

Chapter 2

The Functioning of Coastal Upwelling Systems

Abstract This chapter describes the general physics driving coastal upwelling, various upwelling mechanisms and indicators (e.g. upwelling index), the ecological response to coastal upwelling events, the location of significant upwelling regions, their general biogeochemistry, and various hypotheses for the high abundance of anchovies and sardines in coastal upwelling regions.

Keywords Upwelling · Physical mechanisms · Upwelling index · Biogeochemistry · Ecological response · Theories on fish production

How do you expect to communicate with the ocean,
when you can't even understand one another?

Stanislav Lem (1921–2006)

(Taken from *Solaris*, 1961, reproduced with permission)

2.1 The Physics of Coastal Upwelling

In general, upwelling refers to an upward movement of water parcels in the water column that is maintained over a reasonably long period ($\sim$ several days to weeks), long enough to lift water parcels over a vertical distance of ~ 100 m or more. Here we focus on the classical wind-driven coastal upwelling mechanism that creates the largest and most persistent upwelling regions in the world ocean. Other upwelling mechanisms are described in the last part of this section.

The main forms of wind-driven upwelling are (i) coastal upwelling, (ii) equatorial upwelling, and (iii) ice-edge upwelling (Fig. 2.1). The Earth's rotation and its associated effects, such as the Coriolis force, play a dominant role in the dynamics of upwelling in all three systems. Coastal upwelling owes its existence to the presence of both the coast as an impermeable lateral boundary and relatively

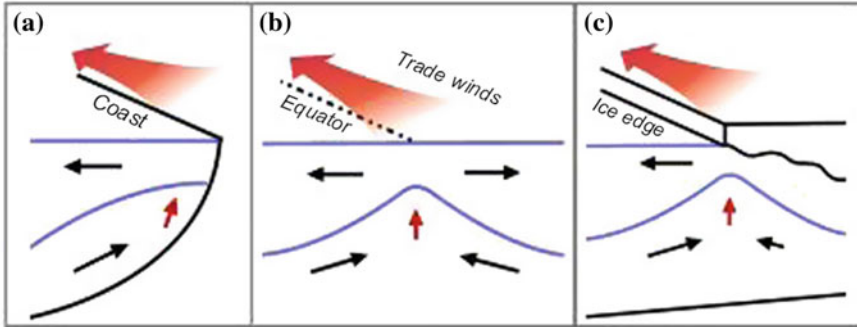
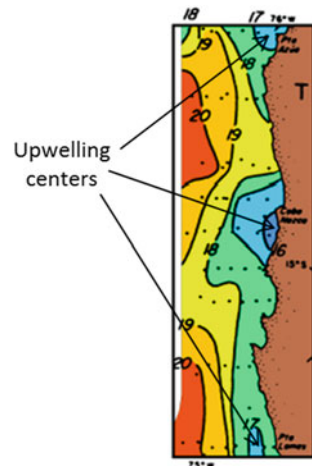


Fig. 2.1 Types of oceanic upwelling: **a** coastal upwelling, **b** equatorial upwelling, and **c** ice-edge upwelling. The *broad brown arrow* shows the direction of the prevailing wind relative to a coast, the equator, or an ice edge. In the case of the coast this shows the situation for the southern hemisphere, with the wind blowing towards the north

shallow water on the continental shelf. Equatorial upwelling is related to the fact that the Coriolis parameter (the constant of proportionality in the Coriolis force) changes sign across the equator. Although the Coriolis force vanishes at the equator it comes into full swing at relatively short distances (>50 km) from it. Due to this spatial variation of rotational effects, the dynamical role of the equator in the upwelling process is similar to that of coasts. Ice-edge upwelling is created via a substantial dampening of the effect of wind stresses on currents under the sea ice.

Depending on typical wind conditions in a region, coastal upwelling can be either a quasi-permanent feature in so-called *major* coastal upwelling systems or a seasonal feature in *seasonal* coastal upwelling systems. While upwelling can occur all along a straight coastline (e.g., off Oregon, see Chap. 4), since coastlines and seafloors are frequently irregular, wind-driven coastal upwelling events are

Fig. 2.2 In warm-water regions of the ocean, coastal upwelling of colder sub-surface water leads to a decrease in sea surface temperatures. This decrease need not be spatially uniform as it can occur at specific upwelling centres. The graph shows in-situ measured sea surface temperatures for the Peru-Chile upwelling system (from Tomczak and Godfrey 2003)



generally localized, and upwelling is not at all uniform. As a consequence, upwelling is more pronounced in certain regions, called *upwelling centres*, than in others (Fig. 2.2). Upwelling centres are often associated with strong frontal flows associated with an *upwelling jet* that breaks up into mesoscale (10–20 km in coastal waters) circular circulation patterns called *eddies*. While most of the primary productivity takes place inside and a short distance downstream of coastal upwelling centres, more quiescent regions adjacent to upwelling centres, called *upwelling shadows*, are important as spawning and nursery grounds for pelagic fish.

2.1.1 Description of the Upwelling Process

Seawater is largely incompressible. Hence, the vertical volume flux induced by upwelling is only possible if the same volume of water per unit time is moved away laterally from a region by a divergence of the horizontal flow. As a result, the trigger of coastal upwelling is the wind-induced offshore movement of surface water, which is replenished with water from below. In the case of equatorial upwelling, the prevailing trade winds induce net surface water movement away from the equator in both hemispheres, resulting in its replacement by sub-surface waters. Given that the upwelled water is generally heavier (denser) than the water it replaces, the associated increase in potential energy of the system requires an external energy source, which is provided by surface wind stresses.

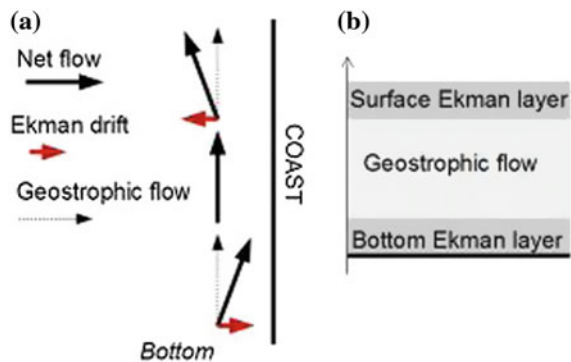
Any dynamical process in the ocean lasting longer than a day, such as coastal upwelling, is controlled by rotational effects, i.e. the Coriolis force. A balance between the Coriolis force and the horizontal pressure-gradient force, known as the *geostrophic balance*, governs the dynamics of horizontal ocean currents in the ocean interior (i.e., at some distance from the sea surface and the seafloor). The geostrophic balance implies that horizontal currents strictly follow isobars (lines of constant pressure). Surface pressure anomalies and, hence, horizontal geostrophic flows extend throughout the entire water column, unless they are weakened by a dynamical adjustment of density interfaces in the ocean's interior, called *baroclinic compensation*. In addition to the geostrophic flow regime, frictional effects become relevant near vertical (and lateral) boundaries. Near vertical boundaries, the balance between friction and the Coriolis force creates departures of the flow from the geostrophic balance, known as *Ekman layers* (see next section for more details), first studied and described by Ekman (1905) (Fig. 2.3).

The general structure of the oceanic circulation in coastal upwelling situations consists of a coast-parallel geostrophic current, called an *upwelling jet*, which is deflected seaward in an Ekman layer near the surface and shoreward in an Ekman layer near the bottom (Fig. 2.4). The coast-parallel component of the wind stress induces offshore movement in the surface Ekman layer which operates to lower the coastal sea level by about $\sim 5\text{--}10$ cm until a dynamical equilibrium is reached. This

Fig. 2.3 Vagn Walfrid Ekman operating a current meter. Photography courtesy of University of Bergen



Fig. 2.4 The general dynamic structure of coastal upwelling. Panel **a** illustrates the horizontal flow structure in water near the surface, in the middle of the water column, and near the seafloor. Panel **b** illustrates the principal vertical structure of the ocean dynamics. In panel (a) the wind is blowing from the bottom of the figure towards the top



drop in sea level is sufficient to create a shoreward pressure-gradient force driving a swift geostrophic upwelling jet of 20–50 cm/s in speed. In turn, the geostrophic flow becomes subject to frictional effects of the seafloor. This creates a shoreward flow in the bottom Ekman layer, which is about 5–25 m thick. This near-bottom flow is the final agent of the upwelling process as it moves near-bottom water shoreward and, as it hits the coast, upward into the euphotic zone.

Some upwelling systems, such as the world's largest upwelling regions found off Peru/Chile, California, northwest Africa, and southwest Africa, exhibit nutrient-rich *undercurrents* at shelf-break depth acting as both a source for upwelled water and as a nutrient trap (Montecino et al. 2005).

2.1.2 Wind Stress and Ekman Transport

The magnitude of the frictional wind stress at the sea surface can be calculated from the formula:

$$\tau = \rho_{air} C_D W, \quad (2.1)$$

where $\rho_{air} \approx 1.28 \text{ kg/m}^3$ is the air density, $C_D \approx 0.001\text{--}0.002$ is the wind drag coefficient (its value depends on turbulence levels in the lower atmosphere), and W is the horizontal wind speed at a reference height of 10 m above sea level. The direction of the wind stress vector is the same as that of the horizontal wind velocity.

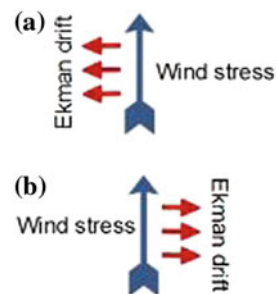
Owing to rotational effects (i.e., the Earth's rotation) and the associated Coriolis force, the response of the surface ocean to wind stress is not straightforward. On timescales of a couple of days and longer, the frictional effect of a wind stress is confined to a surface Ekman layer having thickness of $\sim 50\text{--}100 \text{ m}$ (away from the equator). In the absence of other processes, oceanic currents in the Ekman layer are strictly horizontal but change direction with depth in a spiral fashion, known as the *Ekman spiral* (see Pond and Pickard 1983).

