Chapter 6

Pelagic Ecosystems

CHAPTER SUMMARY

Away from coastal boundaries and above the seabed, the pelagic environment encompasses the entire watercolumn of the seas and oceans. The pelagic environment extends from the tropics to the polar regions, and from the sea surface to the abyssal depths, and is a highly heterogeneous and dynamic three-dimensional habitat. The pelagic is home to some of the most revered and reviled marine inhabitants, but great whales and jellyfish alike are subject to the consequences of pelagic ecosystem variability. Physical processes in the pelagic exert major control on biological activity, and lead to substantial geographic variability in production. Knowledge of biophysical interactions is essential for understanding ecological patterns and processes in the pelagic environment, and will be key for predicting changes there induced, for example, by climatic warming.

6.1 Introduction

The term **pelagic** means '**of the open sea**' and the pelagic realm is a largely open, unbounded environment in which the inhabitants have freedom, within physiological limits, to move in three dimensions. Contrary to the common perception of the sea as an unchanging, relentless expanse, the open ocean is an environment where variability is very much the norm. Patchiness in physical properties (e.g. temperature, salinity, turbidity), biological production, and biomass exists at a range of scales in space (centimetres to hundreds of kilometres) and time (minutes to decades). One of the key challenges to understanding open-ocean function lies in understanding the mechanisms that cause, and consequences of, this patchiness (Mackas & Tsuda 1999).

Despite the fact that much of the open ocean is remote from land, beyond the horizon for land-based observers, it has not escaped human impacts. For example, 90% of stocks of large pelagic fish such as tuna (Scombridae) and jacks (Carangidae) may have been removed by fishing (Myers & Worm 2003), and whole zooplankton communities have

● The open ocean is an highly variable environment.

shifted their spatial distribution (Beaugrand et al. 2002) possibly in response to ocean warming, itself most likely caused by anthropogenically-released greenhouse gasses (IPCC 2001).

The pioneering studies of open-ocean ecology made from vessels with evocative names such as *Discovery, Challenger*, and *Atlantis* have been enhanced in recent years with observations from technologically advanced research platforms that include Earth-orbiting satellites (Bricaud et al. 1999) and unmanned autonomous underwater vehicles (AUVs) (Griffiths 2003). The aim of this chapter is to provide a synthesis of open-ocean ecosystem function and the factors that control it, insight into difficulties associated with sampling the heterogeneous pelagic realm, and some examples of ecological step-changes (regime shift) in the global pelagic environment.

● Despite its apparent remoteness, the open ocean has been influenced strongly by human activities such as fishing and anthropogenic climate warming.

6.2 Definitions and Environmental Features

The pelagic realm spans the entirety of the water column, beginning at the sea surface and ending just above the seabed (the benthic realm; Chapters 7 and 8). The pelagic realm can be subdivided by total water depth and distance from shore. The neritic zone lies adjacent to shore, over continental shelves, and covers about 8% of the Earth's total sea area. Out beyond the continental shelf break, which is delimited typically by the 200 m depth contour, lies the vast, open oceanic zone (92% of the total sea area that covers 65% of the Earth's surface). There are numerous differences between the neritic and oceanic zones, differences that arise not least because of differences in proximity to land and consequent differences in nutrient and sediment loading in the water column (much of the sediment load in the seas and oceans is terrigenous and is delivered by rivers and estuaries; Chapter 4). Sailing out from a coastal port towards the open sea it is common to notice a transition from turbid to clear, blue waters. This transition is obvious not just from the deck of a ship but is visible from space. Indeed, interpretations of satellite remote sensed observations of ocean properties have to distinguish 'Case 1' waters, where the ocean colour is determined predominantly by algal pigments, from 'Case 2' waters where reflections from particulate matter dominate (Fig. 6.1) (Babin et al. 2003). One adaptive biological consequence of the difference in sediment and particulate loading between the oceanic and neritic zones can perhaps be seen in squid anatomy. Myopsin squid inhabit the neritic zone (for example *Loligo forbesi*, which is common in north-west European coastal waters, or *L. opalescens* from the west coast of the USA) and have a membrane across the eye that may serve to protect the eye from particulate irritants suspended in the water: in the open ocean myopsin

● The neritic and oceanic zones are very different, due in part to their differing distances from the coastline.
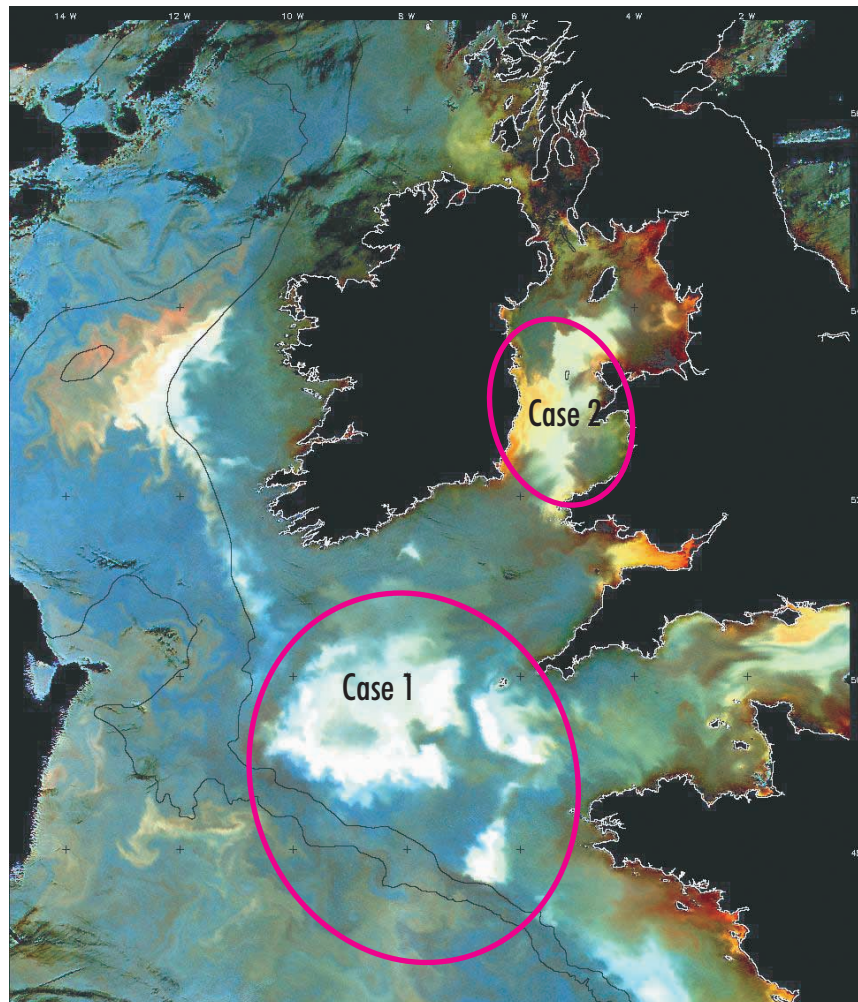
Fig. 6.1 An enhanced true-colour view of ocean colour from the SeaWiFS satellite (18 May 1998 1308 GMT) showing Case 1 and 2 waters around and to the south-west of the British Isles, North-West Europe. Satellite images were received by the NERC Dundee Satellite Receiving Station and processed by Peter Miller and Gavin Tilstone at the Plymouth Marine Laboratory (PML) Remote Sensing Group (**www.npm.ac.uk/rsdas/**). SeaWiFS data courtesy of the NASA SeaWiFS project and Orbital Sciences Corporation.

● The presence of a protective eye membrane in neritic squid may be an adaptation to heavy particulate loading in near-shore seas.

squid are replaced largely by members of the suborder Oegopsina (for example the European flying squid, *Todarodes sagittatus*) in which the membrane is absent, possibly because it is unnecessary.

The pelagic component of the open ocean can be divided further by depth. The upper surface of the ocean is known as the **neustic** zone and, in the tropics especially, is an habitat made harsh by exposure to high

levels of ultraviolet radiation. Floating organisms inhabiting this zone typically have a blue colouration (Fig. 6.2) due to the presence of protective pigments that are able to reflect this damaging part of the light spectrum. The development of the ozone hole in the Earth's atmosphere has resulted in increased levels of UV radiation reaching the Earth's surface (the ozone layer acts as an UV shield), particularly in the southern hemisphere. In the Southern Ocean, Antarctic krill (*Euphausia superba*) may be particularly vulnerable to UV-induced DNA mutation because krill DNA is rich in thymine, which is the base that is most susceptible to UV radiation damage (Jarman et al. 1999). Since krill migrate away from the sea surface during daylight hours, however, their behaviour will probably serve to limit DNA damage, but UV damage to other species remains a distinct possibility.

Light also plays an important role in pelagic ecosystem function away from the neustic zone, both because it drives primary production (Chapter 2) and because it enables visual predation (predators that hunt using the sense of sight). In clear oceanic waters the threat from visual predators is increased because these predators can detect prey over greater ranges (Aksnes & Giske 1993). Shark attacks on humans often occur in turbid waters (Cliff 1991), possibly because under these conditions prey recognition is difficult and humans are mistaken for typical prey such as seals. The upper part of the water column into which light penetrates is called the photic zone. In clear tropical oceanic waters this zone may extend as deep as 200 m (much less in more turbid, temperate locations), although at this depth light intensity will usually be too low to drive photosynthesis (Chapter 2).

