diatoms while other consumers filter phytoplankton drifting through the vegetation canopy of macro-algae. Small fish dash from their protective habitat to prey on zooplankton drifting by and are themselves prey for larger fish, seabirds or seals.

Some species of sea urchins may be voracious grazers on macro-algae. Sea urchins have destroyed many Subarctic kelp forests due to ecological relations that are not fully understood. Few animals eat macro-algae directly because macro-algae produce anti-grazing toxins. However, much of this biomass is detoxified at the end of the growth season when fungi and bacteria decay large amounts of the algal biomass discarded each year. Waves and tidal currents break the detoxified remains into pieces and the fragments settle in places not disturbed by currents becoming digestible for detritus feeders and bacteria that finalize the decay into mineral nutrients.

Intertidal and subtidal algae characterize subarctic shores with moderate exposure to floating ice, but are absent where it is present throughout the year. Icebergs calving from glacier fronts move with tidal currents along the shore and scour away seaweed belts and kelp forests leaving a barren subtidal bottom. Sea ice forced by onshore winds and currents piles up in the intertidal zone and may prevent intertidal life from establishing on the shore. Many arctic shorelines develop an **ice-foot** in early winter, which gradually grows when the intertidal zone gets wet on high tide and freezes a new ice layer at each low-water tide. The ice-foot is completed when it fills the intertidal zone and establishes a vertical front as high as the local tidal range. Some intertidal animal species allow themselves to be trapped by the ice-foot and thus gain protection from sea ice scouring.These organisms contain anti-freeze molecules that prevent ice crystals from forming in their cells. Anti-freeze molecules are produced by a wide range of aquatic and terrestrial species exposed to supercooled water, ice cover or frosty air.

The endemic subtidal fauna typical of the High Arctic is mainly found in brackish waters along the Eurasian and North American continents. The fauna inhabits vast areas of soft bottom that develop where large rivers deposit sediment. Mollusks, polychaetes, brittlestars and crustaceans, including large isopods, are common organisms of the subtidal biota. Marine species with a wider geographic distribution exist farther north, where the shelf slopes into the more saline abyss of the Arctic Ocean. Atlantic water flowing eastward after entering the Arctic Ocean allows a benthic fauna of subarctic and boreal species to exist along the continental slope that borders the Kara, Laptev and East Siberian Seas. A similar situation exists where Pacific water flows through the Bering Strait and along the continental slope bordering the Beaufort Sea.

Deep basins of the Arctic Ocean and the Greenland and Norwegian Seas are inhabited by soft-bottom benthic faunas that experience sub-zero temperatures and feed on detritus sinking from higher water layers. Peculiar biotas have recently been discovered along the northernmost parts of the Atlantic Mid-Oceanic Ridge that runs from Iceland

and Jan Mayen Island into the Arctic Ocean where it forms the Gakkel Ridge. Seawater that fills cracks in rocks on the ocean floor is warmed by geothermal heat and absorbs sulfides before leaving the bottom through mineral pipes called **hydrothermal vents**. The hydrothermal vents are similar to those observed elsewhere in world oceans and are characterized by emission of sulfides utilized by autotrophic bacteria serving as food for specialized animals. Arctic hydrothermal vents seem to differ from those of warmer oceans by not having evolved specialized consumers.

7.4 Function of Aquatic Ecosystems

Synecological Relations

Aquatic organisms tend to occur in dense aggregations. Planktonic larvae of benthic animals may carefully test the bottom quality before they settle in a habitat were they may be stuck for life. They seek places that optimize their chances for survival and growth and many select places where their species are already abundant.

Strong winds generate surface motions resulting in counter-rotating **Langmuir cells** (Figure 7.13) that occur in lakes and at sea. They are recognized by stripes of floating debris and foam where two cells rotate toward each other. Vertical water movements organize and concentrate organisms according to their buoyancy or preferred vertical migration. The result is small-scale habitats where one kind of biota may exist close to another. Once the wind stops the organisms reorganize themselves in response to factors such as light, tidal mixing, intra-specific relations, inter-specific attraction and avoidance.

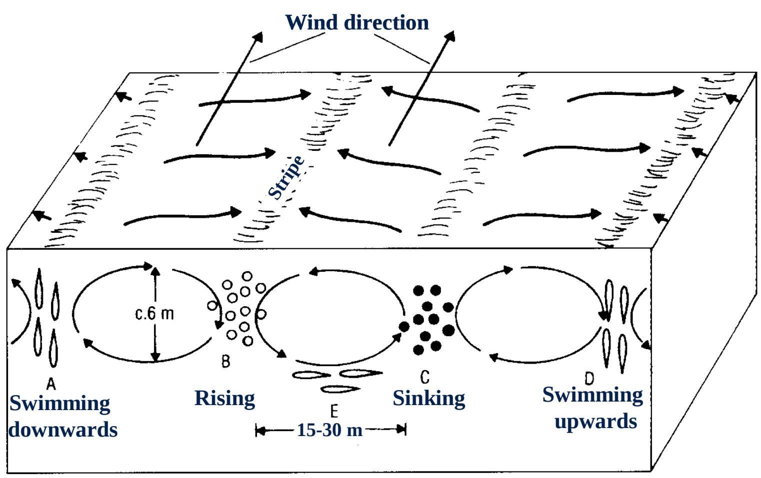

Figure 7.13. Wind-generated Langmuir cells sort plankton into separate biota. Vertical and horizontal dimensions in freshwater may be about 6 and 20m, respectively, but larger in more viscous seawater. Organisms that rise due to positive buoyancy or migrate towards the surface accumulate where water is circulated down. Negatively buoyant organisms that sink or swim down accumulate where water circulates up. Neutrally buoyant organisms are evenly dispersed while nekton may choose the appropriate aggregate of prey. A: Fish eggs, and flagellates and small krill with positive phototaxis. B: Sinking diatoms, and fish larvae and copepods with negative phototaxis. C: Foam and floating debris flow with the wind.

Voluntary aggregation is a tactic used by swarming zooplankton and schooling nekton. It may be related to reproduction, but also serves as a tactic to diminish predation. Organisms that do not aggregate create gradients in their abundance providing predators with a clue to the direction of optimal prey density. Aggregation eliminates these gradients and forces predators to search at random. Predators may cooperate in larger schools that scout for smaller schools or swarms of prey organisms. When members observe a patch of prey a signal goes from one animal to the next and the entire school rushes into harvest the prey. Voluntary aggregation is a behaviour exhibited by many pelagic species that combine simultaneous roles of being prey and predator.

Marine Food Webs

Subarctic production of macro-algae only occurs along coasts and to about 20 m depth in the clearest water. The vertical distribution of macro-algae is less in areas that receive suspended sediments from glaciers or rivers. Ice-algae produce biomass wherever there is sea ice, but their production is low because of limited solar radiation and shading from the ice. Most of the production is therefore due to phytoplankton and occurs in ice-free subarctic waters (Figure 7.14).