Dynamically more important than this vertical structure is the fact that the depth-averaged horizontal volume transport in a surface Ekman layer is at right angles to the wind direction; it is deflected 90° to the right (left) of the wind direction in the northern (southern) hemisphere (Fig. 2.5). This change of direction between the hemispheres is caused by the change of the direction of the Coriolis force at the equator. Moreover, theory reveals that the magnitude of the net volume transport in the surface Ekman layer M —called *Ekman transport* or *Ekman drift*—can be quantified as:

$$M = \frac{\tau}{\rho_{sea}|f|} \quad (2.2)$$

where τ is the magnitude of the wind stress in m/sec, $\rho_{sea} \approx 1026 \text{ kg/m}^3$ is the average seawater density, and f is the Coriolis parameter. The Coriolis parameter exclusively depends on geographical latitude φ and can be calculated from $f = 4\pi/T_{earth} \sin(\varphi)$, where $T_{earth} = 86,400 \text{ s}$ is the period of the Earth's rotation. Hence, only information on wind stress and geographical latitude is required to determine surface Ekman

Fig. 2.5 The simple directional relationship between wind stress and Ekman drift in the **a** southern hemisphere and **b** the northern hemisphere



transports in the ocean, which can be done by landlubbers without the actual need of marine measurements. Note that M carries units of m^2/s which has to be interpreted as total volume transport (m^3/s) per unit width of the flow.

2.1.3 The Upwelling Index

The theory of Ekman layers (and geostrophic flows) (Jenkins and Bye 2006) is fundamental in the understanding of wind-driven coastal upwelling. We believe that Bakun (1973) was the first who initially described the methods used to calculate upwelling indices, presenting monthly, quarterly, and annual indices for 15 near-coastal positions along the North American west coast for the period 1946–71. Daily and weekly means of the upwelling indices at these standard west coast locations were published by Bakun (1975) for the period 1967–73 (Fig. 2.6). A third report in the series (Mason and Bakun 1986) summarized the monthly indices for 1946–71, along with daily and weekly means of the six-hourly indices for 1974–85 at six locations along the U.S. west coast ($33\text{--}48^\circ\text{ N}$).

Continental shelves are generally deep enough for the undisturbed development of a surface Ekman layer at some distance (typically a few kilometers) from the coast. Given that the coast acts as a barrier to flow, offshore Ekman drift follows from the coast-parallel component of the wind-stress vector. In the general case of any possible coastline orientation, this offshore Ekman transport can be calculated from:

$$UI = M \cos(\alpha^*)$$

(2.3)

where α^* is the relative angle between the wind direction and the actual coastline orientation. Coastline orientation is defined such that $\alpha^* = 0$ implies a wind blowing perfectly parallel to the coast with the coast on its left (right) in the

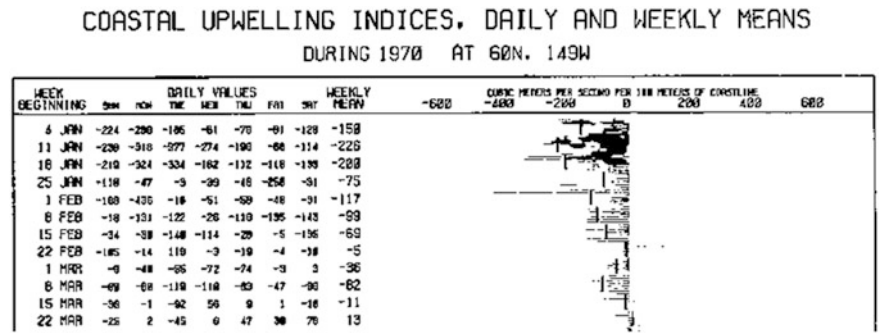


Fig. 2.6 Example of daily upwelling indices published in Bakun (1975)

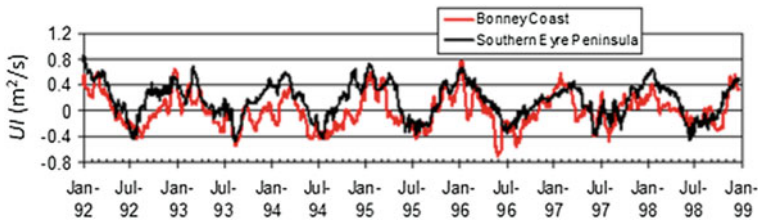


Fig. 2.7 Time-series of the window-averaged (30 days) upwelling index for two upwelling centres of the Great South Australian Coastal Upwelling System (from Kämpf et al. 2004). Indicated is the existence of a seasonal coastal upwelling system in which upwelling occurs during austral summer months

northern (southern) hemisphere. It should be pointed out that, due to volume conservation, UI is a direct measure of the vertical volume transport inherent with upwelling. The dimensional parameter UI is widely known as the *upwelling index*. The upwelling index is the offshore volume transport per unit length of the coastline. The latter is sometimes expressed in kilometres is calculated with reference to a distance of 1 km.

Using coastal wind data, the upwelling index is a simple method to explore and identify coastal upwelling activity in a region (Fig. 2.7 shows an example). Situations in which UI is negative imply an onshore Ekman drift pushing seawater against the coast and density interfaces downward in a process called *coastal downwelling*. Often, prevailing coastal winds create alternating upwelling and downwelling sequences associated with synoptic (3–10 days) variability of weather patterns.

2.1.4 Physical Timescales of the Upwelling Process

It is clear that it takes a certain time before sub-surface water is brought to the sea surface from its initial depth before upwelling starts. To estimate this time, let us consider a coastal ocean consisting of two distinct layers: a warm and lighter surface layer above a colder, denser and nutrient-rich bottom layer. The upper layer has a thickness of H . The density difference between the layers is $\Delta\rho$. The combined effect of magnitude and duration of upwelling-favourable wind stresses can be formulated in terms of a quantity called *wind impulse* (Ω), defined by:

$$\Omega = \frac{|f|}{H} \int_{event} UI dt, \quad (2.4)$$

where H is the undisturbed thickness of the surface layer (Cushman-Roisin 1994). Depending on the magnitude of Ω for an upwelling event, the wind stress causes the

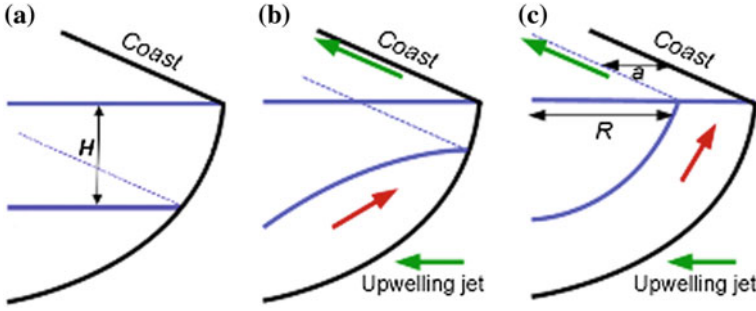


Fig. 2.8 Two possible outcomes of coastal upwelling after a longshore wind event of finite duration. Panel **a** shows the reference state. Panel **b** after a weak or brief wind event, the interface has upwelled but not to the point of reaching the surface. Panel **c** a strong or prolonged wind event causes the density interface to reach and intersect the sea surface, where it forms a front that may depart from the coast under the action of offshore Ekman drift. The latter case corresponds to a mature upwelling that favours biological activity. Adapted from Cushman-Roisin (1994)

density interface to rise towards the coast and it may or may not eventually reach the sea surface, leading to either *partial upwelling* or *full upwelling* (Csanady 1977; Fig. 2.8).

Partial upwelling results in a sloping density interface which does not reach the surface (Fig. 2.8b). Full upwelling, on the other hand, implies the formation of a surface *density front*, which is a narrow frontal zone across which seawater density changes rapidly, also referred to as *upwelling front* (Fig. 2.8c). The upwelling jet coincides with the frontal axis. Sea surface temperatures can vary by several degrees across such fronts. During the process of full upwelling, the upwelling front and the associated upwelling jet continue to move offshore under the action of the Ekman drift as long as the wind forcing continues to exist.

In order to estimate the duration of the partial upwelling phase and to determine the final offshore distance of the upwelling front, we assume that the coastline extends to infinity and that the coastal wind stress varies in time but not spatially. For such a simplified conceptual model, Cushman-Roisin (1994) derived a formula to estimate the distance (a) of the upwelling front from the coast (see Fig. 2.8c), given by:

$$a = \frac{\Omega}{|f|} - R \quad \text{with } R = \frac{\sqrt{g'H}}{|f|} \quad (2.5)$$

where R is the *internal deformation radius* (which is an estimate of the width of the upwelling front) with $g' = \Delta\rho/\rho_o$ g being reduced gravity ($g = 9.81 \text{ m/s}^2$ is acceleration due to gravity). Equation (2.5) can also be used to estimate the time span full upwelling to develop from $\Omega = \sqrt{g'H}$ for $a = 0$.

If we furthermore express the wind impulse (2.5) by an average value of UI for an event of duration Δt , we obtain $\Delta t = RH/\langle UI \rangle$. Using realistic values

($R = 5$ km, $H = 100$ m, and $\langle UI \rangle = 1$ m²/s) gives $\Delta t = 5$ –6 days, which falls within the timescale of synoptic weather events. Hence, full upwelling does generally not occur for relatively short wind events of only 1–2 days or less in duration, but it may follow from a series of consecutive events. According to this simplified conceptual model an upwelling event of a duration of 10–12 days would move the density front a distance of $a = R = 5$ km offshore.