The upper 200 m of the water column is also known as the epipelagic (Fig. 6.3). Light at the red end of the spectrum is absorbed rapidly by seawater and does not penetrate far into the epipelagic zone (Chapter 2). Red colours are effectively invisible at depth, therefore, and many pelagic crustaceans adopt this colour as a means of camouflage against visual predators (Fig. 6.4). Below the epipelagic zone are, sequentially, the mesopelagic (200 m to 2000 m), the bathypelagic (2000 m to 4000 m), and the abyssopelagic (4000 m to 6000 m) zones. As depth increases, organisms in the pelagic environment are faced with increasing physiological challenges: pressure increases by 1 atmosphere for every 10 m increase in depth (Box 6.1; 1 atmosphere $= 1\,\mathrm{kg\,cm^{-2}}$ or approximately the mass of a Mini on an area $25\,\mathrm{cm} \times 25\,\mathrm{cm}$), and in some locations oxygen-minima layers (Rogers 2000) arise at depth because oxygen is depleted by bacteria breaking down material sinking from the sea surface.

In general terms the total mass of biota per unit volume of seawater decreases with depth (Yamaguchi et al. 2002). This is because, with the exception of energy input by chemoautotrophic processes at hydrothermal vents (Chapter 8), biological processes in the deep sea are
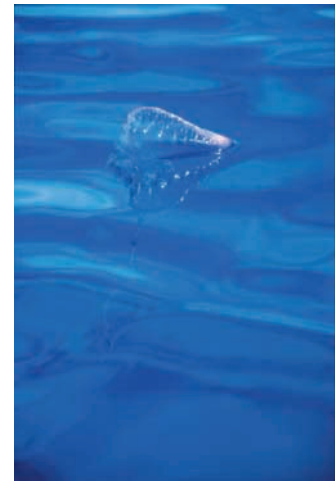

Fig. 6.2 The Portuguese man-o-war (*Physalia physalis*, a colonial Cnidarian) floats at the sea surface and has a blue colouration. Photograph from joaoguaresma.com with permission.

● Organisms that live in the neustic zone are particularly vulnerable to changes in UV radiation.

● Daily and seasonal changes in incident light intensity have profound effects on biological processes in the pelagic environment, driving vertical migrations and seasonal plankton blooms.

● The total mass of biota per unit volume of seawater decreases with depth.
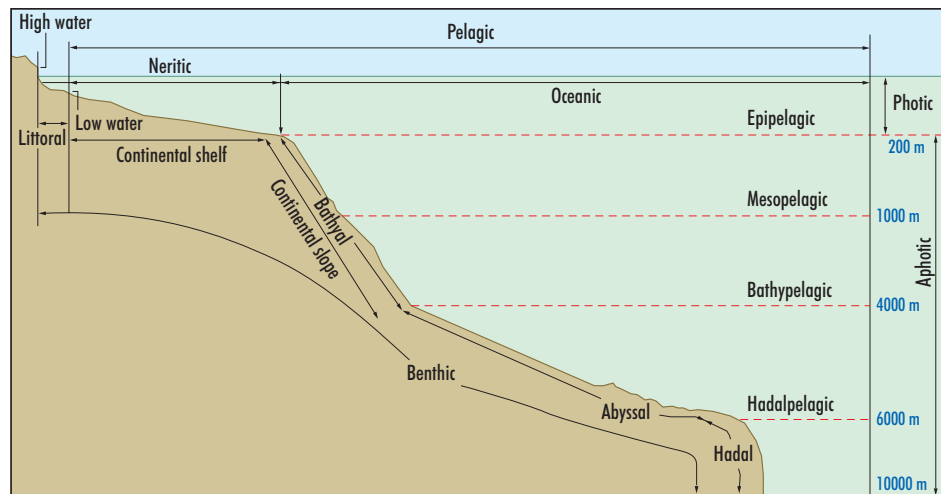
Fig. 6.3 Depth zones.

Fig. 6.4 A mesopelagic zooplankton/nekton sample showing the predominance of red-coloured crustaceans. Photograph: Andrew Brierley.

fuelled entirely by photosynthetically–generated organic matter that sinks from the illuminated surface region. As material sinks further from the surface it becomes distributed through an ever-increasing volume of water. This dilution effect means that as distance from the surface increases, food availability decreases, with the consequence that less animal biomass can be sustained at depth. In the deep pelagic zones,

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Box 6.1 Seawater as a dense and viscous (sticky) medium

Seawater is denser and more viscous than air. The increased **density** offers advantages to some marine organisms, for example providing physical support that reduces the need for skeletal strength, but also presents challenges such as rapidly increasing pressure with depth. Seawater density varies as a function of the concentration of dissolved salts (**salinity**; salinity is reported without units since it is defined in terms of the ratio of the electrical conductivity of seawater to the electrical conductivity of a potassium chloride standard, see also Chapter 4) and temperature (warm water is less dense than cold water). The strength of cohesion, or stickiness, of a fluid is quantified by its **dynamic viscosity**. The dynamic viscosity of olive oil, for example, is 40 times that of seawater. The motion of a particle of a given size and velocity is more impeded through a medium of greater dynamic viscosity (think of marbles sinking through a bottle of water and a bottle of olive oil). For a fluid of a given dynamic viscosity (e.g. seawater) the continuity of motion of a particle is controlled by its velocity and size, and can be quantified by the **Reynolds number** (Re). For a given fluid, Re is simply ((particle velocity × particle size)/dynamic viscosity). Re is dimensionless because the units used in its calculation cancel out. Broadly speaking for small organisms moving at slow speeds Re is less than 1000 and seawater is 'sticky': ciliates, for example, stop the moment they cease swimming. For larger organisms travelling at higher speeds Re is greater than 1000: the inertia of a large pelagic fish, for example, enables it to continue gliding through the water even after it has ceased active swimming (see also Chapter 3).

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energy efficiency is particularly important and animals adopt stealthy, sedentary lifestyles and use cunning mechanisms to ambush prey in darkness (Seibel et al. 2000).

● Energy efficiency is important in the deep pelagic due to the dispersed nature of potential food.

6.3 Pelagic Inhabitants: Consequences of Size

Pelagic organisms can be divided in to two categories on the basis of their locomotory prowess. Plankton are unable to counteract the influence of currents and drift passively in the horizontal plane (ocean currents often exceed 1 knot or $c.0.5\,\mathrm{m\,s^{-1}}$). Plankton can move vertically, adjusting their depth, and do so pronouncedly during diel vertical migrations at dawn and dusk (Fig. 6.5). Diel vertical migrations are a ubiquitous feature of pelagic ecosystems (Hays 2003) and are thought to be driven primarily by the trade off required to enable plankton to feed in the food-rich upper water column and yet to avoid the illuminated upper layer in daylight because of the increased risk of visual predation incurred there at that time (Tarling 2003). Some organisms, such as copepods and chaetognaths, complete their entire life cycle as plankton and are called holoplankton. Others, such as fish larvae and barnacle

● The word plankton is derived from the Greek word planao, which means 'to wander'
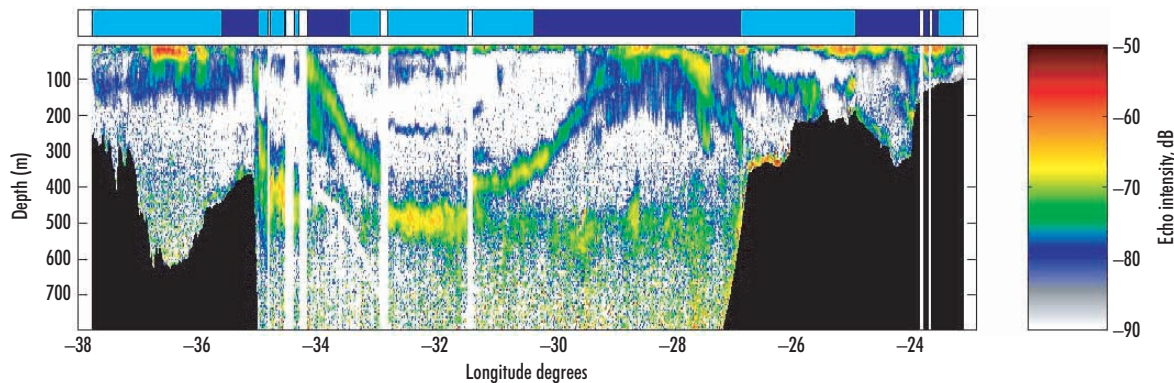
Fig. 6.5 An echogram showing the rapid ascent of zooplankton and nekton (as detected using a 38 kHz scientific echo-sounder) from depth to the near surface at dusk. This migration from 400 m to 50 m takes less than 2 hours. The upper bar indicates periods of day (light blue) and night (dark blue).

● Animals whose larvae have a planktic phase generally produce a relatively high number of eggs for their body mass.

larvae, spend only a part of their life cycle as plankton, either growing or settling out to the seabed as they age, and are called **meroplankton**. A **planktic** phase provides opportunities for dispersal and colonization, but is also a stage that is particularly vulnerable to predation (Pechenik 1999, see also Chapter 13).