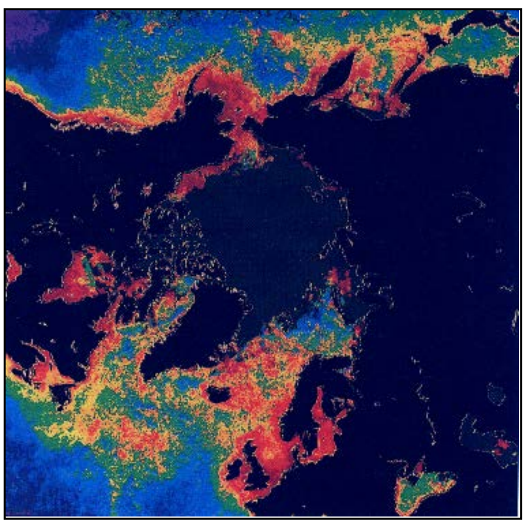

Figure 7.14. Average marine phytoplankton abundance in the Arctic Ocean, and the North Atlantic and North Pacific Oceans. Red: High concentrations. Blue: Low concentrations. Dark blue color in the Arctic Ocean is due to the presence sea ice and does not indicate the abundance of sympagic ice flora (Satellite imagery from NASA).

The population structure of marine phytoplankton is difficult to assess because many species are cosmopolitan and all move by currents. Some species are characteristic producers in coastal or oceanic biota. Others occur unexpectedly or unnoticed until they multiply into dominance for a short period and then disappear. Some become toxic and kill fish and other marine animals in one particular year and seldom or never again. Such toxic blooms are often called **red tides**, although only some toxic species cause seawater to be colored red.

Limiting factors for phytoplankton production are the availability of light and inorganic nutrients. Temperature is of less importance, which explains why phytoplankton production may be greater in higher rather than in lower latitudes. Warm surface temperatures indicate a stable mixed layer that obstructs turbulence bringing nutrients from below into the euphotic layer. Lack of nutrients may force phytoplankton to produce in the pycnocline below the sea surface where light and nutrients are sufficient for growth. Alternatively, stratification is necessary to keep micro-algae within the euphotic layer for a required number of hours per day. This is why production can only occur where pycnolines or the sea bottom prevents mixing deeper than a critical depth (Figure 7.15).

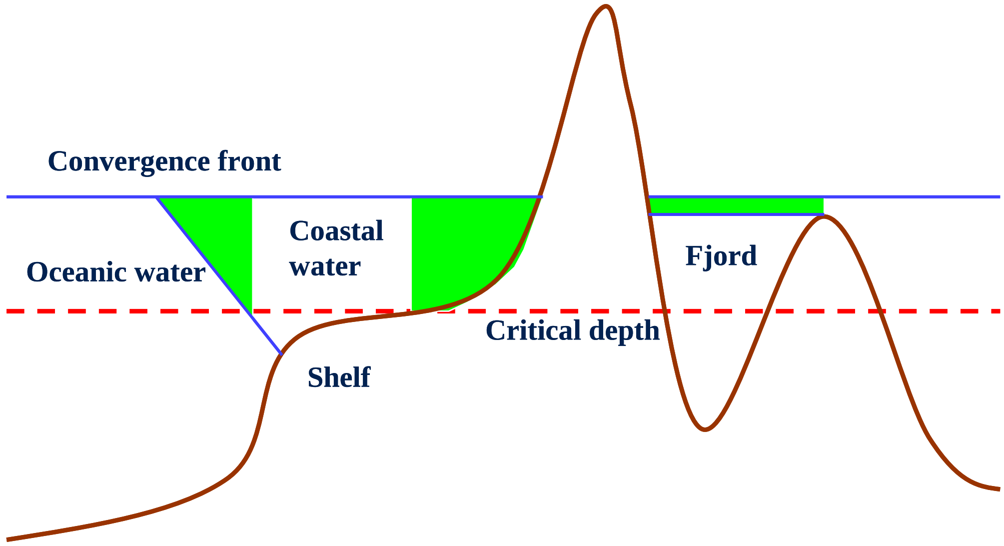

Figure 7.15. Phytoplankton production (green) occurs where pycnoclines (blue) or the sea bottom prevents mixing deeper than a critical depth (stippled red line) determined by water transparency and surface light intensity.

Phytoplankton growth in polar water occurs during summer but depends on vertical mixing during winter, which fertilizes the upper mixed layer with inorganic nutrients from below. In ice-free subarctic coastal waters a spring bloom starts at the vernal equinox (late March) when day-length exceeds 12 hours. The spring bloom is seeded by resting spores from shallow sediments and lasts a couple of weeks stopping when the shortage of nutrients becomes critical. However, estuarine circulation in fjords and tidal mixing in convergence fronts allows continued production throughout summer in pycnoclines where there is enough light from above and nutrients from below. An autumn bloom occurs in coastal waters when winter storms mix new nutrients into the euphotic zone and is terminated after the autumnal equinox when day-length gets shorter than 12 hours.

In oceanic water phytoplankton cannot grow when the mixed layer is deeper than the critical depth for primary production. Production usually starts when solar radiation causes thermal stratification, which is why oceanic phytoplankton grow only during mid-summer. However, the addition of coastal water and freshwater from melting sea ice can strengthen stratification and prolong production if tidal motion or wind mixing adds nutrients from a deeper layer.

Permanent ice-cover in late winter and spring delays the production of phytoplankton in fjords and open seas. Production starts when the ice gets thinner and more transparent allowing penetration of light to ice-algae and phytoplankton. Production is restricted to a few summer months after ice break up, which is why ice-covered waters have low annual production.

Learning Activity 3

Search the internet for satellite images of phytoplankton blooms in the Arctic Ocean and its marginal seas (e.g. Barents Sea and the Beaufort Sea). Note the location of these blooms relative to the Marginal Ice Zone. Also note the time of the year when these blooms appear at the ocean surface.

The **Marginal Ice Zone** (**MIZ**), where polar sea ice meets subarctic water, is a convergence zone where tidal motion, wind and waves mix fresh meltwater with nutrient-rich seawater causing vigorous production of sympagic diatoms while the sea-ice melts. As the ice-edge retreats due to melting, the production system shifts its geographic position and may end up far away from where it started.

When limiting nutrients have been consumed marine phytoplankton do not remain in surface waters. Marine phytoplankton drop to the bottom to escape grazers, but many end up as food for omnivorous benthic animals capable of water filtration and feeding on living micro-algae as well as detritus. The diversity and abundance of arctic and subarctic benthic animals is greatest in shallow water and decreases with depth. A fauna of benthic animals occurs in the deepest parts of all Arctic basins.

The most important first order consumers of phytoplankton in the upper layer of arctic waters are crustacean species belonging to a genus called *Calanus*. These copepods include *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*. These copepod populations have key functions in the Arctic Ocean ecosystem because they channel energy and matter from phytoplankton to most of the ecosystem's food web. *C. finmarchicus* occur in Subarctic waters of the Atlantic Ocean. A population in the Nordic and Barents Seas (Figure 7.16) has a different genetic signature than a population in the Labrador Sea. *C. glacialis* has a circumpolar distribution in Arctic Ocean shelf waters, while *C. hyperboreus* seems to form a pan-Arctic population that uses the Greenland Sea as its main reproductive habitat. *C. finmarchicus* and *C. hyperboreus* invade Subarctic fjords of northern Norway during autumn and winter. The abundance of *C. finmarchicus* is observed to be positively correlated with the fluctuations of a climate index called the North Atlantic Oscillation (NAO). Alternatively, *C. hyperboreus* fluctuates with an index for climate variability known as the Arctic Oscillation (AO). Both relationships indicate that the annual production or geographical distribution of the two population systems respond to changes in the global climate.

