When model and data are shown to be consistent, the specific mechanisms underlying observed patterns in simulated distributions can be identified. If a model is determined to be inconsistent with observations, it may be possible to isolate the specific model assumption that has been violated, and to reformulate the model in a more realistic fashion. Thus, although the assimilation of data into a marine biogeochemical model cannot necessarily overcome inappropriate model dynamics and structure, it can serve to guide model reformulation.

During the 1990s, large interdisciplinary oceanographic programs included model prediction and forecasting as specific research objectives. However, new studies are revealing that much more work needs to be performed before this becomes a realistic and achievable goal. Until high-resolution biological and chemical data are available over large regions of the ocean, and until a much clearer understanding of the intricacies of marine ecosystems is attained, data assimilation in biogeochemical models will be more useful for model improvement and parameter estimation than for model prediction and forecasting. By providing a means for recovering the best-fit set of parameters for a given model, certain assimilation techniques may prove to be a crucial tool for marine biogeochemical modelers.

The importance of inclusion of data in all steps of model development and implementation cannot be emphasized enough. It is through model and data comparisons that models are advanced and better observation systems are developed. Therefore, an important aspect of furthering the development of predictive marine biogeochemical models is recognizing the need for interdisciplinary multiscale observational and experimental networks. The availability of such data will necessitate the development of techniques for input of these data into models, and facilitate the development of data-assimilative marine biogeochemical models.

See also

Data Assimilation in Models. El Niño Southern Oscillation (ENSO) Models. Forward Problem in Numerical Models. Inverse Models. Inherent Optical Properties and Irradiance. Moorings. Ocean Color from Satellites. Population Dynamics Models. Primary Production Processes. Regional and Shelf Sea Models.

Further Reading

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BIOLUMINESCENCE

P. J. Herring, Southampton Oceanography Centre, Southampton, UK
E. A. Widder, Harbor Branch Oceanographic Institution, Fort Pierce, FL, USA

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Introduction

Bioluminescence is the capacity of living organisms to emit visible light. In doing so they utilize a variety of chemiluminescent reaction systems. It has historically been confused with phosphorescence and the latter term is still frequently (and erroneously) used to describe marine bioluminescence. Some terrestrial species (e.g., fireflies) have the same ability, but this adaptation has been most extensively developed in the oceans. Bioluminescent species occur in only five terrestrial phyla, and only in one of these (Arthropoda, which includes the insects) are there many examples. In contrast, bioluminescence occurs in 14 marine phyla, many of which include numerous luminescent species (**Table 1**). All oceanic habitats, shallow and deep, pelagic and benthic, include bioluminescent species, but the phenomenon is commonest in the upper 1000 m of the pelagic environment.