Organisms that are capable of swimming to the extent that they can overcome currents are known as **nekton**. Inhabitants of the open ocean span several orders of magnitude of size, ranging from viruses, bacteria, and protozoa to large predators such as sharks and whales, which may reach many metres in length and body masses of several tonnes. Generally speaking, large organisms are **nektic** and smaller organisms are **planktic**: **micronekton** have intermediate swimming abilities and are of the order of 4 cm in length (for example large euphausiids). This size-related difference in mobility arises in part because of the interaction between size and viscosity (Box 6.1): seawater is essentially a 'sticky' medium for small organisms (Van Duren & Videler 2003) and a constant expenditure of energy is required to maintain their movement. There are exceptions, however, and the Arctic lion's mane jellyfish (*Cyanea arctica*), for example, may attain tentacle lengths of 40 m but is a passive, planktic drifter. The very smallest planktic organisms include viruses and bacteria (Azam & Worden 2004) and protozoa (Struder-Kypke & Montagnes 2002). The small size of these organisms belies their importance to pelagic ecosystem function. Dissolved organic carbon is taken up by bacteria, which are consumed by heterotrophic nanoflagellates and in turn by ciliates in the so-called **microbial loop** at the base of the food chain (Chapter 3). This loop recycles organic matter

that is too small to be consumed by metazoan plankton, and the metazoans are able to prey upon ciliates. The microbial loop therefore fuels the pelagic food chain, and is especially important in oligotrophic waters (Lenz 2000).

As well as impacting mobility, organism size is also a major architect of pelagic food web structure. Pelagic organisms will typically consume food items whole and the size of item that an animal can consume is constrained by its mouth size such that predators are usually substantially larger than their prey (Cohen et al. 1993; Jennings & Warr 2003). This concept is well captured by Brueghel's picture *Big fish eat little fish*, in which small fish are tumbling out of the mouths of successively bigger fish (Fig. 6.6). A more trophically extensive example from the North Sea has unicellular algae such as diatoms (*c*.100 μm diameter), grazed by copepods (e.g. *Calanus finmarchicus, c*.3 mm length), which are in turn predated by herring (*Clupea harengus, c*.20 cm length), which might be consumed by gannets (*Sula bassana*, wing span *c*.180 cm). This strongly size-structured progression is in marked contrast to many terrestrial food chains where small predators (for example hyenas, body mass *c*.40 kg) may cooperate in social groups to take herbivores that are considerably larger (e.g. wildebeest, *c*.250 kg).

Pelagic food webs are often far more complex than the simple four-linked-chain diatom-copepod-fish-bird example from the North Sea. An analysis of a 29-species food web for the Benguela ecosystem undertaken

● Very few pelagic organisms dismantle their prey before eating, a behaviour more common in benthic biota such as crabs.

● In terrestrial systems, animals that forage in social groups can deal with prey items much larger than themselves.
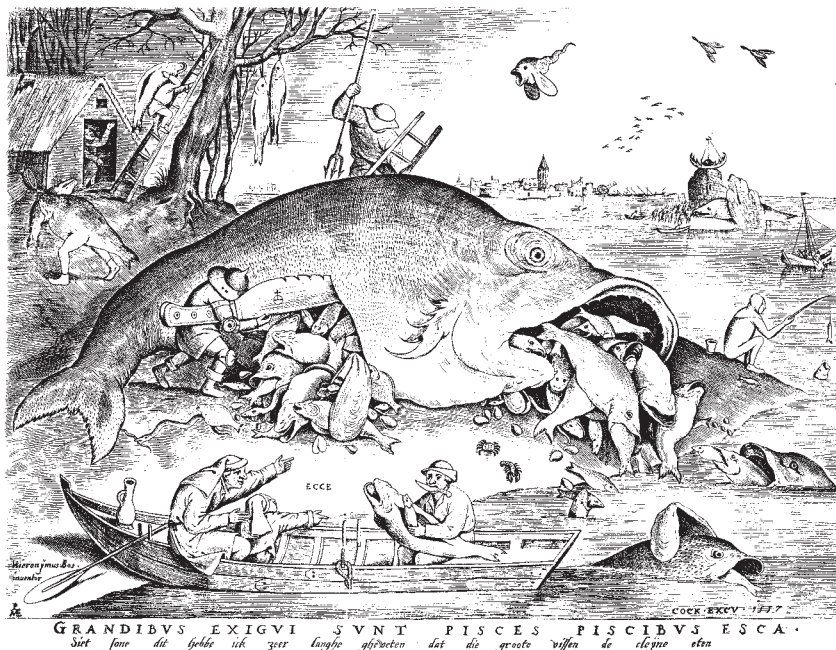

GRANDIBVS EXIGVI SVNT PISCES PISCIBVS ESCA.
Siet sone dit hebbe ick zeer langhe ghewaeten · dat die groote vissen de cleyne eten

Fig. 6.6 '*Big Fish Eat Little Fish*:' after, by Pieter Brueghel the Elder (1557) showing smaller fish tumbling from the mouths of bigger fish. The Metropolitan Museum of Art, Harris Brisbane Dick Fund, 1917. (17.3.859)

● The complexity of food webs means it is difficult (if not impossible) to predict the outcome of selective culling of higher predators on lower tropic levels.

to determine if culling Cape fur seals (*Arctocephalus pusillus pusillus*) would increase hake (*Merluccius* spp.) biomass (Yodzis 2000) noted that there were over 28 million pathways from hake to seals! This complexity of food webs, and the fact that most levels can be controlled either from above (**top-down control**, e.g. by predation) or below (**bottom-up control**, e.g. by food limitation, Verity & Smetacek 1996) renders it very difficult to make predictions of the consequences of bioregulation. In general smaller mean predator : prey body size ratios are characteristic of more stable environments, and food chains are longer when mean predator : prey body size ratios are small (Jennings & Warr 2003). Systems that have shorter food chains are generally much more susceptible to **trophic cascade** effects (Chapter 7).

6.4 Temporal and Spatial Variability in Pelagic Ecosystems

The open ocean is not homogenous. Interactions between physical and biological processes result in variability over a range of temporal and spatial scales, and patchiness is a key feature of pelagic ecosystems. The Stommel diagram (Fig. 6.7) illustrates the scales of variability that are inherent characteristics of pelagic ecosystems, from centimetres to thousands of kilometres and from seconds to millennia, and shows how variations in time and space are interlinked. It is important to appreciate the interplay of temporal and spatial scale, and it is a theme that recurs throughout this book. Phytoplankton are short-lived and are influenced by small-scale mixing processes (Martin 2003). The diel vertical migration of zooplankton at dawn and dusk is restricted to certain times of day but occurs everywhere (Pearre 2003). Fish, which are generally longer lived than zooplankton, are impacted by environmental variability over longer time scales: the Peruvian anchoveta (*Engraulis ringens*), for example, is influenced strongly by the El Niño Southern Oscillation that exhibits decadal scale variability (Chavez et al. 2003, see also Chapters 7, 12, and 14).

● Fish, which are generally longer lived than zooplankton, are impacted by environmental variability over longer time scales.

6.4.1 Physical processes contributing to temporal and spatial variability

The physical properties of the open ocean are heterogeneous by depth, position (latitude, longitude), and over time. In addition to the depth-related changes in light intensity and oxygen concentration already mentioned, vertical gradients in water temperature, density, and nutrient concentration may also exist. Solar heating warms the upper ocean leading to the development of a thermal gradient by depth. In some
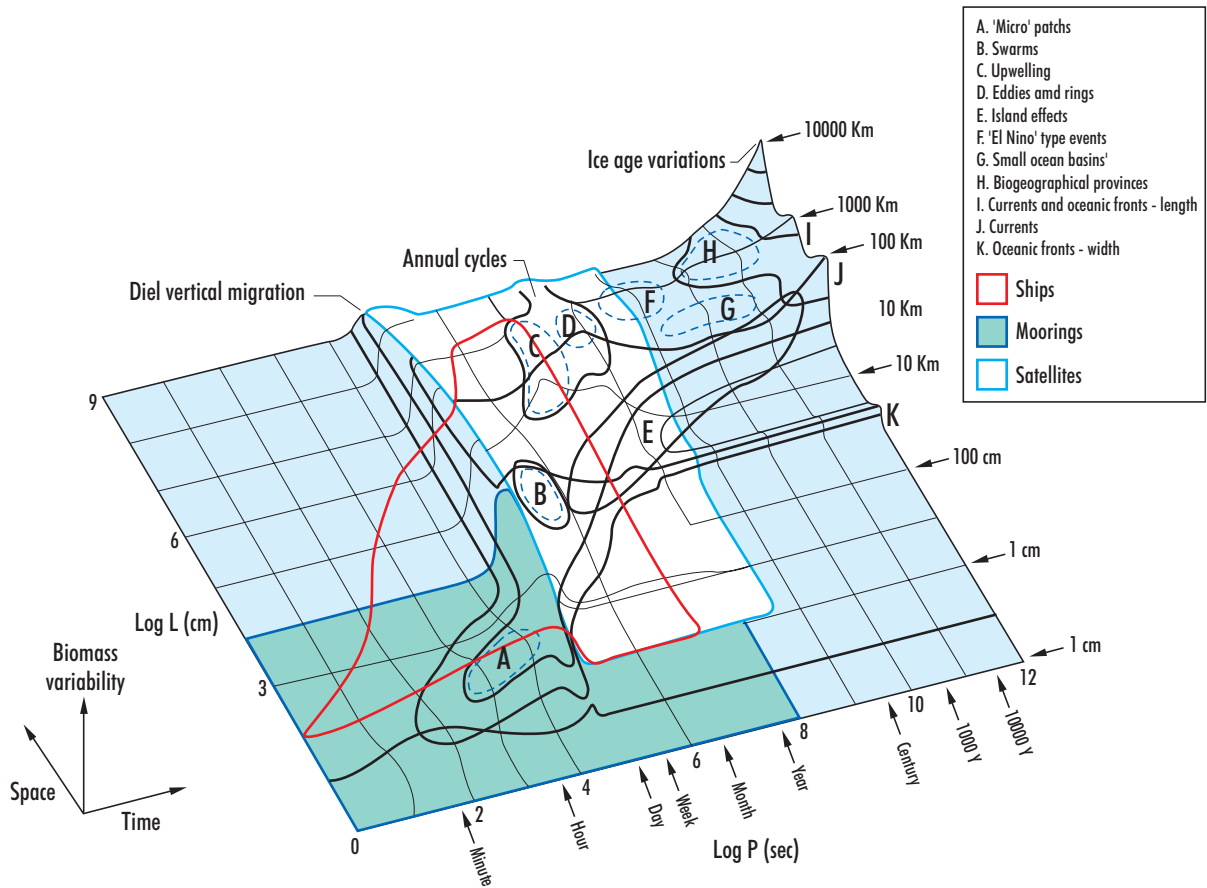
Fig. 6.7 The Stommel diagram, overlain to show the scales that can be sampled with various platforms, and features such as fronts. Modified from ICES Zooplankton Methodology Manual, Harris et al. (eds., 2000), page 36, Copyright 2000, with permission from Elsevier.