Does this imply that the upwelling front is moved to vast distances from the coast for quasi-continuous coastal upwelling ($\Omega \gg 1$) in major coastal upwelling systems? In contrast to the above conceptual model, the transition between partial and full upwelling (i.e., $a = 0$) in real upwelling systems occurs typically at a fixed location (rather than along the entire coast) and the width of the upwelling zone gradually increases with increasing downstream distance from this point. Based on the above example, an upwelling jet with a speed of, say, 0.2 m/s travels ~ 200 km along the coast on a time scale of 10–12 days before it is moved 5 km offshore. Hence, coastal upwelling jets remain relatively close to the shore in smaller upwelling regions. On the other hand, coastal upwelling jets typically become dynamically unstable and break up into a turbulent field of mesoscale eddies. In some upwelling regions, this mechanism leads to a widening of the upwelling zone to several hundred kilometers.

2.1.5 Significance of Upwelling Jets

Coastal upwelling jets are an important part of the wind-driven circulation. On the global scale, such jets within major upwelling systems intensify equatorward flows on the eastern margin of subtropical gyres and thus play an important role in the ocean's meridional transport of heat and freshwater. As such, upwelling jets also transport nutrients and organic matter along the coast. While coastal upwelling centres are largely stationary features, the existence of coastal upwelling jets implies the formation of different biological zones; that is, spatially separated zones of maximum primary, secondary, and fish production form downstream the upwelling region. This separation occurs due to the difference in the time scales associated with the creation of phytoplankton, zooplankton and fish growth, e.g., 5 days for phytoplankton, 25 days for zooplankton, and 2–3 months for small pelagic fish (Hutchings et al. 2006).

On the other hand, upwelling jets are not smooth (laminar) flows. Like other frontal flows (e.g. western boundary currents) upwelling jets quickly become dynamically unstable on time scales of days to weeks and shed *mesoscale eddies*. Mesoscale eddies are circular flow patterns in which the geostrophic flow surrounds a high-pressure (low-pressure) centre associated with an elevated (depressed) sea level. It is the low-pressure eddies (i.e. *cyclones*) that largely sustain upwelled water in their centres. Eddies in the coastal ocean can have diameters as small as 10–20 km, in contrast to the more commonly known open-ocean eddies that have diameters of up to 300 km. As a result of eddy shedding, the width of the upwelling zone generally increases along the

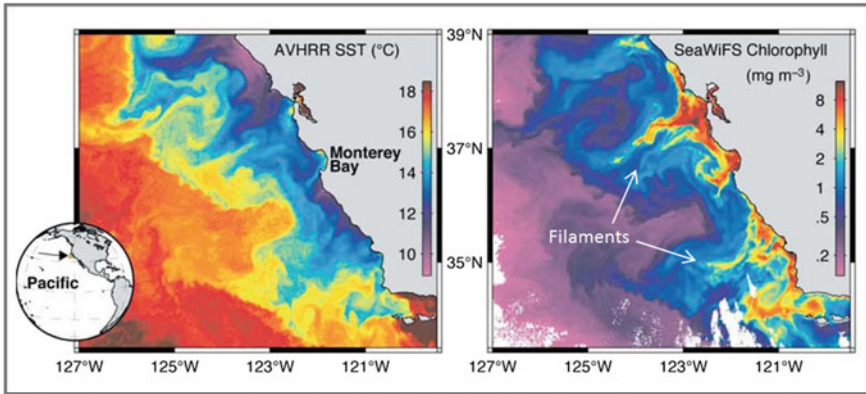


Fig. 2.9 Example of a fully developed eddy field and upwelling filaments seen in satellite images of sea surface temperature and chlorophyll-*a* concentrations in the Californian upwelling system (from Ryan et al. 2005)

coast in the direction of the upwelling jet. In addition, upwelling jets often form turbulent wakes in the lee of headlands or islands. Fully developed eddy fields exhibit specific pathways, called *filaments*, along which upwelled water is advected offshore (Fig. 2.9). Filaments, which can be quasi-stationary or transient features, generally operate as an export mechanism of organic matter to the open ocean (e.g. Aristegui et al. 1997). Eddies also operate to disperse properties of the upwelling centre (e.g. heat anomalies, organic matter and zooplankton and fish larvae) offshore.

As the upwelling front separates from the shore, so does the core of the geostrophic jet (see Fig. 2.8). Despite this, flows within the surface and bottom Ekman layers continue to exist inshore of the geostrophic jet. This implies that upwelling reaches into relatively stagnant coastal seawater that is not subject to the swift geostrophic flow of the upwelling jet. Seawater that has upwelled in this zone is not as rapidly “washed away” as it is in the upwelling jet and, hence, the nutrients contained within it are available for a longer period for biological use.

2.1.6 Coastal Upwelling Regimes

The upwelling process is only of ecological consequence if it actually carries nutrient-rich sub-surface water into the euphotic zone. Hence, the ecological effectiveness of the upwelling process critically depends on the properties of shelf bottom water. Nutrient concentrations in the sea generally increase with increasing water depth. Consequently, dynamical processes that move nutrient-richer seawater from the upper continental slope across the shelf break and onto the continental shelf can substantially enhance the biological productivity in an upwelling region. *nutricline*

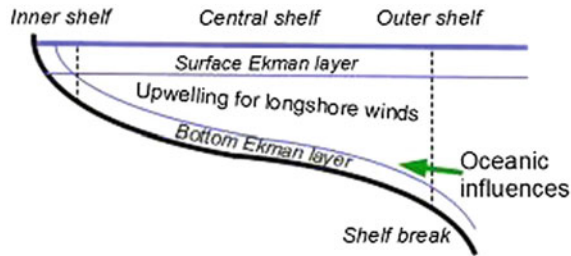


Fig. 2.10 Coastal upwelling regimes. Oceanic influences on the outer continental shelf can precondition shelf waters with nutrient-rich (in some cases, also oxygen-poor) water for subsequent wind-driven coastal upwelling events, which incorporate central regions of the shelf. The inner region of the continental shelf is defined by total water depths <50 m. It is a zone where surface and bottom Ekman layers interfere such that the wind-driven water movement is more aligned with the wind direction

Accordingly, the coastal upwelling dynamics can be grouped into different regimes (Fig. 2.10). Oceanic influences (e.g. the upward tilt of the large-scale nutricline on the eastern side of subtropical gyres, or localized onshore flows in submarine shelf-break canyons) are preconditions for coastal upwelling as they import nutrient-rich waters onto the shelf. The actual wind-driven coastal upwelling process takes place on the central parts of the continental shelf and follows from upwelling-favourable (i.e. coast-parallel) wind stresses. This upwelling excludes near-shore regions of the shelf in which the water is too shallow (<50 m) for the development of spatially separated surface and bottom Ekman layers. Here, the Ekman layers overlap and create water movements that are more aligned with the wind direction. Turbulence mixes waters from the main upwelling zone into nearshore waters.

2.1.7 Indicators of Upwelling

The upwelling index based on the wind stress (2.3) is commonly used as the primary indicator of coastal upwelling events. Another indicator of upwelling events is the lowering of the coastal sea level induced by offshore Ekman transport (Fig. 2.11). Nonetheless, the upwelling-induced signal is relatively weak ($\sim 5\text{--}20$ cm) and low-pass filters have to be applied to extract this signal from other more dominant sea-level oscillations caused by wind waves, swell, tides and coastally trapped waves.

Since the 1970s, satellites have revolutionized our ability to see large-scale changes in the ocean over relatively short time periods. Satellite-derived sea surface temperatures are sufficiently accurate and of high-enough temporal resolution (<1 day) to identify upwelling events and their associated coastal upwelling centres. In warmer oceanic regions, where sea temperature decreases rapidly with depth, upwelling can readily be identified from sudden drops in sea surface temperatures

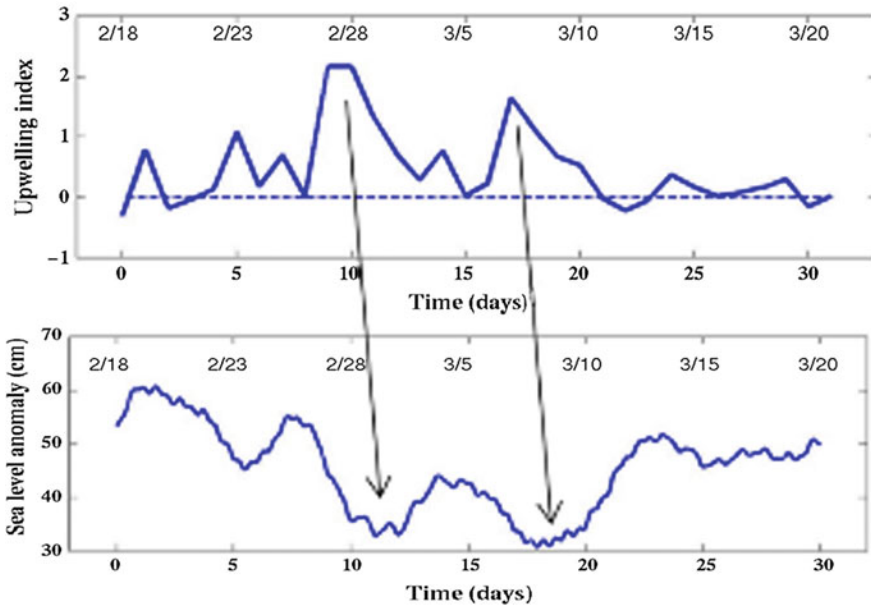


Fig. 2.11 Sea level response (cm) to upwelling-favourable winds for the Bonney upwelling region, Australia. Upwelling index is based on daily averaged wind data for Portland. A moving average window of 5 days in width is applied to sea level data of Portland's tide gauge. Unpublished data. For more information on this upwelling region, see Kämpf et al. (2004) and chap. 8

by >1 °C on the timescale of synoptic weather events (3–10 days). Elevated phytoplankton concentration associated with upwelling events can be inferred from Ocean Color (SeaWiFS) data (Fig. 2.12 shows examples).

