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ULTRAVIOLET STRESS

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Solar ultraviolet (UV) radiation, because of its high energy, damages biological molecules such as DNA, proteins, and lipids. UV radiation penetrates coastal seawater, where it may kill organisms outright, adversely affect diverse physiological processes (embryological development, growth, photosynthesis, immune response), and evoke avoidance behaviors. Marine organisms have evolved biochemical defenses against the direct and indirect effects of UV radiation. The metabolic costs of maintaining these defenses represent a stress, particularly when the defenses must cope with enhanced UV irradiance.

SOLAR UV RADIATION AT THE EARTH'S SURFACE AND UNDER WATER

Because of atmospheric absorption and scattering, solar radiation reaching the earth is lowered in intensity and its spectral distribution is truncated (Fig. 1A). The shortest ultraviolet wavelengths (UVC, <280 nanometers) are absorbed by ozone (O₃) and molecular oxygen (O₂) and do not reach the earth's surface. UVB (the band of wavelengths from 280 to 320 nm) is also greatly attenuated by stratospheric O₃, whereas UVA (320–400 nm) and photosynthetically available radiation (PAR, 400–700 nm) are not.

Owing to the net degradation of stratospheric O₃ by reactions with polluting halocarbons (molecules containing halogen atoms such as chlorine, fluorine, and

bromine), most notably chlorofluorocarbons (manufactured as refrigerants and aerosol propellants), levels of UVB reaching the earth's surface have increased since the 1970s—on average by 50% and 15% in the Antarctic and Arctic, respectively, during seasonal ozone depletion, and seasonally by 4–7% in midlatitudes of the northern hemisphere. UVB, already high in the tropics, has not changed significantly there.

Infrared radiation (>700 nm), which has a low energy content per photon (Fig. 1B) and is manifested as heat, constitutes just under half of the total solar energy incident on the earth (Fig. 1A). PAR (also involved in vision) accounts for roughly half. Combined UVA and UVB constitute only about 5%. Despite this low incidence, because of their high energy content per photon (Fig. 1B), UV wavelengths have large biological effects.

The variable penetration of UV radiation into seawater is caused primarily by regional and temporal differences in its absorption by biologically derived dissolved organic matter and particulate organic matter (including detritus and living plankton). The attenuation of UV radiation is inversely related to wavelength, so that UVA penetrates deeper than does UVB. In clear seawater that is low in productivity, UV radiation penetrates to several tens of meters, whereas in productive coastal waters it reaches maximally to about 10–20 meters, with much variability among waters having different optical properties. In the coastal Gulf of Maine (United States), UVA is 1% of its surface value at about 5 m; the 1% depth there for UVB is 2–5 m, but off Southern California (United States) UVB is detectable to 22 m. Organisms living intertidally and in tidepools potentially are exposed to levels of UVR ranging from a few percent up to 100% of the local surface intensity.

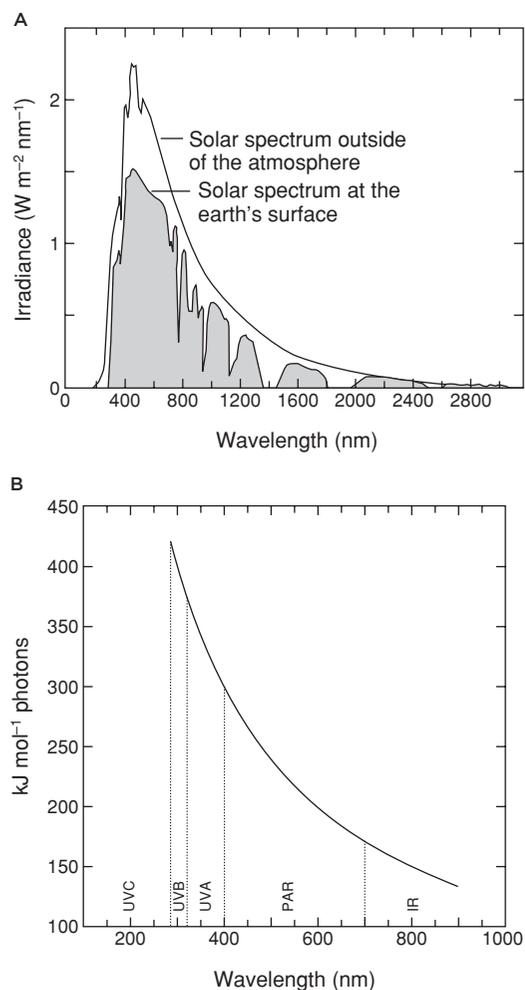


FIGURE 1 (A) The solar spectral irradiance (energy flux at various wavelengths) outside the atmosphere and incident on the earth. Modified from M. Blumthaler and A. R. Webb, *UV radiation climatology*, in Helbling and Zagarese (2003). Reproduced by permission of The Royal Society of Chemistry. (B) The energy content of a photon of light is inversely related to its wavelength (λ). UVC = ultraviolet C; UVB = ultraviolet B; UVA = ultraviolet A; PAR = photosynthetically available radiation; IR = infrared radiation.