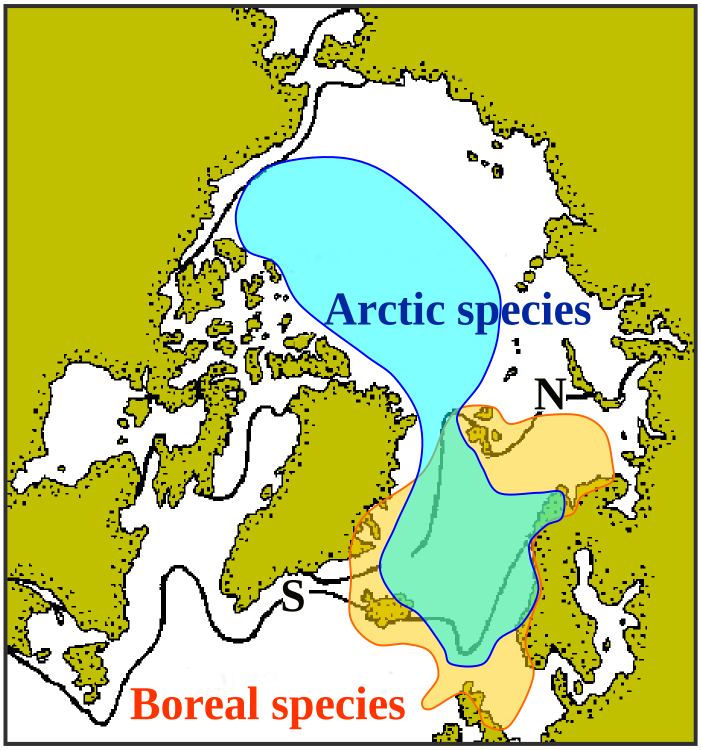

Figure 7.16. The Arctic Ocean with marine zoogeographical borders and the spatial distribution of two copepod population systems. Some eurytopic Arctic species extend their populations to a southern limit marked S. Eurytopic boreal species extend their populations to a northern limit marked N. The area between N and S is the Subarctic Transitional Zone. Blue hatching indicates the pan-arctic population system of *Calanus hyperboreus*. Orange hatching indicates the northeast Atlantic population system of *Calanus finmarchicus* that is an endemic species in subarctic waters.

Pacific and Atlantic subarctic seas are geographically separated, but ecologically connected. Zooplankton are transported in Atlantic water from the Greenland Sea to the Pacific sector of the Arctic Ocean and exchanged with ice-algae from the Pacific sector to the Atlantic sector. This demonstrates that planktonic population systems have wide geographic extensions and contribute to the structure of a large food web that characterizes and unites the Arctic Ocean ecosystem.

Norwegian spring-spawning herring (*Clupea harengus*) is a large planktivorous fish population preyed upon by larger fish, seabirds and marine mammals. Adult herring spawn in Norwegian waters. The Norwegian Coastal Current carries juveniles from spawning habitats to their nursery habitat in the southwestern Barents Sea. All age groups prey on *C. finmarchicus* but the adults prefer the larger *C. hyperboreus* when they occupy their summer feeding habitats in the western Norwegian Sea. Juvenile herring may supplement their copepod diet with other plankton, including capelin (*Mallotus villosus*) larvae, another planktivorous fish population in the Barents Sea. Capelin populations only succeed in producing strong year-classes when juvenile herring are absent in the Barents Sea due to reproduction failure.

The MIZ of the northern Barents Sea provides nursery and feeding habitats for its capelin population. Juvenile capelin in the MIZ are prey for Atlantic cod (*Gadus morhua*) that belong to a population called the Northeast Arctic cod. These cod spawn along the Norwegian coast and their juveniles feed on *C. finmarchicus* while being transported by the Norwegian Coastal Current into their nursery habitat in the southeastern Barents Sea. Older cod are omnivorous and may feed on juvenile herring, capelin and benthic animals in the Barents Sea. Atlantic cod cannibalize smaller members of their own population if prey is scarce.

The food-chains described here are not simple and direct. The smallest phytoplankton are not grazed by copepods, but by micro-zooplankton preyed upon by copepods. Copepods are not eaten exclusively by fish, but also by larger zooplankton like amphipods, euphausids and jellyfish. A large number of fish and marine mammals are adapted to feed on different trophic levels in the food web as they grow. All produce feces and food detritus that fall into the deep sea where much is consumed by a variety of animal species. The Iceland, Norwegian, Greenland and Barents Seas (Figure 7.1) are inhabited by populations that co-exist in a three-dimensional food web that conveys biomass to higher trophic levels within a single ecosystem. Top predators are seabirds, whales, seals (Figure 7.17) and humans who fish and export biomass to a world-wide market.

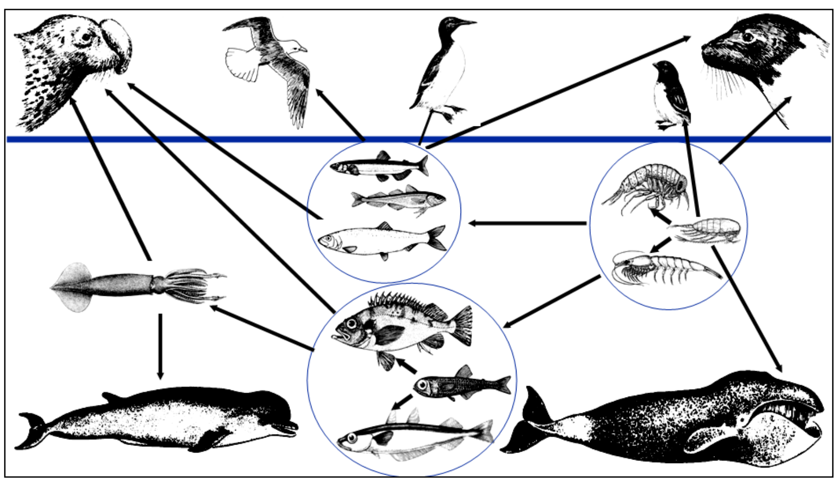

Figure 7.17. Some present and historical populations of the marine food web in the western Norwegian Sea and the Greenland Sea. *Calanus* species are eaten by amphipods and euphausids (1), and some hundred years ago the little auk (2) probably competed with another specialist on *Calanus* feeding, the Greenland right whale, *Balaena mysticetus* (3). The minke whale, *Balaenoptera acutorostrata* (4) is the smallest of all baleen whales. It is an omnivore that migrates from the North Atlantic during summer to feed on zooplankton as well as big fish. Juvenile harp seal, *Pagophilus groenlandicus* (5), and epipelagic (6) and mesopelagic fish (7) feed on zooplankton. Young hooded seal, *Cystaphora cristata* (8) and adult harp seal compete with glaucus gull, *Larus hyperboreus* (9) and guillemot, *Uria lomvia* (10) for epipelagic fish, especially capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*), and herring (*Clupea harengus*). Adult hooded seal and squid, *Gonatus fabrici* (11) feed in larger depths, on mesopelagic fish like northern lantern fish (*Benthosema glaciale*), blue whiting (*Micromesistius poutassou*), and pelagic redfish (*Sebastes mentella*). The bottlenosed whale, *Hyperoodon ampullatus* (12) is a visitor from the North Atlantic mainly feeding on squid during summer.

Capelin (*Mallotus villosus*) is a circumpolar species endemic in the **Subarctic Transitional Zone** (Figure 16). Subject to predation from many species, capelin provides commercially important populations in Icelandic, Canadian and Alaskan waters and the Barents Sea. Capelin populations are regularly preyed upon by Atlantic cod (*Gadus morhua*) in the Icelandic, Barents and Labrador Seas. Alternatively, Pacific cod (*Gadus macrocephalus*) in the Bering Sea only prey heavily on capelin in warm years when capelin do not find refuge in cold water.