regions, combinations of tidal and wind-driven processes cause turbulence and mixing of heated surface water with cooler water below. However, in regions or seasons where winds are light and wave action slight, or in water that is too deep to be mixed completely by tidal flow (Chapter 7), pronounced vertical stratification can become established: warm surface waters then become effectively isolated from cooler, deeper waters by a **thermocline**. Vertical stratification is also promoted in situations where fresh water is introduced. Rain, river run-off, and ice-melt all introduce fresh water to the surface of the ocean. Low salinity waters are less dense than high salinity waters (Box 6.1) and stabilize the upper water column because more energy is required to mix low salinity waters downwards. The strong density gradient between the mixed, buoyant, low salinity surface waters and underlying high salinity waters is known as the **pycnocline**. The depth of the mixed layer,

● Where winds are light and wave action slight, or in water that is too deep to be mixed completely by tidal flow, vertical stratification can develop.

as bounded by the pycnocline or thermocline, will vary depending upon prevailing conditions (Chapters 2 and 7).

As well as causing downward mixing, wind can lead to the upward transport of water from depth. Such wind-driven **upwelling** occurs over a range of scales. At the small scale, **Langmuir circulation** is generated as wind blows steadily across calm water, causing near-surface vortices several metres in diameter to develop parallel to the wind flow (Box 6.2). At the interfaces between neighbouring vortex cells, alternating lines of upward and downward convergence develop. Flotsam accumulates on the surface above the downward zones, leading to the development of prominent, parallel **wind lanes** on the surface. Zooplankton may also accumulate in downward zones because they are able to swim upwards against the flow (Pershing et al. 2001).

At the large scale, wind plays a role inducing flow in most surface currents. Currents do not flow parallel to the direction of the wind but, due to interactions with the **Coriolis force**, when averaged over the whole of the water column, currents move at 90° to the wind. Movement is to

● Langmuir circulation can lead to the accumulation of zooplankton and flotsam, which forms visible wind lanes, at the sea surface.

Box 6.2 Wind-driven circulation processes

As wind blows over the surface of the sea it generates waves and induces vertical and horizontal motion in the water. **Langmuir cells** are small-scale, parallel, helical vortices that are often apparent as a series of **wind lanes** on the sea surface running parallel to the direction of the wind. Vortices are usually not large enough to bring nutrients up from deep water beneath the pycnocline.
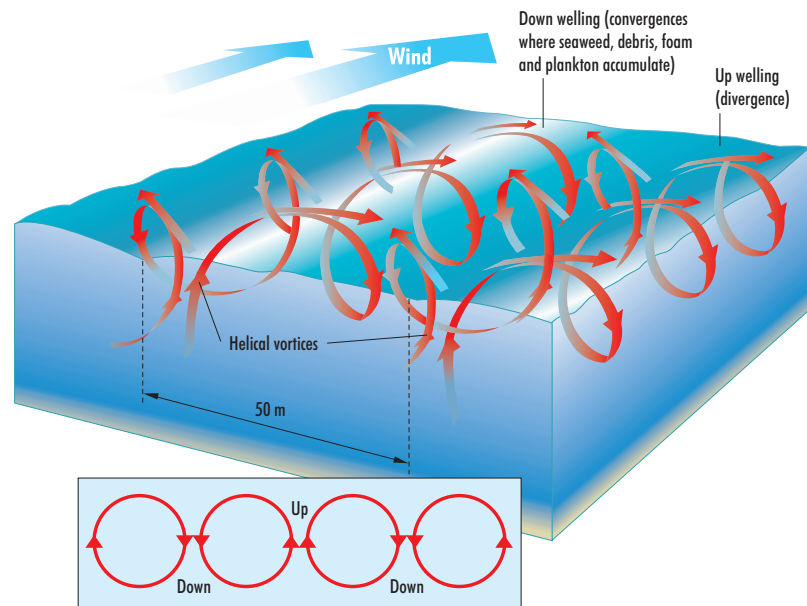
Fig. 1 Large-scale ocean currents are also induced by wind, but occur at angles to the direction of the wind rather than parallel to it. This is because of the interaction between friction and the **Coriolis force**. The Coriolis force is the force experienced by a moving body of water due to the fact that the planet is rotating. The water column can be thought of as a series of horizontal layers. The upper layer at the sea surface is subject to wind friction (**wind stress**) at the top and water friction (**eddy viscosity**) at the bottom. Subsequent layers are impacted by friction with layers above and beneath. Slippage between layers result in an exponential decrease in current speed with depth until, below the **depth of frictional influence**, wind influence ceases. Cumulative impacts of Coriolis force result in an increasing angle of deviation away from the wind with depth. Current vectors in all layers form a spiral pattern known as an **Ekman spiral**. The averaged effect of the spiral is that the mean motion of the wind-driven (Ekman) layer is at right angles to the wind direction. Reprinted from Ocean Circulation, 2nd ed., the Open University Course Team 2001, pp. 42 and 68, Copyright 2001, with permission from Elsevier.
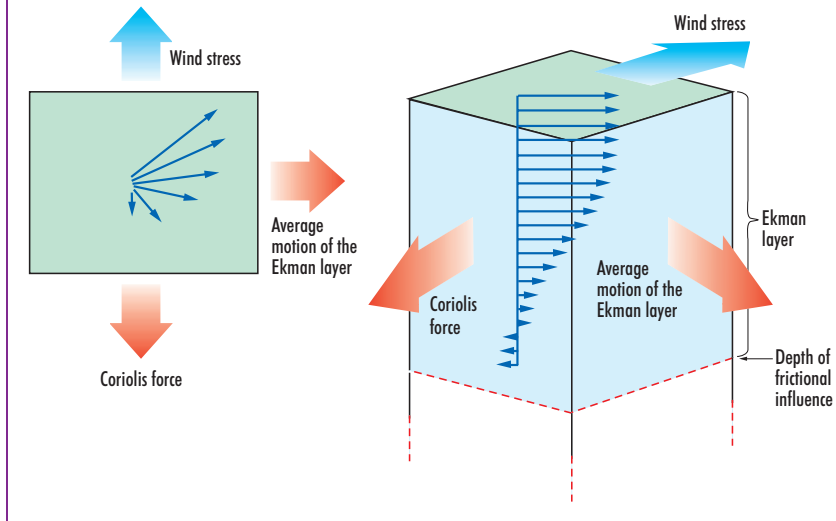

the right of the wind in the northern hemisphere and to the left in the south. This movement is called **Ekman transport** (Box 6.2). It contributes significantly to general ocean circulation and can result in pronounced **upwelling**. In the case of the Benguela Current, for example, and other southern hemisphere **eastern boundary currents**, the prevailing south-easterly winds blow alongshore and drive near-shore Ekman flow away from the coast. This in turn draws cold, nutrient-rich waters from depth to the surface at the coast (Carr & Kearns 2003). Changes in global wind patterns have the potential to affect upwelling and the ecosystems that are dependent upon them (Grantham et al. 2004).

Horizontal boundaries between water masses with different physical properties are known as **fronts** (Box 6.3). Fronts occur at a range of

Box 6.3 Front formation and elevated biological activity at fronts

In the same way that fronts on weather maps mark boundaries between different air masses, fronts in the sea are boundaries between dissimilar bodies of water. Fronts occur off estuaries at boundaries between fresh and salt water, in shelf seas between mixed and stratified waters, at continental shelf breaks adjacent to upwelling regions and, at the global scale, between major current systems. Fronts tend to be sites with higher biological activity that the surrounding water masses, often because nutrients are transported upwards into the stratified euphotic zone at fronts.