BIOLOGICAL EFFECTS OF UV RADIATION

Because their cyclic molecular structures contain conjugated double bonds (i.e., those that alternate with single bonds: C=C–C=C–C=C), in which the electrons are loosely bound, nucleotide bases (especially) and aromatic amino acids containing cyclic side groups (to a smaller extent) readily absorb UVB. The same is true of polymers containing these building blocks: the nucleic acids DNA and RNA, and proteins. These molecules are structurally altered when the loosely bound electrons are raised to higher energy levels on absorbing these energetic wavelengths. In DNA, the most common UVB photoproducts are pyrimidine

dimers, in which two adjacent molecules of the pyrimidine nucleotide thymine are covalently linked in a cyclic structure that blocks transcription of the genetic information into RNA. UVB radiation causes mutations in DNA and can produce melanomas in mammals and fishes.

Deleterious effects on proteins (e.g., loss of function, particularly in enzymes involved in photosynthesis) can be caused by both UVB and UVA, in the latter case primarily via the action of intracellular photosensitizing molecules that transfer the absorbed radiant energy to O_2 , leading to the production of reactive oxygen species such as singlet oxygen, hydrogen peroxide (H_2O_2), and superoxide ($O_2^{\cdot-}$) and hydroxyl (OH^{\cdot}) free radicals. Free radicals are chemicals having at least one unpaired electron and in consequence are highly reactive. Oxygen free radicals and other reactive oxygen species in turn oxidatively degrade proteins, DNA, photosynthetic pigments, membrane lipids, and other cellular constituents, with widespread physiological effects. Reactive oxygen species normally are held in check by natural antioxidants such as carotenoids, ascorbic acid (vitamin C), and enzymes such as superoxide dismutase (SOD) and catalase. When there is an imbalance between the production of reactive oxygen species and the defenses against them, oxidative stress is the result.

Reactive oxygen species are also produced in seawater through the interactions of dissolved organic matter with UV radiation and trace metals, with unknown effects on organisms. Any effects might be pronounced in tidepools, whose isolation at low tide and large biomass could lead to higher concentrations of precursors (dissolved organic matter) and products (reactive oxygen species). At the same time, high concentrations of dissolved organic matter (including algal exudates known to absorb UV radiation) in tidepools might help to protect organisms there from the direct effects of UV radiation.

In rare cases it has been possible to infer the proximal cause of the detrimental biological effects of UV radiation by comparing the absorption spectra of biological molecules with the action spectra—the relative effectiveness of different wavelengths of monochromatic radiation—causing a specified biological effect. However, few empirically determined action spectra are available for marine processes. More commonly, biological weighting functions (polychromatic action spectra generated by successively filtering out shorter wavelengths) have been used to assess the effects of ultraviolet and interacting longer wavelengths on marine processes. The biological weighting functions for mortality in embryos of the copepod *Calanus finmarchicus*, the codfish *Gadus morhua*, and the anchovy *Engraulis mordax* closely match that for damage

to isolated DNA (Fig. 2A), indicating that mortality is related to genetic damage. UVB wavelengths <312 nm are the most damaging, whereas UVA has no effect. Conversely, inhibition of photosynthesis in phytoplankton and corals also involves UVA (probably mediated by reactive oxygen species), an inhibition that is offset by intracellular sunscreens that absorb in this waveband (Fig. 2B and see the section “Mechanisms of Repair and Defense”).

Most commonly, mortality, photosynthesis, growth, or another biological process is measured in the presence and absence of broadband UV radiation, or UVB in particular (UV wavelengths are removed from solar or artificial light sources using cutoff filters), or under artificially enhanced UVB to simulate the effect of ozone depletion. Such studies indicate that shallow-water marine organisms may be killed by levels of UV radiation they likely encounter in nature. These include viruses (whose infectivity is also reduced by UV radiation), bacteria, eukaryotic phytoplankton, macroalgae (seaweeds), diverse invertebrates (planktonic crustaceans and larvae of echinoderms have been most studied), and the larvae of fishes. Some generalizations are possible. UVB is more consistently lethal than is UVA (Fig. 2A), and early developmental stages are more susceptible than later ones.

The intertidal copepod *Tigriopus californicus*, an inhabitant of supralittoral pools in the highest reaches of the intertidal zone and normally exposed to high fluxes of solar UV radiation, is more resistant to UVB than is the planktonic copepod *Acartia clausii*. In the latter species, individuals that survive exposure to UVB produce fewer offspring than do unirradiated individuals. It is unknown whether chronic exposure to UVB in intertidal organisms affects their long-term fecundity. Hatching size in surviving codfish larvae is smaller when they have been exposed to UVB during embryonic development.