Ocean colour data are based on standard blue/green ratio algorithms for chlorophyll-*a* retrieval, which can substantially overestimate phytoplankton blooms in coastal waters in the presence of coloured dissolved organic matter (CDOM or *Gelbstoff*) and suspended sediment (e.g., Garcia et al. 2006; Shanmugam 2011). The fluorescence line height (FLH) is a relative measure of the amount of radiance leaving the sea surface in the chlorophyll fluorescence emission band (e.g., Xing et al. 2007). The chlorophyll-*a* fluorescence peak near 685 nm has been proposed as an alternative option of chlorophyll retrieval (Neville and Gower 1977; Gordon 1979). Many researchers have studied the relationship between chlorophyll-*a* concentration and FLH, and have found a good correlation between these properties (Maritorena et al. 2000; Gower et al. 2004; Gower and King 2007; Kämpf 2015) for relatively low chlorophyll-*a* concentrations of <9 mg m⁻³. Modifications are required at higher chlorophyll concentrations, where the fluorescence peak shifts to longer wavelengths (e.g., Gitelson 1993).

Ocean Color images often show upwelling filaments moving organic matter offshore (Fig. 2.12b). While these filaments and eddies can be generated locally, there are also known interferences from remotely created eddies, e.g., off the

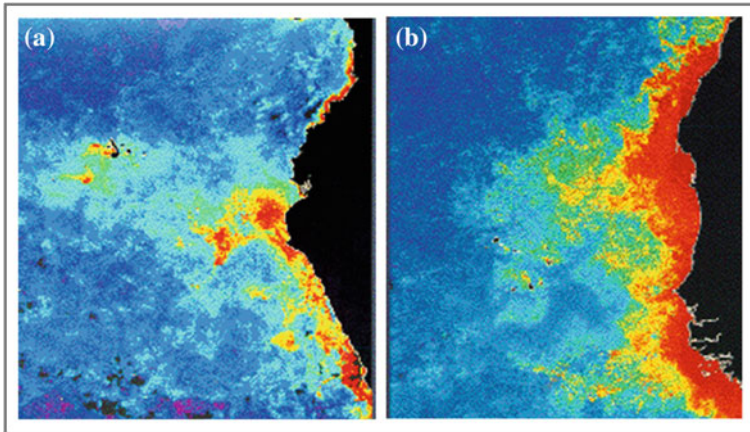


Fig. 2.12 Ocean Color as an indicator of coastal upwelling in waters off **a** Peru and **b** northwest Africa, which are among the most productive in the global ocean. *Red (blue) colours* represent waters of high (low) chlorophyll concentrations. The upwelling is reflected here as chlorophyll-rich bands along both coasts, shown in *red* and *yellow*, up to 100-km wide, and turbulent mixing plumes of productive waters extending $\sim 500\text{--}1,000$ km offshore. Note that island-induced upwelling generates highly productive regions around the Galapagos Archipelago (seen in Panel **a**). Source of images: NASA. http://disc.sci.gsfc.nasa.gov/education-and-outreach/additional/science-ocus/space/ocdst_upwelling_dynamics.shtml [accessed 4 April 2016]

southwest coast of South Africa, where Agulhas eddies call pull shelf water several hundred kilometres into the open ocean and remove large quantities of fish eggs and larvae (Duncombe Rae et al. 1992). In contrast to sea surface temperatures, Ocean Color data can also identify upwelling events in colder oceanic regions, where upwelling-induced temperature anomalies are less pronounced. Other upwelling indicators are high abundances of zooplankton and fish, which can only be measured from sea-based surveys.

2.1.8 Other Upwelling Mechanisms

Apart from the wind-driven coastal upwelling process, there are a number of other physical mechanisms that can produce upwelling in the coastal ocean. These mechanisms are:

- Ekman pumping
- dynamic uplift (shelf-break upwelling),
- tidally-induced upwelling
- upwelling in the wake of islands
- topographically caused upwelling (e.g. in shelf-break canyons), and
- transient upwelling caused by the passage of coastally trapped waves.

Ekman pumping refers to the vertical adjustment of the pycnocline associated with a spatially varying horizontal wind-stress field, known as *wind-stress curl* (Sverdrup et al. 1942), which induces a divergence of horizontal Ekman transports in addition to boundary effects due to the existence of a coast. While the coastal upwelling process involves a cross-shelf transfer inherent with the dynamics of Ekman layers, Ekman pumping exclusively induces a vertical flow. Previous studies indicate that Ekman pumping contributes significantly (>25 %) to the vertical nutrient flux in major eastern boundary upwelling regions (Messié et al. 2009). The important difference between the effects of wind stress and wind stress curl is that Ekman pumping caused by the latter takes place considerably farther offshore, often at the shelf edge, and can occur at faster rates in terms of vertical transport than Ekman transport (Kraus and Businger 1994). Thus, it is separated from the inshore Ekman transport and can provide a second input of nutrients to the system.

Ekman pumping and its associated upward nutrient fluxes have been reported for the California Current (Checkley and Barth 2009; Rykaczewski and Checkley 2008), the Benguela Current (Bakun and Nelson 1991), the eastern Banda Sea (Gordon and Susanto 2001), and the upwelling system around Cabo Frio (Castelão and Barth 2006). Chavez and Messié (2009) suggest that this type of upwelling has different biochemical implications, given that it does not recruit shelf and slope waters that have interacted with the nepheloid layer, and hence brings lower concentrations of iron into the euphotic zone than classical upwelling closer inshore. As a consequence, Chavez and Messié (2009) suggest that the coastal upwelling process stimulates a food web of larger organisms (diatoms, copepods, krill) and accumulation of biomass, whereas the wind-stress-curl-induced upwelling farther offshore leads to relatively low biomass and ecosystem characteristics of high-nutrient-low-chlorophyll regions.

Dynamic uplift (also called *shelf-break upwelling*) is an upwelling mechanism that operates along the inshore edge of western boundary currents (where coastal winds are generally not upwelling favourable). Western boundary currents are geostrophic frontal flows associated with a steep rise of the thermocline from the ocean towards the coast. Being part of large oceanic gyres, their dynamics are largely independent of local wind conditions. On average, western boundary currents are located just offshore from the continental shelf, and their influence does not reach far into the coastal ocean, which establishes its own circulation dominated by local wind and thermohaline forcing. Changes in the current's position (e.g. caused by eddy formation) can lead to upwelling of deeper water onto the outer shelf. The process applies to all western boundary currents, and examples can be found in all oceans on both hemispheres (Tomczak and Godfrey 2003, see also chap. 9).

Tidally-induced “upwelling”, also called *tidal pumping*, is a regional process in which oscillatory tidal flows regularly move nutrient-rich deeper water across the shelf break (Thompson and Golding 1981). Tidal pumping is most pronounced in regions of strong tidal flows in tidal channels between islands located along the shelf break. Although this process is oscillatory rather than steady (similar to the

action of internal waves), it causes the regular appearance of nutrient-rich water on the outer shelf and therefore constitutes a form of shelf-break upwelling.

Fishermen have long known of the enhanced biological productivity in the vicinity of islands (see Fig. 2.10a). The island-wake effect was first scientifically documented by Doty and Oguri (1956). Nutrients, such as nitrate, can be 10 times higher in the wake compared to upstream values (Heywood et al. 1990), and density surfaces can shoal by as much as 100 m. Upwelling in the wake of islands in shallow seas can be explained by the well-known “tea cup effect” (Wolanski and Hamner 1988). Typically, flows around an island create a counter-rotating pair of eddies in the lee of the island. In an eddy, rotating in either direction, there is an inward pressure gradient supporting the centripetal acceleration of the fluid. Friction slows the flow near the bottom, reducing the centripetal acceleration. The pressure gradient remains, is unbalanced, and pushes the near-bottom fluid towards the centre of rotation. This flow convergence drives the upwelling and, in the case of a tea cup, concentrates the “tea leaves” in the cup’s centre (Hasegawa et al. 2004).

Shelf-break canyons are submarine canyons cutting through the shelf break. Depending on their direction, ambient currents at shelf-break depth can trigger localized upwelling of deeper water from the upper continental slope onto the shelf (e.g., Hickey 1997; Allen and Durrieu de Madron 2009). This localized upwelling follows from ambient flows opposed to the propagation direction of topographic Rossby waves; that is, ambient flows that have shallower water (and the coastline) on their left (right) in the northern (southern) hemisphere. Topography Rossby waves are quasi-geostrophic flow disturbances created by water-column stretching/squeezing over topographic undulations. While these waves on their own can only propagate in one specific longshore direction, ambient flows can offset this propagation via the creation of standing wave patterns that consist of stationary but spatially alternating regions of onshore and offshore flows across the shelf break. As such, the canyon-upwelling process can be interpreted as the signature of a stationary topographic Rossby wave, that may induce localized onshore flows near the “crests” of this wave that forms downstream from the canyon (Kämpf 2012). Technically, localized upwelling in shelf-break canyons is also a form of shelf-break upwelling.

Coastally trapped waves are waves of intraseasonal variability (30–60 days periodicity) that attain the largest amplitude near the coast and induce transient upwelling/downwelling in conjunction with onshore/offshore flows across the shelf edge. These waves are often created by coastal winds, but they can also be generated by equatorial Kelvin waves impinging on the coast on the eastern side of the equator. Coastally trapped waves can travel several thousand kilometers along coastlines. After a strong upwelling event, the regional perturbation of the oceanic pressure field (comprising both sea-level and density anomalies) in the vicinity of an upwelling centre may initiate a coastally trapped wave propagating along the shelf break and inducing transient upwelling along its way. These have been observed in coastal tide gauge sea-level records along the coasts of Ecuador, Peru and Chile, as well as in currents measured at moorings along north-central Chile (Shaffer et al. 1997; Hormazabal et al. 2004).