Tidal mixing fronts (also known as shelf sea fronts) occur between tidally mixed and stratified waters. They occur when the intensity of turbulent mixing caused by tidally induced flow over the seabed is sufficient to overcome the barrier to mixing caused by thermal stratification. In simple terms, this is a function of the strength of the tidal flow and water depth; a strong tidal flow will generate sufficient turbulence to completely mix shallow water. On the stratified side of the front, nutrient concentrations in the warm surface waters are depleted and the strong thermal gradient prevents nutrients from beneath being mixed upwards. Phytoplankton growth is therefore nutrient limited and low. On the well-mixed side of the front, although nutrients are not limited, phytoplankton are continually mixed down out of the illuminated surface layer and growth is light-limited. At the front itself stratification weakens sufficiently to enable some vertical nutrient flux but remains strong enough to hold phytoplankton in the photic zone long enough for them to take advantage of the nutrients. Increased phytoplankton production at fronts leads to higher zooplankton standing stocks and increased densities of predators and underlying benthos (see also Chapters 2 and 7).
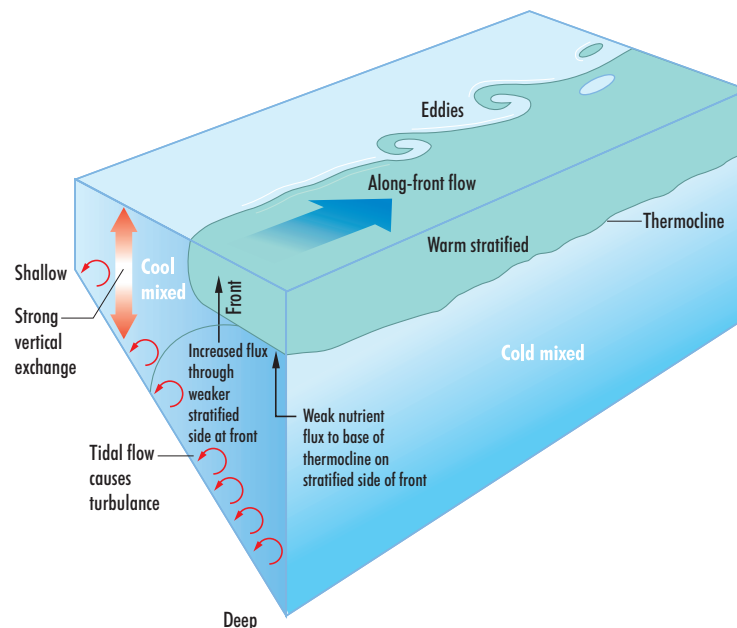
scales, from tidal mixing fronts that separate mixed and stratified waters in coastal seas (Hill et al. 1993) to major oceanographic boundaries such as the North Wall of the Gulf Stream and the Antarctic Polar Front (Taylor & Gangopadhyay 2001). High-velocity current jets associated with fronts can be important long-distance transport routes for many marine organisms: Antarctic krill (*Euphausia superba*) are transported widely throughout the Scotia Sea from breeding centres off the Antarctic Peninsula on frontal currents (Thorpe et al. 2004), and large oceanic squid such as *Illex illecebrosus* take advantage of currents for distribution and feeding (O'Dor 1992). Meanders in fronts can lead to columns of water (core rings) being shed from one side of the front to the other; the retroflection of the Agulhus current around the southern tip of Africa, for example, sheds warm core rings regularly into the south Atlantic (Garzoli et al. 1999) and is an important mechanism for trans-oceanic mixing.

● Most fronts are highly mobile, dynamic features that cannot be represented realistically by single, static lines on charts.

6.4.2. Consequences of temporal and spatial physical variability for pelagic primary productivity and biogeography

The depth to which water column mixing occurs, the mixed layer depth, has major implications for primary production in the open ocean because photosynthesis only takes place in illuminated surface waters. If the mixed layer is deep it is possible that phytoplankton will sink or be carried down below the compensation depth (Chapter 2), reducing net production. In temperate waters, primary production is minimal during winter when light levels and temperatures are low and the upper water column is thoroughly mixed by storm action and convection (Backhaus et al. 2003). Phytoplankton blooms do not commence until calmer, warmer weather in the spring leads to upper water column stratification. From this point on, phytoplankton cells are retained in the upper mixed layer, benefit from the increased illumination from the sun as it reaches higher angles in the sky, and grow and reproduce rapidly. Phytoplankton require nutrients such as phosphate, silicate, and nitrate to grow. As phytoplankton blooms develop, concentrations of these nutrients become depleted and the effective isolation of the mixed layer from the larger nutrient pool beneath means that nutrients are not replenished. In temperate waters, nutrient limitation may inhibit phytoplankton growth throughout the summer months. A second bloom may though occur at the onset of autumn when wind-driven mixing brings nutrient-rich waters from beneath the pycnocline up in to the illuminated surface layer (Diehl 2002).

In regions of the world where upwelling is persistent throughout the year (Box 6.2) nutrients tend not to be limited and annual primary

● Although the development of stratification is a necessary precursor to bloom formation, the persistence of an upper layer that is effectively cut off by density and temperature gradients from the waters beneath can eventually inhibit phytoplankton growth.

● A phytoplankton maximum can develop at the pycnocline late in the season as this is the interface between nutrient-rich deep water and illuminated nutrient depleted surface stratified waters.

● Iron is thought to be one of the key limiting trace elements in HNLC regions, and experimental iron fertilization in these locations has stimulated phytoplankton production (Boyd 2002).

production levels are high. However, in El Niño years, changes in prevailing weather conditions reduce the usually strong upwelling off the coast of western South America and ensuing nutrient limitation has dramatic negative consequences for primary production and fisheries in coastal waters. Tropical ocean basins tend to be permanently stratified and primary production levels are low. As a consequence surface waters in these tropical regions lack particulate matter and are very clear: such waters are termed oligotrophic. Other areas of the world ocean have low phytoplankton biomass despite the presence of high nutrient concentrations. These HNLC (high nutrient, low chlorophyll) regions include the Southern Ocean and Equatorial Pacific, and hypotheses proposed to explain their existence include grazing pressure and absence of trace elements, particularly iron (Chapter 2).

Global variation in the pattern of annual primary production is strikingly clear in images of averaged chlorophyll concentration obtained through satellite imagery (see Fig. 2.3, Chapter 2). Regional coherence in the pattern of annual phytoplankton production has been used as one diagnostic feature in the hierarchical separation of the global ocean into distinct biogeographic biomes and provinces (Longhurst 1998). A biome is the largest coherent community unit that it is convenient to recognize, and Longhurst (1998) distinguishes four in the global ocean, which are characterized by the principal mechanisms driving their mixed layer depth: in the Westerlies biome local winds and irradiance force the mixed layer depth; in the Trades biome the mixed layer depth is influenced by large-scale ocean-circulation processes; in the Polar biome the presence of buoyant, fresh water from ice melt in spring constrains the mixed layer depth; and in the Coastal biome diverse processes including upwelling force the mixed layer depth. Within these biomes, 51 provinces are recognized (Chapter 1). Separation of the global ocean into provinces is very useful because it allows regional differences in physical oceanography to be used to gain understanding, and make predictions, of regional differences in ocean ecology.

● Knowledge that a particular area of ocean lies in a particular province enables predictions to be made regarding ecosystem function there, even if field data for the specific area are lacking.

6.4.3 Consequences for higher trophic levels of variability in primary production

Regions of the world's ocean with high primary productivity support richer pelagic communities, with higher total biomass, than do regions with low primary production. In fact there is a direct linear relationship between the magnitude of annual primary production and nekton (fish and squid) production (Sommer et al. 2002) (Fig. 6.8). This relationship is apparent in the distribution of global fish catches (Chapter 12): nutrient-rich shelf seas and regions with strong upwelling account for the vast majority of the world's commercial catch (Watson & Pauly
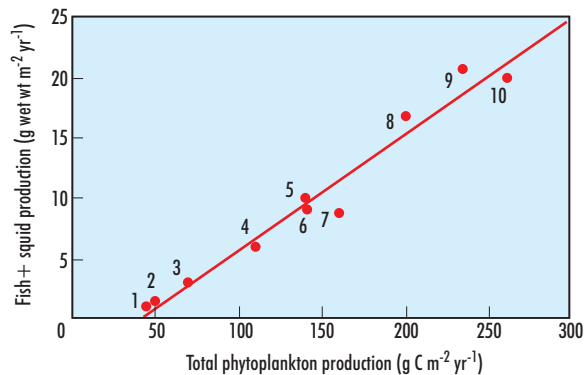
Fig. 6.8 The relationship between primary production and nekton production. Fish and squid production = (0.095 Phytoplankton production) − 3.73, r^2 = 0.96. 1 = Atlantic Ocean gyre centre, 2 = Atlantic ocean gyre boundaries, 3 = Hawaiian waters, 4 = Bothnian Sea, 5 = Gulf of Riga, 6 = Gulf of Finland, 7 = Baltic Sea, 8 = Nova Scotian shelf, 9 = Gulf of Maine, 10 = Mid-Atlantic bight. Redrawn from Iverson 1990. Copyright 2000 by the American Society of Limnology and Oceanography, Inc.

2001), whereas oligotrophic central open-ocean basins contribute little. Commercially important pelagic fish species do not consume phytoplankton directly but usually predate zooplankton and micronekton that are primary consumers. Understanding zooplankton ecology is therefore key to understanding fisheries production.