Broadband UV radiation reduces growth in brown, red, and green seaweeds, as well as skeletal growth in corals having unicellular algal endosymbionts living within the host animals’ cells, consistent with the many demonstrations that UV radiation also diminishes photosynthesis in such organisms. Impaired growth is not simply an effect of a diminished supply of photosynthetically fixed carbon, however, and as in the cases of stunted cod larvae and of nonsymbiotic sea anemones (*Actinia equina* and *Metridium senile*) that grow more slowly under UV radiation, it may reflect a reallocation of resources from growth to resistance against and repair of UV-induced damage. UV radiation reduces the grazing on small phytoplankton

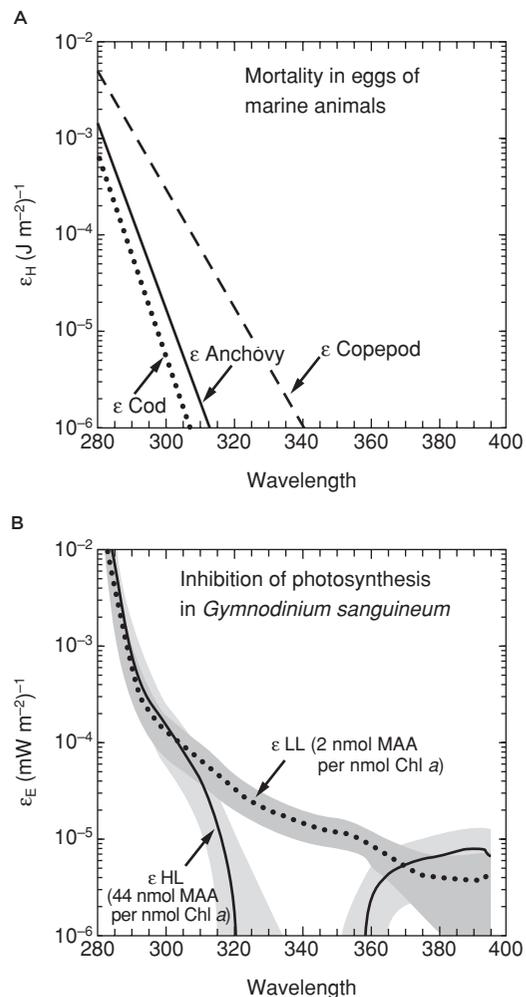


FIGURE 2 (A) Biological weighting functions (ϵ_H), which show the relative effect of different UV wavelengths, indicate that mortality in the eggs of copepods and fishes is related to damage to their DNA by UVB radiation. For comparison, the spectrum for anchovy egg mortality is the action spectrum for damage to naked DNA normalized to the exposure causing 50% egg mortality. Units of ϵ_H are the reciprocal of UV dose ($J m^{-2}$) because mortality is best predicted from cumulative exposure. Here, the eggs of a copepod are more sensitive than those of fishes. (B) Biological weighting functions (ϵ_E ; units are the reciprocal of dosage rate, $mW m^{-2} = mJ s^{-1} m^{-2}$, used in short-term exposures) indicate that the inhibition of photosynthesis by UVA (≈ 320 – 360 nm) in the dinoflagellate *Gymnodinium sanguineum* grown under low light (LL) is offset by the 22-fold higher concentration of UV-absorbing mycosporine-like amino acids (MAAs; see section “Mechanisms of Repair and Defense”) per nanomole of chlorophyll α occurring in cells previously grown in bright light (HL). UVB also exerts strong negative effects in both groups at wavelengths shorter than those absorbed by MAAs. Shaded areas represent the 95% confidence belts for the biological weighting functions. A and B modified from P. J. Neale and D. J. Kieber, Assessing biological and chemical effects of UV in the marine environment: Spectral weighting functions, in Hester and Harrison (2000). Reproduced by permission of The Royal Society of Chemistry.

by heterotrophic nanoflagellates, which should also affect the consumers' growth.

In the case of inhibition of photosynthesis, specific effects of UV radiation include the degradation of the structural D1 protein in photosystem II (a complex of light-trapping molecules, a photochemical reaction center, and electron transfer molecules), and of Rubisco, the primary CO₂-fixing enzyme. Intracellular reactive oxygen species are particularly implicated in photooxidative damage during the exposure of photosynthetic organisms to UV radiation. This includes not only free-living algae but also corals and sea anemones that harbor unicellular algal endosymbionts. Cytological abnormalities, damage to DNA, and oxidative stress in the host or the symbiotic algae have been demonstrated in the anemones *Aiptasia* spp., *Anthopleura elegantissima*, *Cereus pedunculatus*, and in the corals *Montipora faveolata*, *Porites porites*, and *Stylophora pistillata* that have been exposed to UV radiation.

Subtidal seaweeds are generally more susceptible to inhibition of photosynthesis and growth by UV radiation than intertidal macroalgae are. Unlike phytoplankton in a deep, vertically mixed water column that affords a periodic reprieve from UV radiation, algae living intertidally and in tidepools are continuously subjected to UV inhibition of photosynthesis in daylight, although they recover more quickly than subtidal algae when the stress is removed. Differential susceptibility to UV radiation among species is one factor affecting the vertical zonation of seaweeds.

UV radiation inhibits the uptake of inorganic nutrients such as ammonium, nitrate, and phosphate by phytoplankton and macroalgae by an unknown mechanism, perhaps damage to ion transporter proteins or to membrane lipids (important targets of reactive oxygen species). This may be important because the algae normally are nitrogen limited. The pools of algal storage products, including carbohydrates, lipids, and amino acids, are also affected.