2.1.9 Location of Significant Upwelling Regions

Most major and seasonal coastal upwelling systems can be inferred from surface wind maps (Fig. 2.13) when using the rule that upwelling is created by coast-parallel winds driving off-shore transport in the surface Ekman layer. This intuitive method identifies the major upwelling regions off the coasts of California, Peru, Chile, northwest and southwest Africa, and Portugal as well as their associated upwelling jets (i.e., California Current, Peru-Chile Current, Portugal Current, Canary and Benguela Current) (Fig. 2.14). These year-round upwelling regions are referred to as

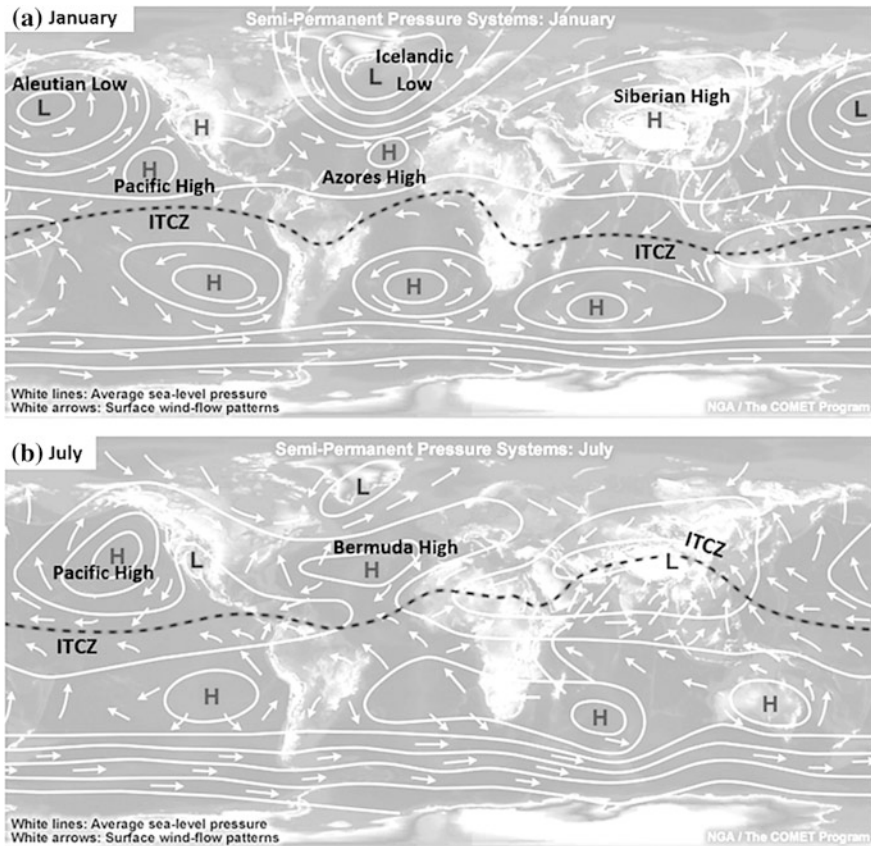


Fig. 2.13 Seasonal variations of surface wind patterns. Can you guess where coastal upwelling regions form? The source of this material is the COMET[®] Website at <http://meted.ucar.edu/> of the University Corporation for Atmospheric Research (UCAR), sponsored in part through cooperative agreement(s) with the National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce (DOC). ©1997–2016 University Corporation for Atmospheric Research. All Rights Reserved

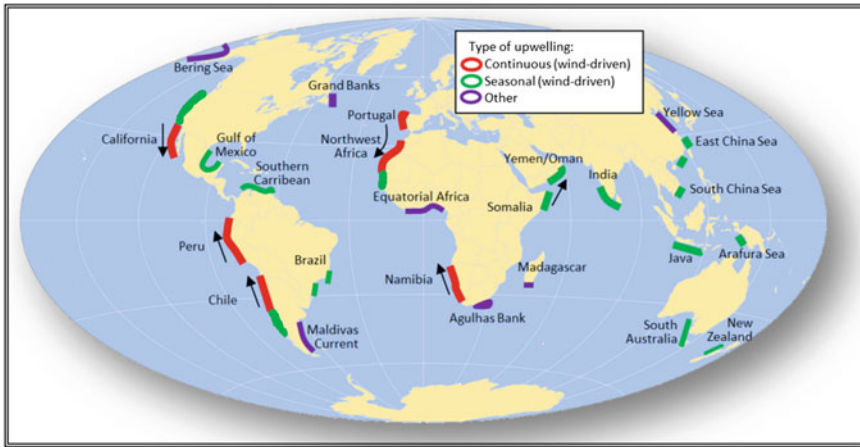


Fig. 2.14 Locations of significant coastal upwelling regions in the world ocean

major coastal upwelling regions, or eastern boundary upwelling regions. While the prevailing winds in these upwelling regions are equatorward, a distinct feature of these systems is the existence of poleward undercurrents that play significant roles in the distribution of nutrients and dissolved oxygen in these regions and also affect the lateral displacement of marine organisms undertaking diel vertical migration.

This method also identifies seasonal upwelling systems off the coasts of Somalia, Yemen/Oman, Sumatra, and in the South China Sea. There are also seasonal coastal upwelling systems along the southwest coast of India and the southern shelves of Australia, which are less apparent from the wind distributions shown in Fig. 2.13. For completeness, the map also includes other types of upwelling/highly-productive coastal regions such as the “Green Belt” of the Bering Sea, the Grand Banks, the Agulhas Bank and the shelf-break region of the Malvinas Current, in which upwelling is caused by dynamic uplift/shelf-break upwelling, and the Irish Sea and the Yellow Sea, where nutrient enrichment/concentration is induced by tidal mixing fronts.

2.2 The Biogeochemistry of Coastal Upwelling Systems

2.2.1 General Description

While the basics of nutrient cycling by phytoplankton and bacteria were described by Harvey (1928), and Redfield et al. (1963) described the ratios in marine phytoplankton of nutrient elements to carbon, much of our understanding of biogeochemical cycles in the ocean including the solubility and biological pumps was informed and motivated by Wallace Broecker’s inference of the deep circulation from

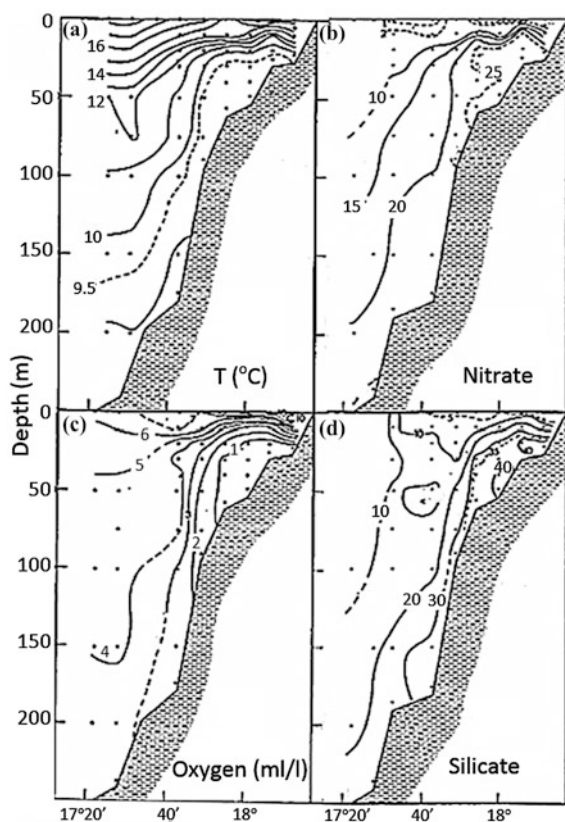
the distributions of chemical tracers in the deep ocean (Broecker and Peng 1982). This led to the international Joint Global Ocean Flux Study (JGOFS), which refined the understanding of processes involved in the biological pump (Ducklow et al. 2001). Broecker's work has since motivated many groundbreaking studies, including CO₂ flux studies in upwelling regions, and related concepts such as that of the *continental shelf pump*, first proposed by Tsunogai et al. (1999) for the East China Sea.

In most upwelling systems, the source of the upwelled water is the offshore intermediate waters, found mostly between 100–300 m below the seasonal pycnocline. Because the wind is such an important component of upwelling systems, the amount of nutrients that is delivered to the surface layer, and hence the theoretical maximum in new production and carbon export, varies with the wind stress. As discussed above, weak winds may lift only small volumes of water onto the shelf, and this water may not reach the euphotic zone. If the winds are too strong, however, it means that the phytoplankton may be unable to make use of the nutrients, either because they are advected out of the coastal zone, or because the increased turbulence means that the surface mixed layer is deepened to such an extent that “seed” cells are removed vertically from the euphotic layer. In either case the potential productivity is lost to the system.

Intermediate wind speeds are therefore needed for maximum production rates, and off California these have been estimated at 7–8 m/s (Ware and Thompson 1991), while in the northern Benguela, minimum wind speeds of about 5 m/s are required to initiate upwelling (Shannon 1985). As wind stress varies very considerably on both seasonal and shorter time-scales, so pulsing of upwelling and the resultant production is seen in all areas, and it is common for maximum production to occur following a wind relaxation, which stabilizes the upper water column and allows phytoplankton to use the nutrients that have been upwelled.

A feature common to all upwelling systems is an increase in nutrients and a decrease in dissolved oxygen on the shelf below the seasonal pycnocline. This occurs both because of the nutrients brought in with the upwelling water mass and through local decomposition and regeneration processes in the bottom water and sediments. A typical example is shown in Fig. 2.15, which shows temperature, oxygen, nitrate and silicate from a line of stations across St. Helena Bay in the southern Benguela system. The main mass of the upwelling water, which contains about 20 µM/kg of both nitrate and silicate, in this figure is from about 175 m depth, but considerably higher concentrations of nitrate and silicate were found at 50-m depth on the shelf, accompanied by reduced oxygen concentrations, which are typically <90 µM/kg during the summer upwelling season, compared to saturated oxygen concentrations of about 225–275 µM/kg for waters having the same temperature and salinity. While it might be expected that the recycled nitrogen appears as ammonia or urea, and sediments in upwelling regions are certainly reducing, nitrification is active in the water column below the euphotic zone so that much of the recycled nitrogen is reoxidized rapidly to nitrate, despite the lower oxygen concentrations. While studies prior to the 1990s assumed that this process was facilitated by nitrifying bacteria such as *Nitrosomonas* (Ward and Carlucci 1985),

Fig. 2.15 **a** Temperature, **b** nitrate, **c** dissolved oxygen, **d** silicate in a section across the shelf off St. Helena Bay, South Africa ($32^{\circ} 35' \text{ S}$, $17^{\circ} 30' - 18^{\circ} 20' \text{ E}$) in February 1979. Data from Bailey and Chapman (1985)



it is now accepted that Archaea, which are much more abundant than nitrifying bacteria, play a large role in the initial oxidation of ammonia to nitrite, after which nitrite oxidizing bacteria convert the nitrite to nitrate (Zehr and Kudela 2011).