Production of ice algae in Arctic Ocean multi-year ice are largely grazed by sympagic crustaceans that fall prey to two closely related species; Polar cod (*Boreogadus saida*) is more common in the Atlantic sector, while Arctic cod (*Arctogadus glacialis*) is more common in the Pacific sector. Both species live in the Arctic Ocean and in ice-covered Arctic marginal seas (Figure 1) and fjords. Spawning occurs in the MIZ where young fish possibly feed on juveniles of reproducing copepods. Polar cod and Arctic cod are both preyed upon by seabirds, and narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) populations that are true Arctic whales on top of the food web. The ultimate carnivore except for humans is the polar bear (*Ursus maritimus*), which feeds mostly on seals and also seabirds or macroalgae when the coasts are ice-free.

Freshwater Food Webs

Rivers and lakes in subarctic regions export biomass downstream and often receive biomass from smaller upstream watercourses. Many organismic systems in freshwater communicate with the sea via **diadromous** species, organisms that migrate between freshwater and marine habitats. **Catadromous** fish that reproduce in the sea and spend life stages in freshwater are few in Arctic waters. For example, one is the European flounder (*Platichthyes flesus*) that mainly lives in brackish habitats, but rivers and lakes may serve as nursery habitats for juveniles. Many diadromous species are **anadromous** meaning their populations spawn and spend juvenile stages in freshwater habitats. For example, lampreys and their juveniles migrate into Arctic seas to grow to sexual maturity. They may feed as predators on small fish like capelin, but their mouths are specialized for parasitic feeding on blood and tissue fluids from larger fish and whales. Lamprey are poor swimmers and may migrate up turbulent rivers when attached to salmon returning from the sea.

Anadromy is particularly associated with salmonids, a family of species well known to people that fish in rivers. All salmonid species spawn in freshwater and bury their eggs in sand or gravel on river bottoms where after some months they hatch. Juveniles look different from adult salmon until they metamorphose into the fry stage, which may last for one or more years. Fry undergo **smoltification** when they prepare for migration to marine habitats. Fry change their external spotted pigmentation to the silvery skin of a **smolt**. This is a type of individual acclimation that includes changes in their **osmoregulation** involving the physiological functions of the gills and kidneys. Salmon in freshwater habitats keep their body fluid salinity higher than their aquatic environment by kidney functions that pump water out of their body, which differs from osmoregulation in marine habitats. Salmon and bony fish drink seawater to replace water that the salt environment drains from their bodies, while specialized cells in their gills pump excess salts from their blood into the ambient water.

The ability of salmon species to return from the sea to their juvenile river habitats to spawn is fascinating and debated by scientists. Some scientists claim that homing is due to sensitive olfactory organs that allows salmon to smell pheromones from their freshwater relatives. Pheromones are potent chemicals released when relatives defecate in river water that is mixed into ocean currents and detected by adults migrating toward their spawning habitats. There is also considerable evidence that the ability to find the correct river depends on imprinting, meaning smolts learn to recognize local waypoints. Regardless, a percentage of returning adults migrate into neighboring rivers to spawn. Accordingly, salmon from different rivers may belong to the gene-pool of a common population system with a wider distribution.

Salmo is an Atlantic genus with two boreal species of salmon, the Atlantic salmon (*S. salar*) and the trout (*S. trutta*), that have established many subarctic populations. The trout is widely distributed in northern Europe and has been transferred to new continents by man. Sea trout are anadromous populations that establish spawning and nursery habitats in large rivers and small streams flowing into the sea. The species is mostly known as stationary brown trout in lakes. Some lake populations became isolated from the sea when post-glacial uplift of the coastal landscapes resulted in waterfalls that prevented the return of sea-run fish. Populations in higher altitude landscapes have been introduced by humans wanting to improve the carrying capacity of their own population system. Ancient runes cut into a stone in the mountain landscape of southern Norway tell that “Eiliv Moose carried fish to Red Lake.”

Seven Pacific salmon species belong to the genus *Oncorhyncus*: cherry (*O. masu*), chinook (*O. tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), sockeye (*O. nerka*) and steelhead (*O. mykiss*). They are boreal species with biogeographical distributions extending into subarctic waters. All are anadromous and may establish stationary stocks in rivers. For example, stationary *O. mykiss* in lakes is known as rainbow trout, a popular sports fishing species that is cultured in freshwater ponds and in marine cage cultures in many countries.

Salmons differ from chars belonging to the salmonid genus *Salvelinus*, a circumpolar genus that confuses fish biologists because scientific taxonomy has established a large number of species and subspecies based on their morphology. At present, scientists maintain Arctic char (*S. alpinus*) as a circumpolar species (Figure 7.18) that establishes the northernmost populations of any fish occuring in freshwater. DNA studies in northeastern Asia suggest Arctic char is predominantly Atlantic and has recently diverged from Dolly Varden (*S. malma*), a char distributed in the Pacific sector of the northern hemisphere. Both are anadromous but form stationary populations in lakes.

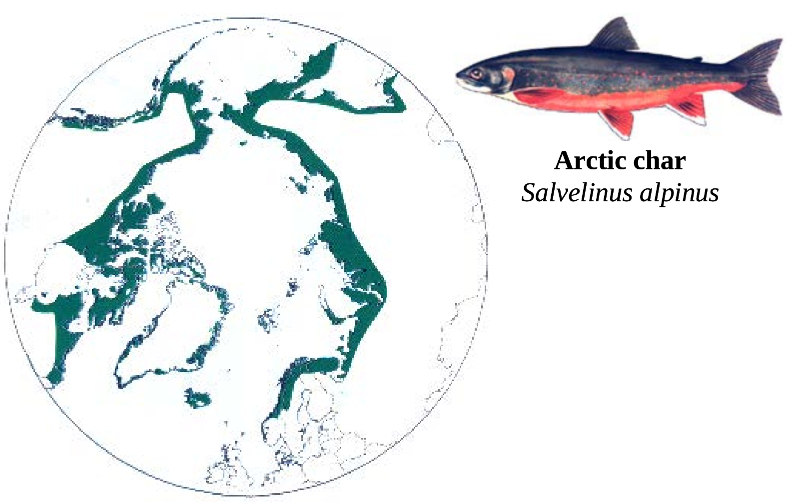

Figure 7.18. The circumpolar distribution of Arctic char, a fish spawning in freshwater. Populations may split into anadromous stocks that do annual feeding migrations into the sea and stationary stocks that remain in rivers and lakes. Stationary stocks occur in lakes where waterfalls prevent the return migration from the sea. (Map from CAFF).

Arctic char cannot leap up waterfalls like salmon and trout, so anadromous populations usually occur in rivers and lakes with short, easy access to the sea. Anadromous populations usually develop three adult stocks. Some juveniles smoltify to migrate to the sea to feed on copepods and other plankton, sympagic and benthic invertebrates, and small fish like sculpins. They stay a little more than one month in the sea before returning to freshwater and may need more than one summer to become sexually mature. Some stationary juveniles mature at a low age and become a stock of small adults, while others grow into large adults over years. Both stationary stocks may smoltify as adults and join the sea-running stock.