Damage to DNA by UVB has been studied in marine bacteria, phytoplankton, and zooplankton, including larvae of invertebrates and fishes, as well as benthic invertebrates such as corals. The relationship between the extent of DNA damage (pyrimidine dimers) and mortality has rarely been assessed, but the two are correlated in larvae of sea urchins. Damage to DNA, and perhaps to actin microfilaments and components of cell signaling pathways, delays the first cell division in the eggs of sea urchins and tunicates, and results in abnormal embryonic and larval development in sea urchins. Delays in the cycle of cell division allow for repair of damaged DNA, which may implicate the UVB-dependent activation of

genes controlling the cycle. Exposure of sea urchin and cod fish embryos to UVB leads to enhanced transcription of the tumor suppressor gene *p53*, whose product delays cell division while DNA is repaired. Irreversibly damaged cells may be removed by apoptosis (programmed cell death), which increases in sea urchin embryos exposed to UVB. The UV inhibition of germination and cellular proliferation in spores of intertidal brown seaweeds is sensitive to temperature, an important consideration in this thermally variable environment.

First demonstrated in mammals, suppression by UV radiation of the immune response to invading substances is also seen in fishes. This might lead to a greater susceptibility to infections.

MECHANISMS OF REPAIR AND DEFENSE

Organisms have been exposed to solar UV radiation since early in the history of life and have evolved mechanisms to deal with its damaging effects. Mechanisms of repairing UV-induced damage to DNA are found from viruses to eukaryotes. Photoreactivation involves the cleavage of covalently linked thymine dimers by a photolyase enzyme that is activated by UVA and blue wavelengths of 370–450 nm in a dose-dependent manner. Therefore, a concern about stratospheric ozone depletion is that it increases the amount of UVB reaching organisms and damaging their DNA without a corresponding increase in the longer photoreactivating wavelengths, which are unaffected by ozone. It also follows that a realistic assessment of the net biological effects of UVB should include allowance for photoreactivation.

Downward movement in the water column (which attenuates damaging UVB more rapidly than it does photoreactivating UVA or blue wavelengths) through vertical mixing or active migration of plankton tips the balance in favor of repair relative to damage, but this defense is less available to sessile intertidal organisms or those confined to tidepools. Photoreactivation has been demonstrated in diverse marine organisms by varying the availability of photoreactivating wavelengths after a UVB insult. A single study of three genera of opisthobranch molluscs (sea slugs), however, did not reveal a correlation between their capacities for photoreactivation by photolyase and their normal environmental UVB regimes.

Unlike photoreactivation, nucleotide excision (dark repair) does not require light and is more complex, involving a suite of enzymes. Dark repair can correct not only pyrimidine dimers but also other structural damage to DNA. It occurs in all taxa examined but has not been systematically studied in marine organisms.

Rather than risking damage that may have further effects before it is repaired, it seems safer to avoid damage in the first place, although the relative metabolic costs of these alternatives have not been compared. Behavioral avoidance of UV radiation is widespread and involves, for example, migrating vertically in the water column (a limited option in the intertidal), seeking shade under the seaweed canopy, under rocks, or in empty shells (employed by tidepool fishes), retracting vulnerable body parts (done by sea anemones, as shown in Fig. 3), and covering the body with reflective shells and other debris (seen in sea anemones—Fig. 3—and sea urchins).

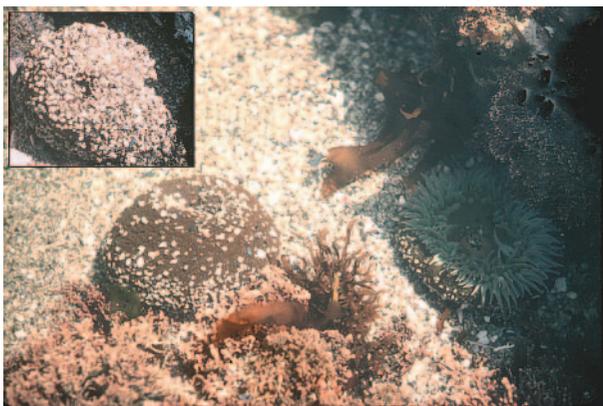


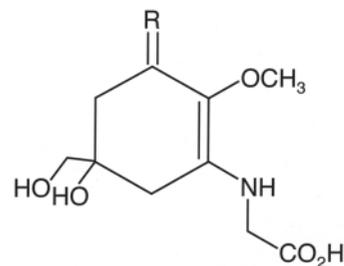
FIGURE 3 Symbiotic sea anemones such as *Anthopleura xanthogrammica* must expose their tentacles and oral disk to some sunlight to allow their algal endosymbionts in those tissues to photosynthesize, as seen in the specimen on the far right. However, sea anemones also reduce the damaging effects of the brightest sunlight by retracting their tentacles and shielding them and the oral disk by contracting the sphincter muscle at the top of the body column like a drawstring (as done by the sea anemone at left). Even the shaded individual on the right has begun to contract its margin where full sunlight has just reached. This avoidance is mediated by PAR and UV radiation. These sea anemones also have attached reflective gravel to the verrucae (adhesive structures) of their columns. Attachment of gravel and shell debris by immersed individuals such as these in tidepools is evoked by UV radiation, so the material serves as a UV sunshade or parasol, particularly when the coverage is extensive (inset). When exposed to air at low tide, the related species *A. elegantissima* responds to low humidity by attaching more debris, which provides a boundary layer that restricts the evaporation of water and reduces desiccation, as well as being a shield against direct sunlight.