Table 1 Representative examples of bioluminescent marine organisms

Organism	*Typical genera*	*Type of luminescence*
Bacteria	*Photobacterium*	Glow
Dinoflagellates	*Ceratium, Lingulodinium (Gonyaulax), Noctiluca, Pyrocystis*	Flashes
Radiolarians	*Collozoum, Collosphaera, Thalassicolla*	Flashes or glows
Cnidarians		
Medusae	*Aequorea, Solmissus, Atolla, Periphylla, Pelagia, Halicreas*	Flashes, scintillating secretions, multiple waves of light
Siphonophores	*Hippopodius, Vogtia, Agalma, Praya, Nanomia, Halistemma*	Flashes and glows, multiple waves of light
Sea pens	*Renilla, Stylatula, Pennatula*	Flashes, multiple waves of light
Polyps	*Obelia, Campanularia*	Flashes, waves of light
Ctenophores	*Beroe, Cestum, Euplokamis, Kiyohimea*	Flashes, waves of light, luminous secretions
Molluscs		
Nudibranchs	*Phyllirrhoe*	Flashes
Pulmonates	*Planaxis*	Flashes, glows
Bivalves	*Pholas*	Secretion
Squid	*Sepiola*[a], *Heteroteuthis, Abralia, Cranchia*, *Chiroteuthis*	Flashes, glow, secretions
Octopods	*Japetella, Stauroteuthis*	Glows
Polychaete worms	*Tomopteris, Chaetopterus, Polynoe, Polycirrus, Odontosyllis*	Glows, flashes, waves of light, secretions
Pycnogonids (sea spiders)	*Collossendeis*	Glows
Crustaceans		
Copepods	*Pleuromamma, Metridia, Euaugaptilus, Lucicutia, Oncaea*	Secretions, flashes
Ostracods	*Vargula, Conchoecia*	Flashes, secretions
Amphipods	*Scina, Cyphocaris*	Flashes, secretions
Mysids	*Gnathophausia*	Secretions
Euphausiids	*Euphausia*	Glows, flashes
Decapod shrimp	*Acanthephyra, Heterocarpus, Thalassocaris, Sergestes, Hymenopenaeus*	Secretions, glows
Echinoderms		
Brittle stars	*Ophiacantha, Amphiura, Ophiomusium*	Flashes, waves of light, glows
Starfish	*Plutonaster, Benthopecten, Brisinga*	Glows
Crinoids (sea lilies)	*Thalassometra, Thaumatocrinus*	Glows
Holothurians (sea cucumbers)	*Paroriza, Laetmogone, Kolga, Enypniastes, Pannychia*	Glows, waves of light
Tunicates		
Larvaceans	*Oikopleura, Megalocercus*	Flashes
Thaliaceans (sea squirts)	*Pyrosoma*[a], *Clavelina*	Glows, slow flashes
Fishes		
Sharks	*Isistius, Euprotomicrus*	Glows
Eels	*Saccopharynx, Lumicongera &*	Glows?
Other fishes: Bathylagids	*Opisthoproctus*[a], *Winteria*[a]	Glows
Gonostomatids	*Cyclothone, Gonostoma, Vinciguerria*	Glows
Sternoptychids (hatchet fishes)	*Argyropelecus, Sternoptyx*	Glows
Stomiiforms	*Astronesthes, Melanostomias, Pachystomias*	Flashes, glows
(dragon fish, loose-jaws)	*Malacosteus, Chauliodus, Stomias, Idiacanthus*	
Myctophids (lantern fishes)	*Electrona, Myctophum, Diaphus, Lampanyctus*	Flashes, glows
Ceratioids (angler fishes)	*Ceratias*[a], *Oneirodes*[a], *Himantolophus*[a], *Linophryne*[a]	Glows, flashes
Morids (deep sea cods)	*Physiculus*[a]	Glows
Macrourids (rattails)	*Coelorhynchus*[a], *Macrourus*[a], *Nezumia*[a]	Glows?
Anomalopids (flashlight fishes)	*Anomalops*[a], *Photoblepharon*[a]	Flashes, glows
Monocentrids (pinecone fishes)	*Cleidopus*[a], *Monocentris*[a]	Glows, flashes
Apogonids	*Apogon*[a], *Siphamia*[a], *Howella*[a]	Glows?
Leiognathids (pony fishes)	*Gazza*[a], *Leiognathus*[a]	Glows, flashes

[a]Symbiotic luminous bacteria.

Biochemistry

Bioluminescence involves the oxidation of a substrate (luciferin) in the presence of an enzyme (luciferase). The distinctive feature of the reaction is that most of the energy generated is emitted as light rather than as heat. There are many different, and unrelated, kinds of luciferin, and biochemical and taxonomic criteria indicate that bioluminescence has been independently evolved many times. Marine animals are unusual, however, in that many species in at least seven phyla use the same luciferin. This compound is known as coelenterazine because it was first identified in jellyfish (coelenterates) and its molecular structure is derived from a ring of three amino acids (two tyrosines, and a phenylalanine). Nevertheless, many other marine organisms use different luciferins. In some animals (e.g., jellyfish) the luciferin/luciferase system can be extracted in the form of a stable 'photoprotein' that will emit light when treated with calcium.

Microorganisms

Bioluminescent organisms are found in all of the oceans of the world and at all depths. The prevalence of the phenomenon has long been known to seafarers, as the light seen at night in the wake or bow wave of their vessels. Three kinds of single-celled marine organisms include species that produce light, namely bacteria, dinoflagellates, and radiolarians, all with different luciferins. Individual luminous bacteria do not luminesce unless there are a lot of them together – colonies therefore become bright. This is because luciferase production is switched on only by the accumulation in the environment of a critical concentration of a chemical released by the bacteria (an autoinducer). Luminous bacteria are to be found free in the ocean but are more commonly encountered as glowing colonies on either marine snow or fecal pellets, or, as luminous symbionts, in the light organs of some fish and squid (see below).