Returns of anadromous stocks of salmons and chars may be massive in some rivers where they provide food for a variety of predators and scavengers. Brown bears are important contributors to terrestrial food-chains. Bears bring onto land large quantities of half-eaten fish that are subsequently consumed by scavenging mammals, birds and insects. Feces and food detritus are decomposed by micro-organisms that fertilize the ground where plants grow. Plant leaves and debris are blown or washed into streams and rivers feeding detritivorous insects and crustaceans that fall prey to juvenile fish.

Many freshwater fish other than salmonids migrate into river deltas and brackish bays where salinities are below 7 psu. Perch (*Perca fluviatilis*) populate lakes and estuaries in Eurasia, and establish population systems in the Bothnian Bay and brackish parts of the Baltic Sea. Freshwater fish feeding in estuaries prey on endemic brackish-water and terrestrial species from wetland biota and on marine zooplankton and nekton. Rivers that allow sea-run stocks of freshwater fish are not closed ecosystems. They receive biomass from two opposite sources, one in marine habitats and the other in terrestrial biota established in the river’s drainage area.

Rivers that do not allow for anandromy only receive biomass from their drainage basins. They may drain a number of streams and lakes that receive terrestrial plant debris washed off the ground. Insect larvae drop from trees hanging over the water and winged adults fly or are blown into the water to be eaten by fish. Freshwater biota feed biomass to terrestrial parts of watersheds when insect larvae grow wings and leave their aquatic habitats.

Large lakes may form ecosystems with their terrestrial surroundings when they do not receive marine biomass by anadromy and production of plankton, and biomass is consumed by animals and decomposers within their drainage basin. Fish species that occupy lakes often belong to population systems where lake stocks exchange genes with other stocks within a larger system of lakes and smaller tributary streams. When this occurs on a large scale large lakes may fail to fill the qualifications of an ecosystem. Fish fauna of a large lake ecosystem may consist of different species representing many feed-back relations stabilizing flows of energy and matter within the ecosystem. Some populations diversify by ontogenetic adaptation into a complex of adult stocks with specialized predation. Arctic char and species within the circumpolar genus of whitefish (*Coregonus*) exhibit these characteristics and form planktivorous stocks feeding on zooplankton and stocks of piscivores that prey on other fish or their smaller relatives. Other fish like the circumpolar northern pike (*Esox lucius*) can only feed by piscivory throughout their adult lives. Piscivores must themselves hide their eggs from being eaten by their own prey and are vulnerable to predation from otters, bears and eagles that may catch large fish in shallow water.

7.5 Controls on Ecosystem Functions

Bottom Up Control

Climate seems to control biological production at lower trophic levels by its regulation of physical processes that provide light and nutrients for primary producers. Clouds reduce the quantity of solar radiation received in aquatic environments and winds and tides are required to mix nutrients from deep layers into the euphotic zone. These factors vary not only with seasons but between years due to global atmospheric processes expressed in the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO). Little is known about how physical factors in aquatic ecosystems regulate biological processes, but the hydrological cycling of water is always involved. Years with large and prolonged freshwater runoff cause groundwater levels to rise and establish seasonal ponds with a range of producers and consumers forming a food web exploited by waterfowl, grazers and predators. Enhanced flooding in rivers increases the discharge of muddy water containing fertilizing nutrients and mineral particles that prevent the photosynthesis of phytoplankton and submerged plants. Plankton brought from lakes into rivers preferably grow when the flow is low and the water clear. Some copepods are known to occupy sediments and become inactive to reduce their transportation downstream when flows are strong. In the sea, adult copepods tend to aggregate in river plumes and coastal convergence fronts, increasing their reproduction when salinity decreases due to increased river discharge.

Top Down Control

Top down control in food webs occurs when animal populations at high trophic levels regulate flows of energy and matter at lower trophic levels. Cannibalistic Arctic char in lakes with only stationary char populations exhibit top down control when they control the stocks of juveniles and small adults. Cannibalism reduces intra-specific competition for limited food sources and stabilizes the population system, which might otherwise burst through the carrying capacity of the environment and crash. Top predators serve the same function within the biota of their population systems.

Polar bears (*Ursus maritimus*) take as many ringed seals (*Phoca hispida*) as their population requires and provide environmental resistance needed by the seal population to keep it within the environmental carrying capacity of its marine habitat. The physical environment of Arctic organisms is highly variable causing polar bear food resources to vary. Male polar bears are known to kill polar bear cubs, which is likely to happen when the males are hungry. Cannibalism may regulate the bear's population to a level that will not overexploit its food resources and allow prey populations to recover.

Polar cod, Arctic cod and capelin are small and typically r-selected species that become sexually mature at a young age and spawn once or a few times in their life time. Capelin are pelagic and feed on zooplankton produced near the MIZ, while Polar cod belong to the sympagic system of polar sea ice, feeding mainly on amphipods grazing on ice algae. Arctic cod is more bathypelagic and may prey on Polar cod. Each is preyed upon by a variety of K-selected seabirds and sea mammals that exert top down control on their populations. These three fish have adapted the same life strategy that makes them mobilize fast population growth when top down control is lifted.

The northeast Arctic population of Atlantic cod preys on capelin and herring in the Barents Sea, which possibly moderates their population development and stabilizes the flows of energy and matter throughout the food web. The cod regulate their own population by cannibalism, which stabilizes the recruitment of individuals to its spawning stock. Top down control is more complicated if many top predators in the Arctic Ocean ecosystem exert direct or indirect effects on large key populations of *Calanus* species. It is likely that plankton populations are more responsive to bottom up control from the abiotic environment.

Role of Migrating Populations

Several large populations migrate between boreal and Arctic habitats. Whale species migrate north during spring to feed. Some feed on pelagic zooplankton and nekton while some, like the Pacific grey whale (*Eschrichtius robustus*), feed on benthos. Whales accumulate blubber that insulates against cold and serves as a fat reserve providing energy for activities in their southern winter habitat. There females give birth, feeding calves nutritious milk preparing them for their first northward migration. Males expend energy in pursuit of females, power displays and mating.

Many seabirds migrate to the Arctic to reproduce. The most extreme migration between habitats is made by the Arctic tern (*Sterna paradisaea*) that nests along the northernmost Arctic coasts and spends every winter in the Antarctic. The Arctic tern, like all bird populations, grows from hatchling to nearly adult size in a few months, all of it in the Arctic summer habitat. In the Arctic, the seabirds of most importance in terms of biomass and ecological influence are populations of different species in the family of auks. They nest in colonies during spring and summer, some densely aggregated in immense numbers. They live for many years and invest their annual efforts into one juvenile that is tended and cared for after leaving the nest. Some of these K-selected birds are observed migrating in flocks of hundreds or thousands seeking feeding habitats during winter, in the MIZ, in oceanic habitats or in Subarctic coastal waters.

Many water-birds nesting and caring for chicks in Arctic watercourses during summer forage in northern marine habitats during winter, but many insect-feeders leave Arctic watercourse habitats to spend winter in more temperate and tropical habitats. The migratory habit is an adaptation that allows species feeding in the Arctic to grow large populations. They are subject to top-down control by migratory birds of prey, which stabilizes the functioning of their population systems and Arctic habitats.

Learning Activity 4

Search various news media for articles that highlight changes in animal migration patterns between Boreal and Arctic habitats.

7.6 Trophic Position of Humans in Aquatic Food Webs

Man is an extremely K-selected species. Parents care for their children until they are sexually mature, but extended tribal family systems and national societies care for their members throughout their lives. Some Arctic cultures have practiced suicide among elders who can no longer contribute to the collective welfare, which may be regarded as the ultimate altruism aimed at preservation of the group.