When productivity is very high, as is often the case in upwelling regions, the sinking and subsequent decomposition of the organic matter produced in the euphotic zone can lead to extremely low dissolved oxygen concentrations in the water column ($<20 \mu\text{M/kg}$). Because nitrate and nitrite have similar oxidation potentials to oxygen, their half-reactions during reduction can be used to provide microorganisms with very nearly the same amount of energy as they would gain from aerobic respiration. This switch from using oxygen to nitrate or nitrite as an electron acceptor can lead to nitrate reduction (when nitrate is converted to nitrite or ammonia) or even denitrification (when it is converted to nitrous oxide or free nitrogen gas) at oxygen concentrations below $5 \mu\text{M/kg}$, and leads to considerably less nitrate being measured than would be expected from the standard 16:1 Redfield ratio of dissolved N:P.

An example, from the Peruvian upwelling system, is given in Fig. 2.16. In this case, a nitrite maximum can be seen at about 200 m depth, which corresponds to

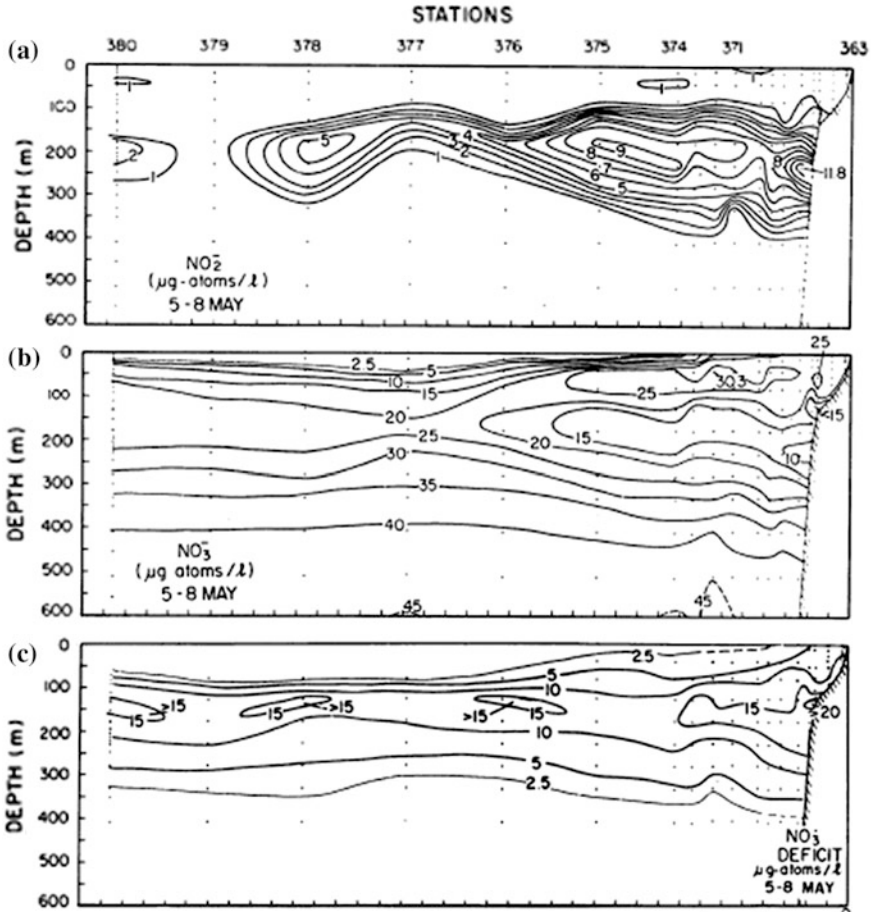


Fig. 2.16 Concentrations of **a** nitrite, **b** nitrate and **c** nitrate deficit (mmol/m^3) at 15°S off Peru (after Codispoti 1983). The nitrate deficit is the amount of nitrate or nitrite reduced to nitrogen gas

the site of maximum nitrate reduction and hence the zone in which nitrogen loss by conversion to gaseous nitrogen is also at a maximum. Oxygen concentrations at this depth are extremely low, with concentrations less than $10 \mu\text{M/kg}$ extending over 1,000 km from the coast into the subtropical South Pacific. Recently, Gruber and Sarmiento (1997) introduced the idea of expressing nitrogen deficits in terms of N^* , calculated as

$$\text{N}^* = [\text{Total inorganic nitrogen}] - 16[\text{PO}_4^{3-}] + 2.9 \mu\text{M/kg} \quad (2.6)$$

where $[\text{Total inorganic nitrogen}]$ equals the sum of nitrate, nitrite, and ammonia concentrations, so that modern values of nitrate deficit differ slightly from earlier numbers.

2.2.2 *Nitrogen Production by Anaerobic Oxidation of Ammonia*

Until the late 1990s, nitrogen reduction was assumed to proceed only via the pathways $\text{NO}_3^- \rightarrow \text{NO}_2^- \rightarrow \text{NO} \rightarrow \text{N}_2\text{O} \rightarrow \text{N}_2$ (heterotrophic denitrification) or $\text{NO}_3^- \rightarrow \text{NO}_2^- \rightarrow \text{NH}_4^+$ (dissimilatory nitrate reduction). However, following the identification of the direct production of nitrogen by anaerobic oxidation of ammonia (Anammox) by bacteria in sewage farms (Mulder et al. 1995; van der Graaf et al. 1995), it is now believed that this reaction, that is,



accounts for much of the loss of nitrogen from the ocean in eastern boundary regions (Lam and Kuypers 2011), both in the water column and within the sediments. Kuypers et al. (2005) showed that up to 5 mM N/m²/day could be lost to the system via this route from the Benguela, and other researchers have shown similar losses from the eastern tropical South Pacific (Thamdrup et al. 2006; Hamersley et al. 2007). Good reviews of the complex interactions of different nitrogen species in upwelling systems and other low oxygen zones are given by Lam and Kuypers (2011) and Zehr and Kudela (2011).

Concentrations of dissolved phosphate and silicate are also enhanced in bottom waters over the shelf in coastal upwelling systems, in a similar way to nitrate. In these cases, however, the cycle is considerably simpler, as they are only found in one inorganic chemical form, although both phosphorous and nitrogen also exist as dissolved organic and particulate forms. Although the Redfield ratio of 16 atoms of nitrogen for every one of phosphate was originally defined from open-ocean North Atlantic data (Redfield et al. 1963), this ratio, or numbers close to it, is found to hold for upwelling regions as well (e.g., Bailey and Chapman 1985). Deviations to ratios less than 16 are assumed to occur because of denitrification (e.g., in the Humboldt Current; Quiñones et al. 2010). However, phosphate concentrations can also vary because of adsorption/desorption reactions within the sediment as the system changes from oxic to anoxic (Suess 1976).

2.2.3 *The Role of Silica*

Silica is an essential component of diatom frustules, and diatoms are the most common phytoplankton species in coastal upwelling systems. The silica to nitrogen ratio in diatoms is usually accepted as being about 1, given their 16:16:1 Si:N:P atomic ratio. Because diatom cells are relatively large, with a small surface-to-volume ratio, they require a high supply of nutrients to enable them to grow (Chisholm 1992). Thus, these organisms are found in high-nutrient and turbulent regimes and transport carbon and silicon both to the seabed and to the open ocean as they sink, are incorporated into zooplankton faecal pellets, or are otherwise

advected out of the coastal upwelling zone. This export results in a silica pump into the deep sea and potential silica limitation in the surface layer (Dugdale et al. 1995). The recycling of the element in the deep ocean is slow because it depends on the rate of dissolution of opaline silica following the decomposition of a protective layer of organic material. Thus its regeneration occurs considerably deeper in the water column than the regeneration of nitrogen and phosphorous and the ratio of silica to nitrate in the surface layer can be reduced to less than 1. In cases where silica is limiting, there is likely to be a shift from diatoms to non-siliceous algae (Officer and Ryther 1980; Egge and Aksnes 1992). This may have major effects on the local ecology, by encouraging harmful algal blooms (e.g., Smayda 1990), but such effects are usually of short duration.

2.2.4 *Upwelling and Carbon Fluxes*

The enhanced production and decomposition rates in coastal upwelling areas means that they are centres for carbon cycling. The observations show interannual variability caused by large-scale ocean effects, such as El Niño-La Niña (see Chap. 3), as well as considerable seasonal and regional variability, which depend to some extent on changes in offshore Ekman transport rates (Thomas et al. 2004). Overall, the world's eastern boundary current upwelling systems show theoretical maximum primary production rates of more than 3 g C/m²/day. More information on seasonality and variability on other time scales will be given in the chapters on individual upwelling regions.

Primary production in all four regions feeds over into secondary production of zooplankton and fish. How much of this primary production ends up as secondary production varies considerably with season and region. The general transfer of carbon from the euphotic zone to the deep sea has been discussed in Chap. 1. However, within upwelling regions, considerable amounts of carbon are also recycled locally on the shelves either as dead phytoplankton or as zooplankton faecal pellets, so that sediments in some regions can contain more than 10 % percent organic carbon by weight (Bremner 1980; Dale et al. 2014). How much of this material is lost to the atmosphere following either oxidation to carbon dioxide or reduction to methane and dimethyl sulphide within the sediments remains unclear, but sulphide emissions are known from both the Benguela and Peru upwelling systems once oxygen levels in the water column drop to zero.