Zooplankton blooms are only able to develop once phytoplankton biomass and production has become sufficient to sustain zooplankton grazing rates. In temperate waters, therefore, peaks in zooplankton biomass occur in spring and autumn slightly after the phytoplankton blooms. In high latitudes, where seasonality is extreme and the phytoplankton bloom is limited to a single spring/summer peak, some zooplankton species survive the dark, food impoverished winter months in deep water in a dormant state called diapause. Copedods including *Calanus finmarchicus* in the sub-Arctic north Atlantic and *Calanoides acutus* in the Southern Ocean build up large stores of lipids during summer feeding, a small proportion of which fuels their survival over winter. At the end of summer, growth and development are arrested and individuals sink, overwintering in a state of hibernation at depths between 500 m and 2000 m (Box 6.4). In late winter or early spring copepods emerge from diapause and migrate to the surface to spawn. Because of the short production season, the timing of reproduction is critical at high latitudes. By using lipid reserves accumulated in the

● GLOBEC (*glo*bal ocean *e*cosystem dynamics) **http://www.pml.ac.uk/globec** is a global research effort to understand interactions between primary consumers, higher trophic levels and fisheries.

● *Calanus finmarchicus* survives food depleted winter months in the north Atlantic by drawing on lipid reserves. This also enables them to produce young in advance of the phytoplankton bloom in the following year.

Box 6.4 Diapause depth, water density, and lipid composition

The overwintering depth of the copepod *Calanus finmarchicus* varies throughout its distribution range in the north Atlantic. In the eastern Norwegian Sea, for example, *Calanus* overwinters at about 800 m whereas in the Iceland Basin overwintering is at around 1500 m (Heath et al. 2004), despite the fact that both locations have similar total water depths (*c.*2000 m). The water column vertical temperature profile varies markedly throughout the north Atlantic: in the eastern Norwegian Sea the temperature at the overwintering depth is approximately 0 °C whereas in the Iceland Basin it is much warmer (4 °C). This physical variation provides much insight into the variation of the overwintering depth. At the onset of diapause *Calanus* becomes physically inactive and sinks passively until it reaches the depth where it is neutrally buoyant. This is the depth at which the density of the copepod is the same as the density of the surrounding seawater, which itself is a function of ambient temperature and salinity. One of the major contributors to variation in density between copepods is lipid composition, such that density decreases as the proportions of lipid increases. Using knowledge of the temperature and salinity at the overwintering depth in several locations, and hence the density there, it has been possible to predict the proportion of lipid that should be expected in individuals overwintering at particular locations. A very good linear relationship has been found between predicted and actual values (Heath et al. 2004).

It is not yet clear what the main evolutionary drivers of variation in copepod lipid composition are. In order to survive the winter individuals need to descend below the depth of winter mixing, and will also have increased chances of survival overwinter if they descend below depths where predators can operate. In Norwegian fjords overwintering is shallower in fjords where visual predators are absent (Bagoien et al. 2001), but the winter distribution of predators in the open ocean is not yet known. Ironically, therefore, individuals that feed too successfully over summer and lay down excessive lipid reserves may be unable to sink to depths below predators; this would provide a strong selective pressure against over consumption and may be one reason why some copepods enter diapause early in the year when the phytoplankton bloom is still in full swing. Since current flow is different at different depths, the overwintering depth will also have a profound influence on the location at which individual *Calanus* surface after diapuse. In order to complete its life cycle successfully *Calanus* has to surface at a location where offspring can be spawned and hatch and eat, and descend to overwinter to complete the life cycle. It is likely that few depths will enable this to be achieved, providing another source of selection. It is clear that the life cycle of *Calanus* is tied very closely to its environment; understanding the environmental space-time dynamics will be vital to gaining full understanding of regional variability in *Calanus* abundance and consequences to higher trophic levels such as fisheries.

previous year to fuel reproduction, these copepods can spawn early, independent of the present year's phytoplankton bloom, and ensure that their young are in place to fully exploit the short livid phytoplankton bloom.

The timing of the phytoplankton bloom not only influences zooplankton secondary production but also places a significant control

upon organisms that predate upon zooplankton. Developing fish larvae 'surf on the wave of zooplankton production' and the **match-mismatch hypothesis** (Cushing 1990) proposes that larval fish survival will be greatest in years when the period of plankton production overlaps most closely with the period of larval food demand. Satellite data that revealed between-year variations in the timing of the spring phytoplankton bloom support this hypothesis with regard to haddock (*Melanogrammus aeglefinus*) on the shelf east of Nova Scotia (Platt et al. 2003; Fig. 6.9). An index of larval haddock survival (size of age 1 year class divided by spawning stock biomass) showed that two exceptionally strong year classes occurred when the peak of the spring phytoplankton bloom was between 2 and 3 weeks earlier than the long-term average. An early bloom may result in lower larval mortality caused by starvation.

● Survival of larval fish is greatest when the overlap between the period of planktic food availability and food demand by fish is greatest.

Spatial as well as temporal coherence is required between production and consumption if high-biomass pelagic communities are to develop. At the large scale, it has been suggested that iron fertilization in regions of low primary productivity could enhance production up the food chain to zooplankton and fisheries, and that the increased photosynthesis could also lead to an increased drawdown of atmospheric carbon dioxide that may mitigate against climate change. Complex trophic interactions, however, make implementation of this far from straight-forward (Buesseler & Boyd 2003; Gnanadesikan et al. 2003). At the smaller scale, patchiness is essential for maintaining ecosystem function. If phytoplankton and grazers were mixed homogenously then resource depletion would soon occur, whereas spatial segregation enables higher
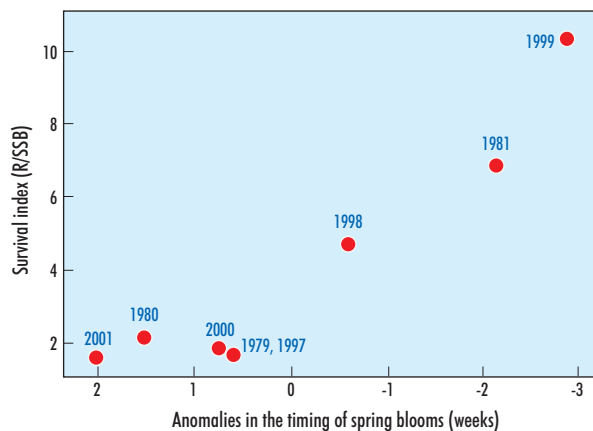

Fig. 6.9 Larval haddock survival (size of the year class at age 1 (R) divided by spawning stock biomass (SSB)) against deviation from the mean time of the annual peak in phytoplankton production. Timing of the peak of the spring phytoplankton bloom explains 89% of the variance in larval survival, providing strong support for the match-mismatch hypothesis. Redrawn from Platt et al. 2003 with permission from the author.

● If phytoplankton and grazers were mixed homogenously then resource depletion would soon occur, whereas spatial segregation enables higher overall biomass to be maintained.

● Conservation measures aimed at reducing conflict between wildlife and fishers need to take in to account the fact that predators forage at production hotspots that occur at oceanographic features such as fronts.

overall biomass to be maintained (Brentnall et al. 2003). Furthermore, if zooplankton did not aggregate in high densities then pelagic filter feeders such as basking sharks and baleen whales would not be able to survive on a diet of these organisms. Whales incur high energetic costs while foraging (Acevedo-Gutierrez et al. 2002) and it has been estimated, for example, that Right whales (*Eubalaena glacialis*) require copepod prey concentrations to exceed a minimum threshold of 4500 individuals m^{-3} of seawater just to balance the energy expended during feeding (Beardsley et al. 1996).

Frontal regions tend to be characterized by increased primary production and to support particularly rich pelagic communities (Box 6.3). Fronts are therefore sites of intense feeding activity and are targeted by mobile predators including fish, squid, marine mammals, and birds (Durazo et al. 1998). The exact mechanisms by which predators locate prey in the wide expanse of the open ocean remain largely unknown and different cues are likely to be important at different spatial scales (Fauchald et al. 2000). In some ecosystems prey are located regularly in production 'hot spots' (Davoren et al. 2003), attracting larger predators in a predictable manner. Conservation measures aimed at reducing conflict between wildlife and fishers need to account for geographic variability such as this in ecosystem management plans. Fisheries for Antarctic krill, for example, may in future be required to operate outside the foraging areas of land-based central-place foragers during their breeding season (Constable & Nicol 2002).

6.5 Sampling the Open Ocean

The sometimes-extreme horizontal, vertical, and temporal patchiness that is characteristic of pelagic ecosystems, and the huge size range of organisms inhabiting the open ocean, present considerable difficulties for quantitative sampling.