Some Indigenous Arctic peoples have expressed moral thinking and justice aimed at sustainable harvesting of living resources in areas they control. There are still cases of strict tribal regulation of fishing for salmon in rivers, sharing of catches and the right to fish in lakes referred to tribal legislation. In the past taxation of tribes and marketing of commodities like otter and beaver furs organized by national states created competition for resources, which disrupted and over-ruled tribal traditions and caution causing over-exploitation and extinction of living Arctic resources.

European nations began the industrial exploitation of Arctic resources in the 17th century after Willem Barents discovered Spitsbergen and opened the region for hunting of the Greenland Right whale, a population of the Arctic bowhead whale (*Balaena mysticetus*). Oil was extracted from the blubber and used for various purposes. Baleen plates used by whales to feed on copepods were processed into flexible items used in corsets and other products. Hunting did not take into account that the Greenland Right whale was an extreme K-selected species growing slowly, becoming sexually mature at about 20 years and giving birth to one or two calves every third year. The low reproduction rate and unregulated hunting drove the Atlantic population into extinction after 200 – 300 years. During the last decades individuals have been observed in Svalbard waters, indicating migration from the Pacific side where the population is sustainable and growing. Culling is allowed on a small scale only by Indigenous peoples with historical and cultural rights.

Steller's sea cow (*Hydrodamalis gigas*) is an example of the extinction of an Arctic mammal population. First described in 1741 during the Russian exploration of the Bering Sea, it was soon harvested for commercial purposes and became extinct about 30 years after of its discovery. It fed exclusively on kelps and was an easy target for hunters.

Today, several Arctic sea mammals are harvested for traditional and commercial use. Canadians, Norwegians and Russians hunt three separate populations of harp seal (*Phoca groelandica*) in the Labrador Sea, the Iceland and Greenland Seas and the White Sea, respectively. They are primarily culled when they aggregate in large numbers to give birth to juveniles and mate. Juveniles are no longer culled; the skin, meat and blubber are landed and sold. The species is an important source of food and material for Indigenous technology and artifacts.

The small ringed seal (*Phoca hispida*) is circumpolar but divided into several sub-species. Some occupy continental freshwater lakes and are regarded as glacial relics separated from the ocean by post-glacial uplift as are ringed seals inhabiting Bothnian Bay in the Baltic Sea. The populations are not subject to industrial culling, but may be the most important resource for High Arctic Indigenous peoples who use them for consumption, clothing and dog food. The species digs a den in the snow that covers its breathing hole and shelters a single white-furred pup in late winter. Marine populations feed on zooplankton, sympagic crustaceans and small fish, especially Polar and Arctic cod. The species is a subsistence prey organism for polar bears.

The Polar bear (*Ursus maritimus*) is a marine top carnivore known to kill and eat humans given the opportunity in seasons when its natural prey is scarce or absent. Its circumpolar distribution consists of about 20 distinct populations. Females hibernate in dens dug into snow, usually on hillsides, where they give birth to 1 – 3 cubs that feed on milk until the mother leaves the den to hunt on the sea ice. Females may take refuge on land if males are likely to kill and eat the cubs. Humans have killed polar bears for their white winter fur, but commercial hunting is now banned in most Arctic sectors. Canada allows a quota for sports hunting and Indigenous peoples are allowed to kill Polar bears for cultural purposes.

Human control of predators to protect the subsistence of our ancestors has a long history. Killing sea eagles (*Haliaetus albicilla*) and otters (Lutra lutra) that prey on adult eider ducks (*Somateria mollissima*) and gulls that feed on juvenile eiders was common in Arctic Norway to protect artisan production of high priced eider down. Changes in the global economy and a growing awareness of feed-back control in ecosystems is causing changes in competition with predators, however humans continue to cull populations of seals in coastal waters to reduce the infestation of parasitic nematodes in marketed cod fillets.

Previous human generations harvested local biota with primitive technology to make a sustainable living, but their fishing of large oceanic populations represented little top down control. The last half century saw the development of large ships with acoustic instruments for detecting fish and powerful machinery for handling fishing gear. Industrial fishing of Arctic waters has the power to extinguish entire fish populations and radically change the trophic structure of the ecosystem's food webs. Humans are beginning to understand that exploitation of living resources can no longer be based on fisheries harvesting single species without regard to the effects on other species. Model simulations indicate that tactical multi-species harvesting can maintain trophic structures and increase the harvest.

One of the most serious issues discussed in fisheries management today is the use of trawls and nets that select the largest individuals of exploited populations. Genes that escape this fishing pressure survive in fish that grow slowly and mature sexually at small size demonstrating survival of the fittest in contemporary evolution. This is now evident in populations of Atlantic cod (*Gadus morhua*) that inhabit Subarctic waters. Big fish with genomes for fast growth, large size and delayed sexual maturation may become extinct.

The present use of marine resources is the result of economic considerations. Some of today's harvest is marketed for human consumption, but an increasing amount is processed to produce formulated feed for farmed fish, poultry, pigs and pets (Figure 7.19). Marine biomass is now a limited commodity causing prices to increase. The aquaculture industry looks for new resources and attempts to develop methods that allow exploitation of zooplankton at lower trophic levels. Considering a 90 percent loss of energy on each trophic level, harvesting at low levels may allow for an increased harvest, but the bottom up effects on higher trophic levels have not been evaluated.

Drifting sea ice of the Arctic Ocean and the East Greenland Current is characterized by the food web of sympagic ice algae and ice fauna, and associated populations of Polar and Arctic cod. The Arctic Ocean also receives considerable input of planktonic biomass from the Subarctic food web of the Iceland, Norwegian, Greenland and Barents Seas, and less influential contributions from the Bering Sea.

Although many species at high trophic levels establish separate population systems in the Arctic Ocean biome and Subarctic waters of the Atlantic and Pacific sectors, they are integrated sub-systems of the larger Arctic Mediterranean ecosystem. The main issue in this respect is that the population systems of three *Calanus* species are primary consumers that link the Arctic Ocean and the Subarctic seas into one common ecosystem.

Many fundamental ecological processes in Arctic seas are forced by hydrological cycling of water. The discharge of freshwater from two continents and the trophic connections between the sea and many freshwater and terrestrial systems indicate that future management of Arctic living resources must rest on multidisciplinary ecological research. Rational ecosystem-based management of the Arctic Mediterranean ecosystem requires international coordination and united efforts from nations surrounding Arctic seas.