Sessile organisms must rely on mechanisms to block or screen out UV radiation. These include shells, tests, egg capsules, and other coverings, as well as biochemical sunscreens that absorb UV radiation and harmlessly dissipate its energy. The latter include melanins and mycosporine-like amino acids (MAAs), and less demonstrably, carotenoids and macroalgal phlorotannins (polyphenolic compounds consisting of multiple six-carbon rings containing three conjugated

double bonds and attached $-OH$ groups). Carotenoids seem to protect more by quenching reactive oxygen species (especially singlet oxygen) and photo-excited chlorophylls than by dissipating UV radiation directly. The phlorotannin content of the brown seaweed *Ascophyllum nodosum* increases under UV exposure, but its sunscreen effectiveness (it absorbs in the UVB) has not been evaluated.

Melanins (complex pigments formed by the oxidation and polymerization of the aromatic amino acid tyrosine) broadly absorb UVA and UVB and occur in the epidermis of marine invertebrates, including sea anemones, flatworms, polychaetes, echinoderms, and arthropods (crustaceans and insects), as well as in the integument of fishes. Increased deposition of melanin following exposure to UV radiation (the familiar tanning response in littoral humans) occurs in bony fishes and sharks, as well as in the sea anemone *Metridium senile*, where it presumably enhances photoprotection.

Mycosporine-like amino acids are, taxonomically, the most widespread sunscreens in marine organisms. They are small cyclic molecules in which variation in a side chain changes their absorption characteristics (Fig. 4). The 20-odd identified MAAs absorb UVA and UVB radiation in the range 309–360 nm, providing a broadband UV filter. They absorb UV radiation efficiently (far more so than DNA and proteins in this waveband), and thus intercept UV radiation before it damages other biological molecules, dissipating the energy as heat and without forming potentially damaging active intermediates. MAAs are colorless and transparent to PAR, important



Mycosporine-glycine: R = O; $\lambda_{\max} = 310$ nm

Palythine: R = NH; $\lambda_{\max} = 320$ nm

Diverse MAAs: R = N of amino acid or other amine;
 $\lambda_{\max} = 330\text{--}360$ nm

FIGURE 4 General structure of mycosporine-like amino acids (MAAs), natural sunscreens that are widespread among marine organisms. Chemical substitutions (R) on the central cyclic structure modify its wavelength of maximum absorption (λ_{\max}), whereby organisms that contain multiple MAAs have a broadband UV sunscreen.

because algae and symbiotic invertebrates such as sea anemones must transmit these solar wavelengths in order to photosynthesize.

MAAs are natural products of metabolism in algae and cyanobacteria, but are also accumulated by marine consumers from their food and subsequently concentrated in epidermal tissues and in eggs, where they afford a concentration-dependent protection of the embryos against UV radiation. Tidepool sculpins (fishes in the family Cottidae) contain UV-absorbing compounds in their skin's mucous layer, the absorption spectra of which are indicative of MAAs that occur also in the ocular lenses of fishes. Overall, the degree of UV absorption by sculpin mucus is correlated with differences in incident UV radiation associated with latitude and intertidal height. Corals and seaweeds in shallow water accumulate higher concentrations of MAAs than do deep-dwelling representatives of the same species, and the biosynthesis of MAAs is stimulated primarily by UV radiation and also by intense PAR. Biological weighting functions indicate that MAAs protect photosynthesis from UVA in free-living dinoflagellates (Fig. 2B) and corals. MAAs released from algae are an important fraction of the UV-absorbing dissolved organic matter in seawater.

The activities of antioxidant enzymes (notably superoxide dismutase) also increase with exposure to UV radiation in algae, invertebrates (including nonsymbiotic but especially symbiotic species), and larval fishes. The upregulation of SOD indicates that it is a defense against the secondary effects of UV radiation acting via the intracellular generation of superoxide radicals and other reactive oxygen species derived from them.

UV RADIATION AND THE INTERTIDAL ENVIRONMENT

Although the intertidal zone has not been extensively studied with particular reference to UV radiation, littoral organisms are exposed to the highest local solar irradiances in the marine environment. Accordingly, they have evolved adaptations to avoid or repair UV-induced damage. The available evidence suggests that, although the increased UVB irradiance since the 1970s has demonstrable short-term effects on shallow-water organisms, it has not caused major changes in littoral communities, probably because the organisms' defensive mechanisms thus far have been able to cope with this increase.

Nevertheless, maintaining elevated defensive and repair capacities imposes a cost, and the manifestations of long-term UV stress on community productivity are uncertain. Subtidal bottom-dwelling organisms, and those living deeper in the water column, have proved more sensitive

to UV radiation and seem more at risk from its effects under ozone depletion. Confined tidepools may provide natural reaction vessels for studying the photochemistry of dissolved organic matter and its dual attributes of attenuating UV radiation and generating reactive oxygen species, as well as natural laboratories for evaluating the potential biological effects of these chemicals.

SEE ALSO THE FOLLOWING ARTICLES

Light, Effects of / Metamorphosis and Larval History / Photosynthesis / Reproduction / Symbiosis / Water Chemistry

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UPWELLING

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Upwelling is the vertical motion of seawater from depth toward the sea surface. Water moves upward to supply regions where wind causes surface waters to diverge. Upwelling fuels the incredibly productive food web found in the coastal ocean, and the circulation it generates is key to the transport of organisms across and along the continental margin.