Early studies of the open ocean depended almost completely on nets to sample living organisms. Netting remains an important component of biological oceanographic research, but the systems in use today are considerably more complex than those used in the pioneering days (Wiebe & Benfield 2003). These days nets are often equipped with depth, temperature, salinity, and other sensors. Data from these sensors can be relayed to the ship in real time, either along conducting cables or via acoustic links, and enable nets to be placed accurately in the section of the water column of particular interest (Brierley et al. 1998). Optical particle counters (OPCs) can be used instead of nets to obtain estimates of zooplankton numerical density (Heath 1995), and photographic and video devices allow high-quality images of ocean inhabitants to be obtained

> ### Box 6.5 Microlayers
>
> Advances in the resolution of optical and acoustic sampling technology have lead to the discovery of widespread 'thin layers' of high biological activity in the ocean. These layers, which range in thickness from a few centimetres to a few metres, may be many kilometres in horizontal extent and may persist for several days. They contain densities of organisms several orders of magnitude higher than adjacent depth zones, and layers at different depths in the same area may contain distinct plankton assemblages. Thin layers produce microenvironments of physical, chemical, and biological parameters. Microlayers sometimes occur at the pycnocline as zooplankton forage on material that is suspended there, but may be deeper or shallower. Layers tend to occur in stratified water where current sheer is low. The species or populations that comprise each distinct thin layer probably aggregate in response to different sets of biological and/or physical processes. The existence and persistence of planktic thin layers generates great biological heterogeneity in the water column, and may go some way to explain the 'paradox of the plankton' in which high species diversity occurs in small, apparently homogeneous bodies of water.

(Benfield et al. 1996). Light is attenuated rapidly by seawater though, and visual sampling is often constrained by water clarity (Chapter 2). Sound, on the other hand, propagates very efficiently through seawater, as is testified by the long-range vocal communications of some whales. Scientific echo-sounders can be used to detect and quantify abundance of zooplankton and fish (Holliday & Pieper 1995), and ever-increasing sampling resolution is detecting biologically important features such as micro-layers (McManus et al. 2003), which are likely to be of very major importance to pelagic ecosystem function (Box 6.5).

At the larger scale, organisms that must come to the sea surface to breath (e.g. seals, whales), or that forage over the sea surface (e.g. seabirds) can be counted at sea by observers on research vessels. Although much biological oceanographic data is still collected from ships, logistic constraints place restrictions on the amount of time that ships can spend at sea. In order to make longer-term observations, or observations over large extents of ocean, other sampling platforms or techniques are required. Moored instruments can be used to collect long time-series of data from spot locations (Schofield et al. 2002). Autonomous underwater vehicles (Box 6.6) have the potential to be able to operate in weather conditions that curtail sampling from ships, and in addition can work in environments that are impenetrable to ships. Earth-orbiting satellites are able to provide coverage of the entire surface of the global ocean on a weekly basis and deliver near-synoptic information on, for example, sea surface temperature, chlorophyll concentration, and frontal position (Miller 2004).
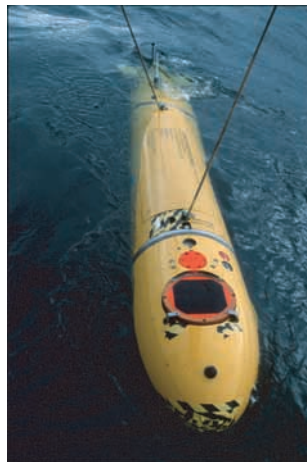
Satellites can also be used to track the movements of larger animals as they forage at sea over extended periods of time (Thompson et al. 2003).

● While modern imaging and acoustic technology has improved our ability to sample the ocean realm, we continue to be reliant upon often-rudimentary nets to obtain biological samples.

● Satellites can relay information from tags attached to air breathing animals such as whales and turtles, collecting data about their behaviour and patterns of movement in real time.

Box 6.6 **Autonomous Underwater Vehicles**

Autonomous Underwater Vehicles (AUVs) are unmanned submersibles that can be programmed to navigate in three dimensions underwater. They can carry a variety of scientific instruments and are able to make measurements in parts of the ocean that are inaccessible, either physically or operationally, to conventional research platforms such as ships. The *Autosub* AUV, for example, has been equipped with a scientific echo-sounder and deployed on missions beneath Antarctic sea ice. There, it has made observations on the distribution of krill under ice, and of ice thickness, that were impossible to make using ice-breaking research vessels (Brierley et al. 2002). *Autosub* is among the largest of AUVs presently available to the scientific community, with an instrument payload capacity of 100 kg (weight in water). *Autosub* is 7 m long × 1 m in diameter, weighs 2400 kg, is powered by manganese alkali batteries, propeller-driven, has a range of about 800 km, and a maximum depth capability of 1600 m. Web link: **http://www.soc.soton.ac.uk/ OED/index.php?page = as**

Leatherback turtles (*Dermochelys coriacea*), for example, have been tracked in the north Atlantic (Hays et al. 2004). Leatherbacks are critically endangered, and a major source of mortality for them is capture by pelagic fisheries. Knowledge of Leatherback distribution and dive characteristics obtained via satellite telemetry could lead to the implementation of conservation measures designed to reduce the interaction of turtles with fisheries, and thus reduce by-catch.

The capacity of scientists to be able to collect data from the pelagic realm seems ever to be increasing. Plans are afoot to establish a series of permanent, automated ocean observatories that will be able to deliver multidisciplinary data continuously in real time, year on year. Although these systems will contribute enormously to our understanding of ocean ecosystem function, they will present new challenges in terms of extracting meaningful summaries from potentially overwhelming quantities of data.

6.6 Pelagic Fisheries

Fisheries for pelagic species have the potential to be among the most sustainable and least damaging to the environment. Shoaling species like

the Atlantic mackerel (*Scomber scombrus*) and North Sea herring (*Clupea harengus*) form single-species aggregations and by-catch is minimal (Chapter 12). Indeed, at the time of writing, stocks of these two species seem to be bucking the global trend of decline and are thriving under good management and regulation. Myctophids, or lantern fish, are small mesopelagic fish that form a major component of oceanic deep scattering layers. They have been fished historically in the south-west Indian Ocean and in the south Atlantic, but fishing ceased in 1992 because of unfavourable economics and market-resistance, and myctophids are not presently under threat.

Planktivorous forage fish such as sardine and anchovy have vital ecosystem functions, particularly in upwelling zones, where they typify mid-trophic-level wasp-waist ecosystems (Cury et al. 2000). Abundance of these species can fluctuate wildly under variable environmental regimes and high fishing pressure and may result in major ecosystem changes. Fishing for large tropical pelagic fish including tuna and jacks has also had substantial impact. Analyses of long-lining data suggest that 90% of biomass of large pelagic fish may have been removed (Myers & Worm 2003). Open-ocean fisheries have tended to develop ahead of management procedures (maybe by as much as 15 years) and, in the case of pelagic long-line fisheries, it is possible that the estimated pre-exploitation biomass to which management processes are anchored are unrealistically low because they represent already-depleted stock levels. This 'missing baseline' presents particular difficulty for the long-term restoration of stocks because the size of the stock pre-exploitation remains unknown, and thus it is very difficult to say when or if restoration has been achieved. Not only has long-lining hit pelagic fish hard, but it has been and is still responsible for substantial declines in albatross populations. Albatrosses take baited long-line hooks as they are thrown from fishing vessels, drowning as the long-line sinks, and some populations are showing marked and continuing decline (Tuck et al. 2001). Seine netting for tuna also suffers from by-catch, particularly of dolphins, although, following international outcry, practices are in place to reduce the impact to levels that are now ecologically sustainable (Hall 1998).

Squid are fished on the open seas, mostly using hooked, coloured lures (jigs) at night to catch animals attracted to bright lights. The high intensity lights used to attract squid to jigs are so bright that they can be seen from satellites, and this has opened a new mechanism for potentially monitoring and managing open-ocean squid fisheries (Rodhouse et al. 2001). Robust management is particularly important for squid because they are short lived, often semelparous (spawn once and die), species and therefore vulnerable to over-fishing since there are few cohorts to provide a buffer from failure of any single generation. Squid also respond rapidly to changing oceanographic conditions and it is

● Fisheries for pelagic species have the potential to be among the most sustainable and least damaging to the environment.

● It is possible that the estimated pre-exploitation pelagic fish biomass to which management processes are anchored are unrealistically low because they represent already-depleted stock levels, the so called 'missing-baseline' effect.

● The whole issue of 'dolphin-safe' tuna remains the subject of debate and there are moves in the United States to ease legislation relating to the definition of the product.

● Semelparous animals such as squid are particularly vulnerable to over-fishing as their populations are not composed of multiple cohorts that provide a safety net against over-exploitation.

● The 1988 regime shift in the North Sea may have been caused by a change in the North Atlantic Oscillation.

becoming increasingly clear that it is essential to understand interactions between squid and their ocean environment in order to predict inter-annual variations in recruitment. Recruitment of the squid *Illex argentinus* to the Falkland Islands fishery, for example, increases in years when water temperatures over the squid egg-hatching grounds are favourable (16 to 18 °C). In years when movement of the highly dynamic front between the Brazil and Falkland currents displaces waters of favourable temperature from over the hatching area, recruitment is reduced (Waluda et al. 2001).

6.7 Regime Shifts in Pelagic Marine Ecosystems

Ecologists have long recognized that ecosystems may exist in 'multiple stable states'. In the oceans, conspicuous jumps from one state to another have become known as regime shifts (Scheffer et al. 2001). Shifts typically take less than one year to occur and regimes may persist for decades (Hare & Mantua 2000). Regime shifts may be driven by climatic changes, fishing pressure, or both, and may be manifest in parameters that measure physical and biological ecosystem state. In the north Pacific, statistically significant regime shifts in 1977 and 1989 are apparent in a composite index of 100 biological and physical time series including the Pacific Decadal Oscillation (PDO), zooplankton biomass estimates and salmon catches (Fig. 6.10).