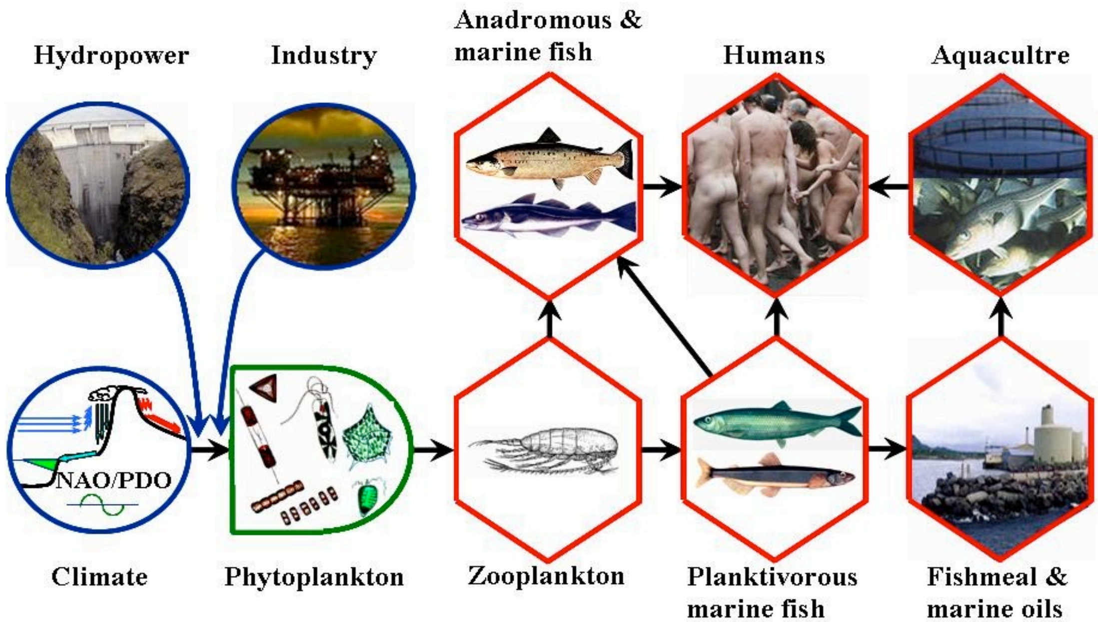

Figure 7.19. Main components in sub-arctic food webs harvested by circumpolar nations. Global climate controls trophic flows of energy and matter bottom up, and humans exert top down control by fishing on commercial stocks. Marine biomass is marketed for direct consumption or processed to increase qualities and profits. Production of hydroelectric energy and emissions of CO_2 from fossil fuels interferes with natural climate forcing of the ecosystem's food web. Circles: Forcing factors. Bullet: Producers. Hexagons: Consumption with trophic loss of energy.

Aquatic Ecosystems in the Arctic

Arctic watercourses that receive only terrestrial biomass and no marine biomass imported by diadromy may be studied as self-contained ecosystems, while anadromous populations link rivers to widespread marine food webs. Salmon species are more numerous and probably more influential in the Pacific Subarctic food web than in the Atlantic Subarctic food web where marine fish species are more influential. This feature distinguishes the two Subarctic regions separated by the Arctic Ocean and the Arctic continental shelf seas of Eurasia and North America. Arctic seas and the two Subarctic regions share populations at low trophic levels and are united by a panarctic food web. The Arctic Mediterranean ecosystem is a conceptual model that unites marine, freshwater and terrestrial science. It establishes a framework for ecosystem-based management that meets environmental challenges raised by the effects of global climate change and explains how Arctic human societies may exploit local resources in sustainable ways.

Conclusion

The buoyancy of aquatic organisms is why energy fluxes in food chains in lakes and oceans are mainly vertical. Aquatic organisms link the upper euphotic zone of producers and primary consumers with the deeper dysphotic and aphotic habitats of higher order consumers and decomposers. Ocean currents disperse populations of plankton over large spatial distances and marine fish populations migrate between distant habitats during their multi-annual life cycles, making marine ecosystems much larger than freshwater ecosystems.

Freshwater ecosystems consist of streams, rivers, lakes and the drained landscape. Plants growing on land and on shallow bottoms produce significant parts of the biomass consumed in freshwater biota. Crustaceans are important consumers in most freshwater and marine biota, but they differ in some respects. Being nearly absent in seawater biota, insects are unique consumers in freshwater ecosystems. Echinoderms that occupy many trophic levels in marine food webs are missing in freshwater. Many fish populations that spawn in freshwater form anadromous stocks of small fish that migrate to feed in the sea. They return as much larger fish and supply significant amounts of marine biomass to the food web of their reproduction and nursery habitats in rivers and lakes. Terrestrial mammals and birds prey on adult anadromous fish in rivers and their feces and food remains fertilize the landscape vegetation. Rivers with anadromous stocks are parts of the marine ecosystem, which is more evident in the Pacific sector than in the Atlantic sector of the Arctic.

Producers of marine biomass in the Arctic are mainly micro-algae. Some are benthic in shallow water and sympagic in the polar sea ice, while most of the production is planktonic associated with the marginal ice zone and oceanic convergence fronts. Benthic macro-algae are the seaweeds and kelps that produce biomass along Subarctic shores, but are absent along Arctic shores where floating ice prevents their establishment.

Polar sea ice originates from freezing of freshwater discharged from large rivers into circumpolar continental shelf seas. Thick multi-year ice results from eastward flows of brackish water along Siberia and water retention in the Beaufort Gyre before the sea ice enters the Transpolar Drift to be transported across the Arctic Ocean and into the Greenland Sea. Ice-algae that grow under the ice are eaten by crustaceans that convey biomass to high trophic levels within the sympagic biome that contains populations of small fish, seabirds, seals and whales. Subarctic plankton biota in the Atlantic and Pacific sectors are connected due to wide geographic distributions of pan-arctic copepod populations that support production of commercially exploited fish populations, including anadromous fish.

Bears and man are top predators in the wide-spread Arctic Mediterranean ecosystem. Whale stocks that occupy wintering habitats in the North Atlantic and North Pacific oceans migrate into Subarctic waters to prey on several trophic levels in the ecosystem’s food web. Their ambulation between northern and southern habitats is similar to the migration pattern of birds that exploit Arctic watercourses and wetlands. Populations of top predators exert top down control on lower trophic levels and may modify the direction of energy flow within the ecosystem’s food web. Bottom up control is mainly due to the global climate which causes biological resources to fluctuate in concert with atmospheric processes in the North Atlantic and North Pacific oceans.

Discussion Questions

1. Discuss criteria that limit spatial dimensions of population systems. Explain why ecosystems are larger than populations systems.
2. How do food webs, energy flow, cycling of matter and control systems interact with biodiversity?
3. Discuss major differences between terrestrial and marine ecosystems.

Study Questions and Answers

1. What distinguishes an ecosystem from an organismic system?

   An ecosystem is the conceptual model of a geographical space where a community of consumer and decomposer populations digest nearly all biogenic energy contained in biomass produced by the ecosystem's populations of autotrophs. Although the food-web may be subject to interannual changes, the conservation of energy within spatial dimensions of the ecosystem allows predictable and accountable energy budgets that can be simulated by numerical modelling on annual and interannual scales. An organismic system is a temporary biota that functions as a common habitat for organisms representing some different populations that make an ecosystem. Organismic systems import and export biomass by seasonal migration or transport by abiotic forcing, which is often highly variable making energy budgets unpredictable on any temporal scale.

2. Suggest two cases of food-chains that demonstrate conservation of energy within a biome and two that demonstrate leakage of energy between biomes.

   Example: Birch leaves grazed by insect larvae are preyed upon by juvenile migratory songbirds, some of which fall prey to local owls and predators in their wintering habitats on lower latitudes.

3. How may abiotic variables interact with growth in populations of herbivorous poikilotherms?

   Examples:

   - Their metabolism increases with temperature.
   - Temperature regulates the seasonal growth of food.
   - The salinity of seawater prevents stenecous freshwater species from feeding on marine biomass.

4. List biological features that distinguish r-strategists from K-strategists.
   - r-strategists are small, have short generation times, produce many eggs at a young age and do not protect their progeny.
   - K-strategists are large, become sexually mature at high age, produce few offspring and protect their progeny.