WIND FORCING OF UPWELLING

Coastal upwelling is driven by the wind, more specifically by the divergence of surface currents driven by the wind. As wind blows over the ocean surface, it pushes

a thin surface layer downwind. The wind stress is communicated down into the upper ocean by the viscosity of water, that is, the friction between water layers, with lower layers moving slower than those above. Because the earth is rotating, there is a Coriolis force to the right (to the left in the Southern Hemisphere) of the wind-driven currents when facing downstream. The following discussion is valid for the Northern Hemisphere. Eventually a balance is achieved between the wind stress and the Coriolis force, and the resulting upper-ocean currents are to the right of the wind. Water velocities are strongest at the surface and decrease with depth while turning in a clockwise direction. The currents near the sea surface are 45° to the right of the wind. Looking down from above, a line connecting the tips of the velocity vectors is a spiral, the so-called Ekman spiral, named after V. W. Ekman, who detailed this motion in 1905 during his Ph.D. research, motivated by the observation by F. Nansen and others that icebergs in the Arctic Ocean moved to the right of the wind rather than directly downwind.

The Ekman layer is a surface boundary layer, and the depth to which the wind-driven currents penetrate, typically 20–50 m, is called the Ekman depth. When the currents in the entire Ekman layer are summed up, the net transport of water, referred to as the Ekman transport, is exactly 90° to the right of the wind. This remarkable result is the driving force behind coastal upwelling. Alongshore winds, blowing with the coast to the left when facing downwind, drive surface currents offshore. To compensate for the loss of water at the surface near the coast, water is upwelled from depth (Fig. 1).

Upwelling is forced primarily by alongshore winds according to the argument just stated, but there are at least

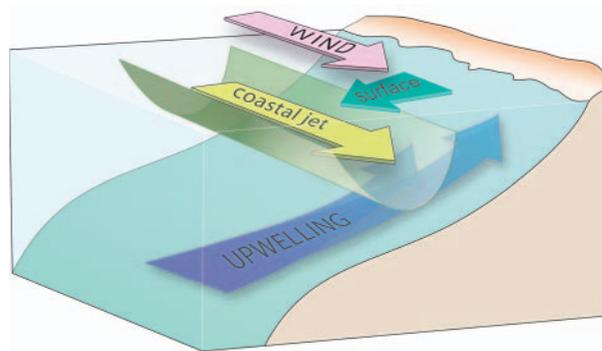


FIGURE 1 Schematic wind-driven upwelling and ocean currents. Surface water is driven offshore by an alongshore wind and the Coriolis force. Cold, salty, nutrient-rich water is upwelled to resupply the offshore surface flow. The resulting cross-shelf temperature (density) gradient creates a strong, surface-intensified coastal upwelling jet flowing in the direction of the wind. Drawing by J. Barth and D. Reinert.

two other ways that wind can drive upwelling. Additional upwelling can be driven by cross-stream variations in the strength of the wind. Where alongshore winds are stronger, say offshore or near coastal headlands, the resultant Ekman layer transport is greater than in adjacent regions with weaker winds. To conserve mass, water is upwelled from below. In some regions of coastal upwelling, this “curl-driven” upwelling can account for one-third or more of the total upwelling. A second source of upwelling originates from winds blowing in the offshore direction. These winds can drive a thin (a few meters thick) surface layer directly offshore in a surface “log layer,” requiring a supply of water from below to conserve mass near the coast. This effect is small compared with the efficiency of alongshore winds in driving upwelling.

Coastal upwelling occurs anywhere where winds blow parallel to the coast, but it is especially prevalent along the eastern boundaries of the ocean basins at mid to high latitudes. Alongshore winds blowing toward the equator are created by air moving around high-pressure systems (clockwise in the Northern Hemisphere) over the eastern ocean basins, for example around the North Pacific High. These winds are intensified by the presence of low-pressure systems over the adjacent warm continents. There are four major eastern boundary current regions dominated by upwelling in the world’s oceans: the Benguela Current region off southwest Africa, the Canary Current region off northwest Africa and the Iberian Peninsula, the Humboldt Current region off Peru and Chile, and the California Current system off the west coast of North America (Fig. 2). The remaining eastern boundary, along the west coast of Australia in the Indian Ocean, is dominated by the Leuwin Current, which is not primarily wind-driven.

QUANTIFYING UPWELLING VELOCITY AND TRANSPORT

Upwelling velocities are measured in tenths of millimeters per second but, summed over a day, result in water parcels moving upward 10–30 m, a significant fraction of the total water depth over the continental shelf. Such small vertical velocities are virtually impossible to measure directly with a mechanical or acoustic current meter, but the effect of upwelling is easy to recognize by the presence of cold water at the surface near the coast (Fig. 2).