Regime shifts present major challenges for scientists attempting to manage fisheries. In the North Sea a regime shift in 1988 was evident from plankton time-series data from the Continuous Plankton Recorder (CPR) surveys (Reid et al. 2001). It has been suggested that this shift was caused by increasing flow of Atlantic waters into the North Sea, an increase that was correlated with a change in the North Atlantic Oscillation Index (NAOI). Recruitment of cod (*Gadus morhua*) in the North Sea has declined since the mid 1980s and it is possible that changes in the plankton following the regime shift have had a negative impact on the supply of food to young cod (bottom-up control) (Beaugrand et al. 2003). In the face of such possible environmental impacts on fisheries, it is clear that future attempts to manage fisheries will need to take environmental factors into account as well as data on fish population dynamics and catch levels. This realization has led to calls for the development of an holistic, ecosystem approach to fisheries management (Pitkitch et al. 2004; Chapters 12 and 15).

Although not necessarily a symptom of regime shift *per se*, jellyfish appear to have increased in prominence in many pelagic marine eco-systems worldwide in recent years (Mills 2001). Jellyfish blooms have occurred in the Bering Sea, the northern Benguela current and elsewhere,
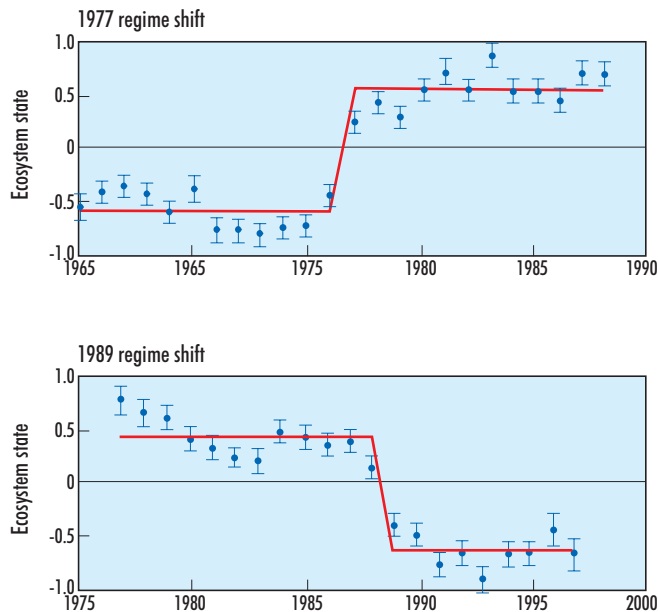
Fig. 6.10 Mean and standard error of a composite index of 31 physical and 69 biological parameters from the north Pacific between 1965 and 1997, showing significant step changes or 'regime shifts' in 1977 and 1989. The physical time series represent atmospheric and oceanic processes, while the biological time series all relate to oceanic species ranging from zooplankton to salmon and groundfish. Each of the time series was normalized before plotting and statistical analysis by subtracting the mean across both regimes and then dividing the data for each regime by the standard deviation for that regime. Standard errors for each year were computed as $s/\sqrt{n}$, where s is the standard deviation across all variables within a year and n is the number of time series used in the calculation ($\leq$100). Redrawn from Scheffer et al. 2001 with Nature Publishing Group's copyright permission and permission from the author.

possibly in response to climate and fishing effects. Indeed, it has been suggested that jellyfish-dominated communities are the inevitable end point in pelagic ecosystems perturbed by fishing (Pauly & MacLean 2003). In the North Sea, correlations between the abundance of jellyfish and an Index describing the periodically fluctuating North Atlantic Oscillation (NAOI) have been detected (Lynam et al. 2004). Furthermore it seems as though the recruitment of herring (*Clupea harengus*) in the North Sea is adversely effected by high jellyfish abundance (although it is not clear as yet whether this is due to predation by jellyfish on herring eggs or larvae, competition between jellyfish and herring for zooplankton food, or both). Complex interactions between climate and jellyfish may therefore impact fish stocks, even in the absence of fishing, and could have major implications for the recovery of fish stocks even after any cessation of fishing.

● Jellyfish-dominated pelagic communities may be one consequence of overexploitation of pelagic fish stocks.

● The NAO is presently in a high phase, possibly restricting jellyfish abundance. If the NAO were to switch phase, climatic inhibition of jellyfish abundance may be relaxed and their numbers may increase with adverse consequences for fish stocks.

There has been an almost exponential rise in the incidence of the term 'regime shift' in the scientific literature since the early 1990s. It is possible that this is because the incidence of regime shifts is increasing, or that accumulating time-series of data are enabling more changes to be detected. A note of caution is perhaps necessary regarding this apparent increasing prevalence however: simulation studies looking at random, independent time series with the same frequency content as the Pacific Decadal Oscillation have shown that techniques used to identify 'regime shifts' may find them in noise. Detection of step-changes does not therefore necessarily provide evidence of processes leading to any meaningful regime shift (Rudnick & Davis 2003) since the step changes may be artefacts of the data.

6.8 The Future for Pelagic Marine Ecosystems

With an ever-increasing human population, and an ever-growing demand for food protein, it seems likely that pressure on the open ocean is likely to continue to grow. There is a history of fisheries advancing further from shore, into deeper and more distant waters, as conventional coastal resources are depleted and this looks set to continue. Fishing effort has already had major impacts on the global ocean. As traditional fish species are removed, fishing effort turns from these higher-trophic-level predators to smaller species. This phenomenon has become known as **fishing down the food web** (Pauly et al. 1998) and is ecologically unsustainable.

Humans are not just altering the open-ocean ecosystems by removing biomass but are also degrading it by addition. The incidence of waste in the ocean is increasing, with floating rubbish potentially distributing species far beyond their usual ranges, leading to alien colonizations of distant shores (Barnes 2002). Introductions of alien species in ballast water from cargo ships has also had devastating effects on pelagic ecosystems, such as the introduction of the ctenophore *Mnemiopsis leydii* to the Black Sea (Kideys 2002). This ctenophore, a native of the eastern USA, was predatory upon fish eggs and led to the collapse of the Black Sea anchovy fishery. Dumping CO_2 at sea in an attempt to reduce further increases in atmospheric concentrations is being investigated (Hunter 1999). As well as the addition of objects and organisms, human activity has also increased noise levels in the ocean. Low frequency noise from shipping, oil-exploration, and military activities may adversely impact cetacean communication and foraging (Croll et al. 2001) by masking the sounds these animals generate. Killer whales (*Orcinus orca*) in the waters of Washington State, USA, increase the lengths of their calls significantly (by about 15%) in the presence of whale-watcher

● The incidence of waste in the ocean is increasing, with floating rubbish potentially distributing species far beyond their usual ranges leading to alien colonizations of distant shores.

boat traffic, and probably do so in an attempt to overcome the noise generated by these boats that may mask their usual calls (Foote et al. 2004).

A recent forecast of the likely state of aquatic ecosystems in 2025 identified climate warming as the most significant single threat (Chapter 14), and climate changes have already had measurable impacts on sea ice extent and zooplankton distributions (Polunin, 2005). Perhaps the biggest climate-related threat to pelagic marine ecosystems arises from the possibility that increased warming and consequent freshening of the Arctic may switch off the north Atlantic current and hence perturb global ocean circulation (Rahmstorf 2002). It is probable that changes like this have happened multiple times during the Earth's history, and occurred over very short periods. If, as some models predict, this were to happen again in the near future, the consequences for the Earth's ecosystem and climate would be so severe that concern for the state of the pelagic realm would probably not be at the top of humanity's agenda.

● CHAPTER SUMMARY

- The pelagic realm is highly heterogeneous, and production is patchy in both space and time. Generally production is higher closer to land, because of increased nutrient input (rivers, upwelling), and close to the surface because of light availability. There is a direct link between primary production and fisheries production.

- Organism size has a major bearing on mobility in the pelagic environment. Plankton are generally small ($<$10 mm long) and are unable to swim against currents and drift passively on them. Larger organisms (nekton) can move actively against currents. Plankton can however move vertically and undertake pronounced diel migrations.

- Pelagic food webs are size-structured: small organisms are consumed by a succession of larger grazers or predators. Most biomass occurs at the lowest trophic levels (grazers) and gradually decreases at increasingly higher trophic levels.

- Environmental heterogeneity and the large range of pelagic organism-size (from plankton to whales) presents a severe challenge for sampling the pelagic environment. Technological advances provide the means to collect ever-increasing quantities of data, but net sampling remains important for collection of biological material.

- Pelagic fish that form large single-species shoals should be amongst the most straightforward to manage and can be exploited with little risk of bycatch. Nevertheless, even pelagic species that inhabit remote locations far from land have been impacted severely by fishing.

- Pelagic ecosystems can suffer step-changes, shifting rapidly from one state to another. Such regime shifts may be due to impacts of climatic change, and have major implications for ecosystem management.

● **FURTHER READING**

Longhurst (1998) provides an excellent description of the causes and consequences of geographic variability throughout the world's ocean. Mann and Lazier (1998) give a broad coverage of biological responses to physical processes in the ocean. A useful plankton atlas of the North Atlantic was published in Volume 278 of Marine Ecology Progress Series (2004). This provides a summary of Continuous Plankton Recorder (CPR) methods, and describes how this invaluable long-term record has become an important implement in our understanding of how pelagic ecosystems respond to global change. Steele (2004) provides a brief review of regime shifts and their definition. His article is the first article in a special issue dedicated to regime shifts.

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