Whether eastern boundary systems are sinks or sources for carbon dioxide is equally unclear; Torres et al. (2002) suggest that northern Chile is a source, while Santana-Casiano et al. (2009) and Monteiro (2010) believe that the Benguela is a net small sink. In this case the sink in the southern Benguela outweighs the source in the north, with the boundary being at about 20° S, but both systems show considerable seasonal and interannual variability. Other eastern boundary systems also show high variability, depending on season, wind strength and direction, and there is presently little consensus on the issue.

2.3 The Ecology of Coastal Upwelling Systems

2.3.1 Biological Response to Coastal Upwelling Events

The biological response to coastal upwelling events in terms of primary and secondary production depends strongly on:

- Existing ambient conditions (illumination and available nutrient concentrations in shelf bottom waters);
- The intensity and duration of upwelling-favourable wind conditions;
- Biochemical factors (i.e. possible nutrient limitation, interaction with oxygen-minimum zones, development of harmful algae blooms and subsequent oxygen depletion),
- The availability of a seed population of phytoplankton (this may be in the form of resting spores on the bottom), and
- Complex food-web dynamics including human interference, such as the harvest of forage fish (sardines, anchovies, pilchards).

The upwelling process moves water and its nutrients from the bottom of the shelf into the surface mixed layer (Fig. 2.17). As nutrient-enriched water moves upward, it can lead to sub-surface phytoplankton production near the base of the euphotic zone, particularly during partial upwelling events, which cannot be detected from satellite measurements. Full upwelling, i.e., when the upwelled water intersects the surface, generally creates the strongest biological response, but the magnitude of the

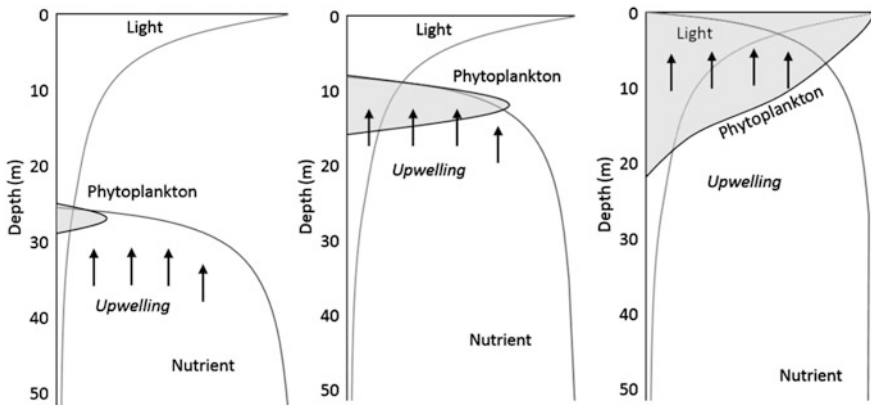


Fig. 2.17 Schematic of the response in phytoplankton production to upwelling of nutrient-rich sub-surface water. Shown is the typical summer situation for temperate waters in which thermal stratification triggers sub-surface phytoplankton production in a narrow zone near the base of the surface mixed layer. As the upwelling continues, this zone is moved upward in the water column to a level of greater light intensity, which increases production. The maximum possible production occurs for full upwelling

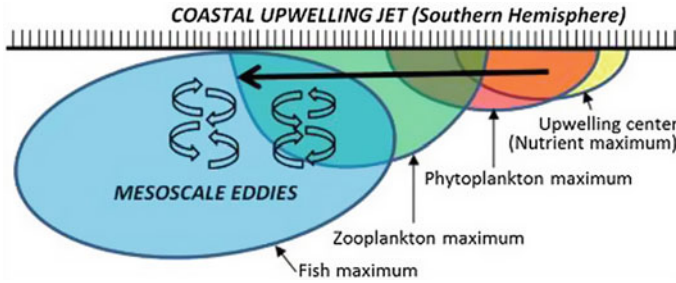


Fig. 2.18 Zonation of different trophic levels of the marine food web in upwelling regions (*top view*). Shown is the case for the southern hemisphere. The coastline is located along the top of the graph

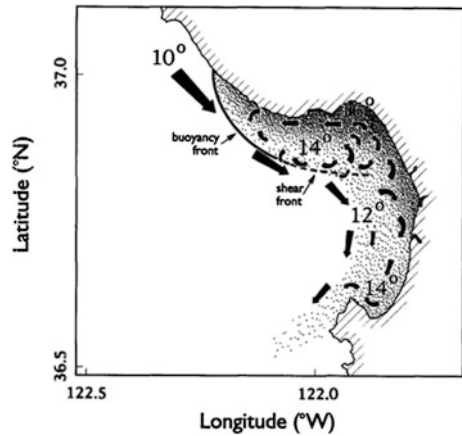
response depends on whether the wind stress is maintained or relaxes to allow a phytoplankton bloom to develop.

The formation of a coastal upwelling centre implies that the nutrient source is a rather regional and localized feature. Given the formation of a coastal upwelling jet and biological response times, the zones of maximum phytoplankton concentration, maximum zooplankton abundance and fish abundance do not form at the same location. Instead, there is a natural zonation and the fish maximum is generally located farthest away from the nutrient maximum (Fig. 2.18). The distance between the centres of individual zones depends on the speed of the upwelling jet and integral biological response times (e.g., doubling time of phytoplankton cells). The effect of mesoscale eddies (created by the upwelling jet) is to increase the width of the upwelling zone with increasing distance from the upwelling centre. If, however, there is a natural physical feature, such as a headland or an eddy system confining the upwelled water, then the trophic succession can take place in the same area.

2.3.2 The Significance of Upwelling Shadows

Upwelling shadows, also known as *retention zones*, are relatively quiescent regions typically located downstream of upwelling centres in embayments that are sheltered from the swift and highly energetic upwelling jets (Fig. 2.19 shown an example). In addition to upwelling centres where nutrient fluxes into the euphotic zone fuel primary production, upwelling shadows form another important ecologic role in the food web dynamics of upwelling systems as these provide sheltered breeding and feeding grounds for fish species. The name “upwelling shadows” was introduced and described by Graham et al. (1992), who analyzed the zooplankton abundance in northern Monterey Bay, California, USA, although the idea of such retention zones trapping water close to the coast thus allowing blooms to develop had been considered earlier (e.g., Shannon et al. 1984; Taunton-Clark 1985).

Fig. 2.19 Hypothetical circulation in the Monterey Bay upwelling shadow. Arrows indicate currents and numbers show water temperatures. The shaded area is the retention zone where current speeds are reduced (from Graham and Largier 1997)



2.3.3 Timing and Duration of Phytoplankton Blooms

A major control on production is the timing and duration of individual phytoplankton blooms. These depend to a large extent on the transition from a well-mixed to a stratified water column, and lead to changes in the dominant species at different times during a bloom (Hutchings et al. 1995). As the bloom ages and nutrient concentrations decrease, there is a shift from small to large, colonial or chain-forming diatoms that use “new” nitrogen, and then to smaller species that use recycled nitrogen, while the importance of the bacterial loop in recycling carbon and nutrients from dead phytoplankton cells and chemical exudates increases.

Continuous upwelling-favourable winds ensure a constant supply of nutrients to the euphotic zone, but if the winds are too strong, then the increased turbulence means that phytoplankton cannot grow close to the upwelling region, but are moved well downstream and may be advected offshore and away from the coast. Productivity in many regions depends on the fact that upwelling is intermittent, so that phytoplankton growth can occur once the upwelling winds relax and the upper part of the water column stabilizes. This then allows time, typically about 5–10 days, for dense phytoplankton blooms to develop. Zooplankton generation times are considerably longer than this, of the order of 25 days, so moderate upwelling likely leads to the maximum populations of zooplankton and hence to increased forage fish stocks. Adult zooplankton can also migrate vertically to take advantage of the presence of undercurrents; this means they can stay in the vicinity of a bloom for long periods, even though larval and juvenile forms develop only in the surface layers (Hutchings et al. 1995).

As a result of the general unpredictability of coastal upwelling systems, the small forage fish typically exhibit serial spawning patterns. Instead of spawning only once a year, as many demersal fish do, they spawn multiple times at short intervals.

This allows them to take advantage of times when the conditions for survival and growth of their larvae are optimal, and minimizes the chance that all the larvae will be lost from the system through physical effects, such as eddies, predation, or starvation. Despite this adaptability, these fish do experience large changes in recruitment and biomass, depending on such factors as parent stock size, egg production, predation, availability of food resources, and physical conditions. The “window of opportunity” after hatching, during which time fish larvae can find a suitable food source, is probably only about 2 or 3 days (Hutchings et al. 1995), after which they exhaust the energy in their egg sacs and die.

Changes in the physical environment and the ecosystem biology, such as those described above, mean that feeding patterns can change from the generally accepted typical short food chain that leads from phytoplankton to zooplankton to forage fish to predatory fish. If thermal stratification is intense, so that upwelling and diatom blooms are reduced, then the plankton population changes to smaller species that use recycled nutrients, leading to an increase in smaller zooplankton and a reduction in the amount of primary production that goes to support fish biomass (Mann 1993). This then alters the whole food web as more recycling goes on in the water column and the general productivity of the system slows down. It may also mean that forage fish switch from eating zooplankton to feeding directly on phytoplankton cells, and/or lead to changes in species dominance, e.g., a switch from sardines to anchovy. Such coherent changes in dominance over decadal time scales, based on changes in the abundance of fish scales in laminated anoxic sediments, have been seen in several coastal upwelling regions (Baumgartner et al. 1992). Whether these changes are dependent on large-scale environmental variability, such as that caused by particularly intense El Niños, remains unclear (Arntz et al. 2006), as is the existence of long-range teleconnections between different upwelling regions, as suggested by Shannon and Nelson (1996).

2.4 Theories on High Fish Production

Because of the importance of recruitment to sustaining fish populations, there have been many studies on what conditions are required for maximum recruitment to occur. We give here brief descriptions of four examples that are applicable to upwelling systems.