The offshore surface Ekman transport ($M = \tau/\rho f$, in $\text{m}^2 \text{s}^{-1}$) is estimated by dividing the wind stress (τ , in newtons m^{-2}) by the density of water ($\rho \approx 1024 \text{ kg m}^{-3}$) and the Coriolis parameter (f), equal to twice the rotation rate of the earth times the sine of the latitude (about

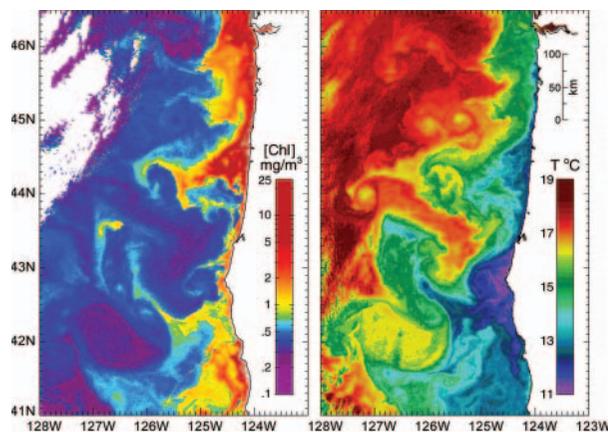


FIGURE 2 Sea-surface temperature (right) and chlorophyll (left) measured by satellite along the U.S. West Coast on September 26, 1998. Image by J. Barth and D. Reinert. Data courtesy of T. Strub.

0.0001 s^{-1} at mid-latitudes). Wind stress is equal to the wind speed squared, multiplied by the density of air (1.3 kg m^{-3}) and a drag coefficient, which is dependent on wind speed and details of the atmospheric boundary layer structure but is about equal to 0.0014 . As an example, a 20-knot wind yields an offshore Ekman transport of $1.9 \text{ m}^2 \text{ s}^{-1}$. If this transport is distributed over a 30-m-deep layer, the offshore velocity is 0.06 m s^{-1} , or about 5 km per day. This formula for offshore surface Ekman transport is used to compute the “Bakun Upwelling Index,” a value commonly used in studies of wind-driven coastal upwelling and ecosystem response.

Since the offshore surface Ekman transport must be balanced by upwelling from below, an estimate of the cross-shelf width (L) over which the upwelling occurs may be used together with a conservation-of-mass argument to calculate the vertical upwelling velocity. In the example above, using $L = 20 \text{ km}$ yields an upwelling velocity of one tenth of a millimeter per second (10^{-4} m s^{-1}) or about 10 meters per day.

COASTAL CIRCULATION IN AN UPWELLING REGION

Upwelling dramatically influences seawater properties near the coast. Because sea water is colder, saltier, and higher in nutrients at depth, water upwelled near the coast is considerably different from surface waters farther offshore. The boundary between cold, salty, nutrient-rich waters inshore and warm, fresh, nutrient-poor waters offshore is called the upwelling front. Upwelling fronts can be strong and sharp with temperature differences of a few to $10 \text{ }^\circ\text{C}$ over a half to 10 km, easily detected,

for example, in satellite sea-surface temperature images (Fig. 2). Note that because salinity is “conserved” (that is, it is not altered by surface warming, as is temperature, nor consumed or produced through biological and chemical processes, as are nutrients), it is the most faithful tracer of upwelling.

Another physical consequence of upwelling is that sea level goes down by tens of centimeters as surface waters are forced offshore, an effect measurable with a tide gauge. In addition to the few to ten cm s^{-1} offshore surface Ekman velocities described in the preceding section, an even weaker compensatory onshore flow at depth— weaker because the required onshore transport is distributed over a layer thicker than the surface Ekman layer—is established to supply the upwelled water (Fig. 1). This compensatory or return flow can occur at mid-depth, in the bottom boundary layer, or both, depending on details of the vertical stratification of the water column and the bottom slope. The proportion of upwelled water supplied from mid-depth or from near the bottom has important consequences for the water properties supplied to the nearshore and the rocky intertidal.

The presence of cold water next to the coast creates a density gradient across the shelf (the upwelling front) because it is denser than warm water found offshore. This density gradient adds to the difference in sea level across the shelf to form an onshore pressure force, which is balanced by an offshore Coriolis force associated with a strong coastal upwelling jet flowing in the direction of the wind (Fig. 1). The horizontal scale over which this balance is achieved is called the Rossby radius of deformation and is a fundamental scale in geophysical fluid dynamics. For coastal upwelling in a stratified fluid, it is the first internal Rossby radius of deformation (L_i), determined by the strength of the stratification (N in s^{-1}), the local water depth (H), and the Coriolis parameter ($L_i = NH/f$), that is most important. Over the continental shelf and slope, L_i varies from 5 to 20 km. From this follows a typical cross-shelf scale of the upwelling front and the width of the alongshore coastal upwelling jet.

The coastal upwelling jet is surface intensified and strongest in a core, associated with the upwelling front, often located over the mid-shelf (about 80–100 m bottom depth, for example off the U.S. West Coast). The upwelling jet can reach speeds of $0.5\text{--}1.0 \text{ m s}^{-1}$ and carry about $0.25\text{--}0.5$ million meters cubed per second of water downwind, equal to 15–30 times the transport in the Mississippi River. Although the surface and deep compensatory currents can move material across the shelf at about 5 cm s^{-1} , the wind-driven alongshore currents are ten or more times faster, so

that water parcel trajectories are not two-dimensional but are, in fact, helical motions along the coast.