5. How may the balance between euryecous and stenecous species influence the biodiversity of an organismic system?

   Euryecous species have wide fundamental niches and may play ecological roles that compete with several stenecous species with narrower fundamental niches. Stenecous species require very specific environmental conditions which optimize their competitiveness. Abiotic conditions must be stable to allow for a rich biota with many stenecous species.

6. Select a typical Arctic organismic system and discuss how the five functional components of the larger ecosystem cause its biodiversity to change with the seasons.

   Many consumers leave northern birch forests when low temperature and short days cause plants to shed their foliage. Leaves are left on the ground to be decomposed by fungi and bacteria, but mineralization stops when soil water freezes. Inorganic nutrients are stored until the spring thaw makes them available for plant roots, which allow trees and herbs to grow new leaves. Forest biodiversity increases when invertebrate eggs hatch into larvae and herbivorous and carnivorous consumers migrate into forest habitats from different winter habitats to feed and breed. In contrast, forest biota becomes less diverse during winter when only stationary consumers are present constituting a much simpler food-web.

Glossary of Terms

Aerosols: A suspension of solid or liquid particles in a gas.

Anadromous: A term relating to animals that live their lives in the ocean and migrate to a freshwater river to breed.

Benthos/Benthic: The collection of organisms living on or in sea or lake bottoms; the benthic environment.

Bioluminescence: the production of light by living organisms.

Bottom Up Control: Bottom up control in ecosystems refers to ecosystems in which the nutrient supply and productivity and type of primary producers (plants and phytoplankton) control the ecosystem structure.

Catadromous: A term relating to animals that live their lives in fresh water but migrate to the ocean to breed.

Convergence Front: Convergent fronts occur when the water masses on both sides of the front are moving towards the front and hence each other. At convergent fronts, the water is often warmer than in the surrounding area, and a buildup of water at the front leads to a slightly higher sea level. This buildup causes increased pressure on the water column, and leads to downwelling at the front.

Coriolis Force: The Coriolis force results in a deflection of fluid flows (to the right in the Northern Hemisphere and left in the Southern Hemisphere).

Diadromous: Organisms capable of migrating between fresh and salt water.

Estuarine Circulation: In an estuary, the outflow (seaward) of low-salinity surface water over a deeper inflowing layer of dense, high-salinity water.

Estuary: A partially enclosed coastal body of water with one or more rivers flowing into it, and with a free connection to the open ocean.

Euphotic Zone: The layer of sea water that receives sufficient light for photosynthesis to occur: it varies with the season and latitude but is generally less than 200 metres deep.

Eutrophication: An aquatic environment rich in inorganic and organic nutrients that promote a proliferation of plant life, especially algae, which reduces the dissolved oxygen content and often causes the extinction of other organisms.

Freezing Point Depression: Freezing-point depression describes the phenomenon in which adding a solid material to a fluid produces a decrease in the freezing point of the fluid. The resulting solution has a lower freezing point than the pure fluid did. This phenomenon is what causes sea water (a mixture of salt in water) to remain liquid at temperatures below 0°C, the freezing point of pure water.

Global Thermohaline Circulation: The term thermohaline circulation refers to a part of the large-scale ocean circulation that is driven by global density gradients created by surface heat and freshwater fluxes. The adjective thermohaline derives from “thermo” referring to temperature and “haline” referring to salt content, factors which together determine the density of sea water.

Halophytes: A plant adapted to living in salty soil, as along the seashore or in tidal flats.

Hydrothermal Vents: A hydrothermal vent is a fissure in a Earth’s crust from which geothermally heated water issues. Hydrothermal vents are commonly found near volcanically active places such as areas where tectonic plates are moving apart at the seafloor.

Langmuir Circulation: This form of water circulation results in the occurrence of thin, visible stripes, called windrows on the surface of the ocean parallel to the direction that the wind is blowing. If the wind is blowing at a speed that exceeds 3 m s^{-1}, it can create parallel windrows of alternating upwelling and downwelling about 5–300 m apart. These windrows are created by adjacent elliptical water cells (extending to about 6 m depth) alternating rotating clockwise and counterclockwise. In the convergence zones debris, foam and seaweed accumulates, while at the divergence zones plankton are caught and carried to the surface. If there are many plankton in the divergence zone fish are often attracted to feed on them.

Marginal Ice Zone (MIZ): The marginal ice zone is generally defined as a transition region from open water to pack ice with changing ice concentration, thickness, and floe sizes.

Nekton: Marine and freshwater organisms that can swim freely and are generally independent of currents, ranging in size from microscopic organisms to whales.

Orographic Uplift: Where the flow of air is forced up and over barriers such as highlands or mountains. Moist air being forced aloft begins to cool, consequently condensation forms, and rain or snow begins to fall. By the time the air reaches the leeward side of the barrier, it sinks and warms, resulting in decreasing relative humidity, cessation of precipitation, and the dissipation of clouds.

Osmoregulation: Maintenance of an optimal, constant fluid pressure in the body of a living organism.

Overturn: The circulation, especially in the fall and spring, of the layers of water in a lake or sea, whereby surface water sinks and mixes with bottom water; it is caused by changes in density differences due to changes in temperature, and is especially common wherever lakes and oceans are ice covered in winter.

Pelagic: The pelagic environment can be thought of in terms of an imaginary column of water that extends from the sea surface to the seafloor. Conditions change deeper down the water column; the pressure increases, the temperature drops and there is less light.

Phototaxis: Movement of an organism toward or away from a source of light.

Phytoplankton: Phytoplankton are photosynthesizing microscopic organisms that inhabit the upper sunlit layer of almost all bodies of fresh and salt water.

Pycnocline: A pycnocline is the layer where the density gradient is greatest within a body of water.

Rain Shadow: An area having relatively little precipitation due to the effect of a topographic barrier, especially a mountain range, which causes the prevailing winds to lose their moisture on the windward side, causing the leeward side to be dry.

Sigma-t (water density): Small changes in ocean water salinity are responsible for large changes in vertical circulation (i.e. thermohaline circulation). For this reason, oceanographers measure salinity with a great deal of precision (e.g. 1.02667 gcm^{-3}). Density is commonly converted to a sigma-t (σ_t) value. For example, a sample of sea water exhibits a density of 1.02667 gcm^{-3} in contrast to the density of pure fresh water with a density of 1.00000 gcm^{-3}. We derive the sigma-t value for the ocean water as follows:

$$\frac{1.02667\,gcm^{-3}}{1.00000\,gcm^{-3}} = 1.02667;\ (1.02667 - 1) \times 1000 = 26.67;\ \sigma_t = 26.67.$$

Subarctic Transition Zone: Relates to those marine environments in which surface waters consist of a mixture of Polar water and Atlantic Ocean or Pacific Ocean water.

Sympagic: An environment where water exists mostly as ice, including ice caps, glaciers, and sea ice. Sea ice is permeated with channels filled with salty brine.

Thermocline: A distinct layer in a large body of water, such as an ocean or lake, in which temperature changes more rapidly with depth than it does in the layers above or below.

Top Down Control: In ecology, top-down control refers to when a top predator controls the structure or population dynamics of the ecosystem.

Zooplankton: Tiny, free-floating or motile organisms, composed mainly of small crustaceans and fish and invertebrate larvae, in lakes and oceans; the animal constituent of plankton. Unlike phytoplankton, zooplankton cannot produce their own food, and so are consumers.

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