2.4.1 *Bakun's Triad*

Bakun (1996) postulated that marine systems having high productivity of upper trophic levels have three key requirements: (i) Bottom-up enrichment, with high nutrient input and subsequent primary productivity; (ii) Aggregation through physically mediated processes that operate to concentrate food resources, and

(iii) Retention through physically-mediated processes that prevent the loss of weak swimmers before they can complete their life cycle.

Mackas et al. (2006) discussed this triad of requirements for the eastern boundary upwelling systems and found that all methodologies and indices agree that the highest nutrient supply and primary productivity are in these regions. Aggregation and retention are mainly associated with the ability of planktonic organisms, including larval fish and invertebrates to travel horizontally due to selective diel migration (taking advantage of flows of opposite directions at different depth levels), and the existence of upwelling shadow zones, where current movements are limited or form gyral systems that retain organisms in the area (see Mackas et al. 2006; and references therein).

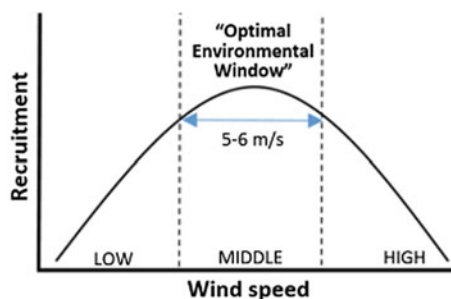
2.4.2 The “Optimal Environmental Window” Hypothesis

The “optimal environmental window” hypothesis is based on observations of the variability of oceanographic conditions and forage fish populations (anchovy and sardines) in the large upwelling zones (Cury and Roy 1989). The basic concept is that the link between recruitment and upwelling intensity is very nonlinear. The best conditions for larval survival and hence the development of abundant anchovy and sardine populations occur following moderate upwelling intensities (Fig. 2.20) rather than very strong or weak intensities.

A gradual wind speed increase in the upwelling zone leads initially to increased production. However, too low a wind speed means the resulting reduced upwelling does not provide nutrient transport to the surface, hindering both phytoplankton and zooplankton development. This defines a minimal level of vertical turbulence promoting larval survival. Successful larval transition to the active feeding stage requires an intermediate level of turbulence, which regulates the frequency of encounter of the larval and their particulate microplankton food above the critical level (Rothschild and Osborn 1988).

As shown, this mechanism is critical for sardine, anchovy, cod, herring, pollock, and some other species of pelagic fishes (see Klyashtorin and Lyubushin 2007; and

Fig. 2.20 Schematic of the “optimal environmental window”. Based on data from Cury and Roy (1989)



references therein). However, with a further increase in wind speed the population growth is slowed, and maximum production requires an optimal wind speed of about 5–6 m/s. This wind speed range, which corresponds to average upwelling intensities and high recruitment, is labelled the “optimal environmental window”. Further increase of wind speed and upwelling intensity increases offshore larval transport from the more favourable coastal environment into the open sea, where their mortality increases significantly (Parrish et al. 2000). In addition, excessive turbulent mixing disrupts the supportive local aggregates of small plankton required for the successful transition of fish larvae to their more mobile active feeding stage (Lasker 1978; Owen 1981).

2.4.3 Lasker’s Hypothesis of a “Calm Ocean”

According to Lasker (1978), the microplankton required for initiation of active feeding by anchovy larvae comprises unicellular flagellate algae and copepod nauplii, which are irregularly distributed in the upper ocean, forming patches and often occurring as microlayers. Increased concentrations of anchovy are found in these microlayers, where they are observed to survive best. This layered structure is stable at low turbulence, but is disrupted by storms or strong winds, which cause intensive mixing of the surface layer. It has been found that a minimum 5-day stable zero-wind weather situation is required to form patches and microlayers of higher food organism concentrations. These periods of the so-called “calm ocean” that promote high survival of larvae were named “Lasker windows”.

2.4.4 Cushing’s “Match/Mismatch” Hypothesis

Based on the multi-year studies in the North Atlantic, Cushing (1990) formulated the underlying reasons for development of abundant recruitment of herring, cod, and other fish with drifting pelagic eggs. While the North Atlantic is not an upwelling system, the basic principles of this hypothesis can still apply. Since there is only a short season for phytoplankton and zooplankton development in this region, favourable conditions for high survival and growth of fish larvae are rather short-term. Ultimately, their survival, and thus breeding success, depends on the massive occurrence of copepod nauplii (the main food of larvae during their transition to active feeding) coinciding with the hatched larvae. When these events coincide, larval survival and the probability of a subsequent abundant generation developing increases. Without such a coincidence, recruitment decreases.

Seawater temperature strictly determines the rate of development of both eggs and larvae and the plankton that directly affect fish recruitment. Optimal vertical turbulence in the surface layer significantly accelerates zooplankton reproduction

and promotes high survival of larvae. In contrast, high intensity wind mixing (regular spring storms, for example) destroys the oceans' upper layer structure and negatively affects survival of larvae, and thus the population recruitment.

2.5 Marine Food Web Structure in Coastal Upwelling Systems

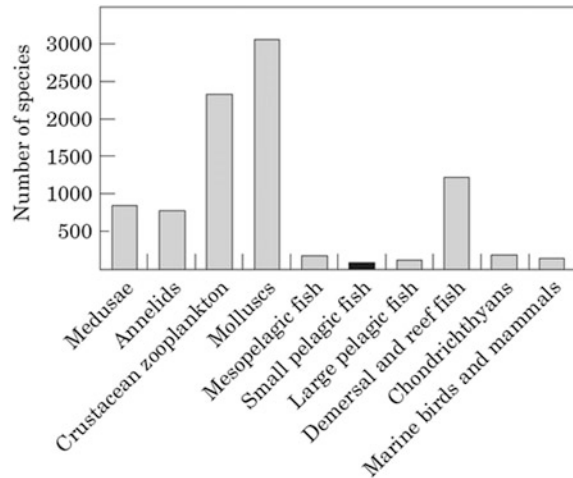
Upwelling regions are important sources of marine productivity, and they attract hundreds of species at different trophic levels to create biodiversity hot spots. Many marine ecosystems typically contain a large number of species at the lower (e.g. planktonic) trophic levels. They also contain a substantial number of predatory fish, seabirds, or marine mammals that feed at the upper apex and near-apex trophic levels. However, in many of the highly productive ecosystems of the world, and particularly in upwelling regions, there tends to be a vital intermediate trophic level occupied by small, plankton-feeding pelagic fish that is typically dominated by only one (e.g. sardine), or at most a few, species (Bakun 1996).

For example, in South Africa's marine fauna, which is particularly rich and well documented, the three phyla mollusca, crustacea, and chordata are represented by 3062, 2333, and 2492 species, respectively (Gibbons et al. 1999). Among the 2000 marine fish species recorded, about 70 % are demersal, benthic, or reef species; in contrast, only 6.1 % large and 3.7 % small pelagic fish species are found (Fig. 2.21). Species diversity is relatively high at the bottom of the food chain (e.g. 429 copepods, 2262 gastropods) and at its top (92 species of marine birds and 41 species of marine mammals). This wasp-waist richness pattern appears to be a common characteristic of upwelling systems.

Food webs of eastern boundary current upwelling systems share various common structural characteristics, such as the dominance of pelagic over demersal consumers, the cell/body size and coarse-taxonomic-level community structure in both plankton and fish, and dominant life history adaptation strategies. A microbial loop consisting of heterotrophic bacteria, very small photosynthetic autotrophs, and unicellular microzooplankton is present in the plankton in all regions, but this is overlaid by another plankton food web consisting of medium-to-large photosynthetic autotrophs grazed by metazoans. For more details, see the reviews by Hutchings et al. (1995) and Mackas et al. (2006).

Apart from a high primary productivity by medium-to-large cell size diatoms, which is generally localized in time and space, patterns of productivity and consumption are leaky and time-space lagged (see Fig. 2.19). Mesozooplankton biomass is usually dominated by a few species of medium and large copepods, one or two euphausiid species, and one or more chaetognaths, all taking advantage of behavioural and life-history adaptations (Mackas et al. 2006). As noted previously, upwelling trophic levels typically have a wasp-waist structure (Cury et al. 2000), whereby the wasp-waist species (sardines) have localized spawning and nursery

Fig. 2.21 Biodiversity of South Africa's marine fauna. Taken from Cury et al. (2000)



areas within the larger region and life spans that are short relative to decadal environmental variability. Dominant resident predators include hake and migratory fish (jack mackerel and tuna) that enter the upwelling system to feed, but spend part of their life offshore. Larger predators, such as fish, squid, seabirds and whales, survey the entire upwelling zone, targeting individual prey aggregations (Batchelder et al. 2002). The diversity of benthic macrofauna can be high, except where it is diminished in zones of hypoxia. Nearshore benthic species with meroplanktonic larval often rely on shoreward frontal displacement associated with upwelling relaxation in order to return to their settlement sites (Mackas et al. 2006).

The interaction of multiple time scales also influences behaviour of zooplankton and larval fish. In the Benguela Current, for example, various zooplankton and fish larvae undertake diel vertical migration, rising to the surface at night and descending into darker regions during the day. The usual explanation for this behaviour is predator-avoidance during daylight, but it has been shown that this behaviour interacts with the seasonal patterns of currents such that it retains the animals at a given latitude and distance offshore (e.g., Peterson et al. 1979; Peterson 1998). Moreover, some zooplankton and anchovy larvae use advanced techniques of diel vertical migration for moving onshore to more suitable spawning areas (see Mackas et al. 2006; and references therein).

2.6 Summary

This chapter described the functioning of the upwelling process in terms of physical and biogeochemical processes and marine food web dynamics, all closely inter-linked and constrained by a large range of temporal and spatial scales and complex interactions. Generally, wind-driven coastal upwelling is the dominant upwelling

mechanism creating highly productive coastal ecosystems and lucrative coastal fisheries. The next chapter details influences by the large-scale circulation, the natural variability of upwelling, and anthropogenic influences including eutrophication, global warming and exploitation of marine resources.

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