ECOSYSTEM RESPONSE TO COASTAL UPWELLING

Upwelling has profound consequences for coastal pelagic and benthic ecosystems. Nutrients are supplied to near-shore and intertidal habitats. Wind-driven currents transport the larvae of rocky-intertidal organisms to and from the coast and, potentially, over great distances alongshore. Phytoplankton blooms occur in continental shelf waters as nutrient-rich water encounters the euphotic zone. Upwelled nutrients include nitrate, phosphate, and silicate, necessary for phytoplankton growth, and trace metals such as iron, which influence the rate of photosynthesis in phytoplankton. These phytoplankton form the base of the food web, supporting zooplankton populations that are, in turn, preyed upon by fish and other large consumers. This efficient upwelling-driven food web supports over 25% of the world's fish catch.

The cold, salty, nutrient-rich upwelled water is the source of water to the rocky intertidal zone. This is demonstrated by the strong relationship between temperatures measured right on a rocky intertidal outcrop adjacent to tide pools off Oregon and temperatures measured directly offshore on the open, wind-driven continental shelf (Fig. 3). Cold, upwelled waters near the coast also help produce fog, which can be a hazard to navigation or supply life-giving moisture to arid regions inshore of upwelling regions, for example the Namib Desert. Cold ocean temperatures from upwelling also increase the strength of the daily sea breeze, intensifying the land–ocean temperature contrast, which forces air landward during the late afternoon.

Besides supplying nutrients to the euphotic zone, the wind-driven surface velocities transport the larvae of rocky-intertidal organisms offshore. The onshore, compensatory

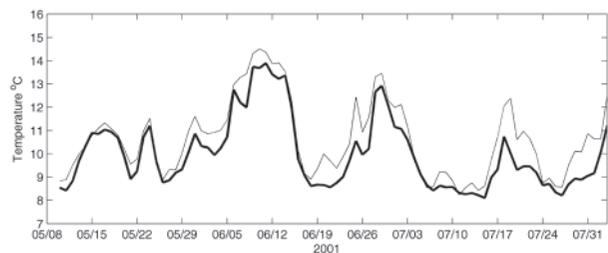


FIGURE 3 Time series of temperature measured on a rocky intertidal outcrop (thick curve) adjacent to tidepools off Oregon, showing high correlation with temperatures measured directly offshore at the surface (thin curve) in 30 m of water. Drawing by J. Barth, A. Kirincich, and F. Chan. Data courtesy of Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO).

flow feeding the upwelling transports water and the material it contains (eggs, larvae) shoreward. These cross-shelf motions are critical in removing and supplying the eggs and larvae of rocky-intertidal organisms to and from the shore. The swift, alongshore coastal upwelling jet can similarly transport eggs and larvae hundreds of kilometers alongshore. This alongshore transport and its variability are important for the connectivity of rocky-intertidal populations through dispersal of their larvae.

TIME- AND SPACE VARIABILITY OF COASTAL UPWELLING

The description above assumes steady, time-independent wind forcing. In reality, coastal winds vary over a wide range of periods. The dominant variability occurs with 2- to 10-day periods, the “weather band,” as atmospheric weather systems transit coastal regions. Weather-band variability can break up periods of strong, upwelling-favorable winds with intervals of low winds (relaxation) or downwelling-favorable winds. When upwelling-favorable winds relax, alongshore flow on the shelf, especially near the bottom and nearest the coast, can reverse and flow opposite to the previously established downwind currents. During wind relaxation, the across-shelf surface Ekman transport ceases, and during downwelling-favorable winds, surface transport is shoreward. Thus, relaxation and downwelling events are important for onshore recruitment of invertebrate larvae (crabs, barnacles, bivalves, and molluscs).

Depending on latitude, coastal winds can also vary strongly on a seasonal cycle, with sometimes rapid transitions between summertime upwelling-favorable winds and fall–winter downwelling-favorable winds. Lastly, year-to-year or “interannual” variability is introduced to coastal upwelling from events, such as El Niño/La Niña cycles or enhanced transport of high-latitude, subarctic water into coastal upwelling regions. This interannual climate variability influences the properties of upwelling source waters (warmer, nutrient-poor water during El Niño; colder, nutrient-rich water during enhanced subarctic transport events) and the strength, timing, and duration of coastal winds.

Further complexity to the circulation and ecosystem consequences described in the previous paragraphs is introduced by three-dimensional processes such as flow instability, alongshore variations in wind speed and flow–topography interaction. The coastal upwelling jet and front are unstable and can break down into meanders and eddies, which increase the amount of frontal habitat and expedite across-shelf transport of nutrients, larvae, phytoplankton, and other water properties (Fig. 2).

This instability process is analogous to how the atmospheric jet stream meanders to create high- and low-pressure weather systems (eddies). When the upwelling jet interacts with coastal topographic features (capes, bays, submarine canyons and banks), strong three-dimensionality is introduced into the system, including the formation of upwelling hot spots with increased primary production; the separation of the jet from the coast, thus injecting water and the material it contains into the deep ocean; and the creation of retention or low-flow regions where organisms can be preferentially held in place near the coast. Each of these processes contributes to the variability in ocean “weather” and, hence, the influence of the coastal ocean on rocky intertidal habitats.

SEE ALSO THE FOLLOWING ARTICLES

Currents, Coastal / El Niño / Fog / Nutrients / Seawater / Wind

FURTHER READING

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