There are many species of luminous dinoflagellates and they are the usual cause of sea surface luminescence, visible in the bow wave or wake of a boat or the turbulence caused by a swimmer, whether man, fish, or dolphin. They can accumulate in dense 'blooms,' some dense enough to be recognized as red tides, and individual dinoflagellates flash when subject to sufficient shear force (e.g., in turbulence). Because they live close to the surface, their light would be invisible by day. In fact most species have a circadian rhythm that conserves the luminescence by turning it off during the day. These organisms, and probably the radiolarians too, defend themselves against planktonic predators by their flashing, which has the added 'burglar alarm' benefit of alerting larger predators to the presence of the original grazer.

Plankton

Other common planktonic luminous organisms are copepod and ostracod crustaceans, cnidarians (jellyfish and siphonophores) and comb jellies. Copepods are in effect the insects of the sea and are the commonest planktonic animals. Many species are luminous. Most of them do not flash but have glands on their limbs or bodies from which they squirt gobbets of luminous secretion into the water as a defensive distraction. Ostracods, though less abundant, also produce luminous droplets from groups of gland cells. Usually this is a defense, but the males of some shallow-water species of *Vargula* swim up off the bottom to signal to the females. They encode a luminous message in the combination of the frequency of their light puffs, their swimming trajectory, and the timing of their displays. The displays are equivalent to complex smoke signals, or skywriting, using light. Occasionally both copepods and ostracods may swarm in such numbers that their secretions light up the wave crests or the entire ocean surface. The luciferin of *Vargula* (previously named *Cypridina*) was the first to be identified and is a tripeptide similar to coelenterazine, but made up of three different amino acids. Certain other ostracods use coelenterazine instead.

Copepods and ostracods, like bacteria, dinoflagellates, and most other marine organisms, produce blue or blue-green luminescence (**Table 1**). These wavelengths penetrate oceanic water best, so they are visible at the greatest range. Many cnidarians and comb jellies also produce blue light, but in a few the luminescence is a vivid green. These animals have incorporated a green fluorescent protein into the luminous cells, or photocytes. The energy from the luciferin–luciferase reaction is transferred to the fluor and is therefore made visible as green light. Some species of jellyfish, siphonophores, and comb jellies can not only flash but also pour out a luminous secretion. The secretion may include scintillating particles, which flash independently in the water. In other species of cnidarians the light-emitting cells (photocytes) are situated all over the surface of the body and a stimulus can set off one or more waves of light that may circle over the surface for several seconds. None of these animals has image-forming eyes, so their bioluminescent displays must be aimed at other animals, probably as a

defense against predators or simply to protect their very fragile tissues from accidental damage by a blundering contact.

There are many luminous worms, though most of them spend their time on the sea floor. Syllid worms (fireworms) come to the surface in shallow waters for a luminous mating display, whose timing is linked to the phase of the moon. They have a greenish light, while the pelagic worm *Tomopteris* is very unusual in producing yellow light (**Table 1**). Scale worms when attacked can shed their scales, which then flash independently. A similar tactic is used by luminous brittlestars; when grasped they shed their arm tips, leaving them to flash and writhe in the predator's grip, like the lizard that sheds its tail. Many other echinoderms (relatives of brittlestars) are bioluminescent, including sea cucumbers, sea stars and sea lilies. Most of these live on the deep-sea floor and, like the jellies, lack image-forming eyes. Other bottom-living luminous animals include species of sea-spiders, acorn worms, snails and clams, as well as cnidarians such as sea pens and gorgonians.

In the plankton and the nekton (those animals that can swim reasonably well) are many other luminous animals, including arrow worms and *Pyrosoma*. The latter forms a cylindrical colony of sea-squirt-like individuals, each of which has two patches of luminous cells. The cells contain bacteria-like organelles, which are uniquely intracellular. The colonies will respond to illumination by producing a slow glow of several seconds duration, and are often seen at night from the decks of ships. Only among the crustaceans, fish, and squid are the photocytes frequently associated with accessory optical structures, including reflectors, lenses, collimators, light guides, and filters (**Figures 1** and **2**). The result is a complex light organ or photophore.

Photophores have not been developed in luminous amphipods nor in the mysid *Gnathophausia*, but those in euphausiid and many decapod shrimps are

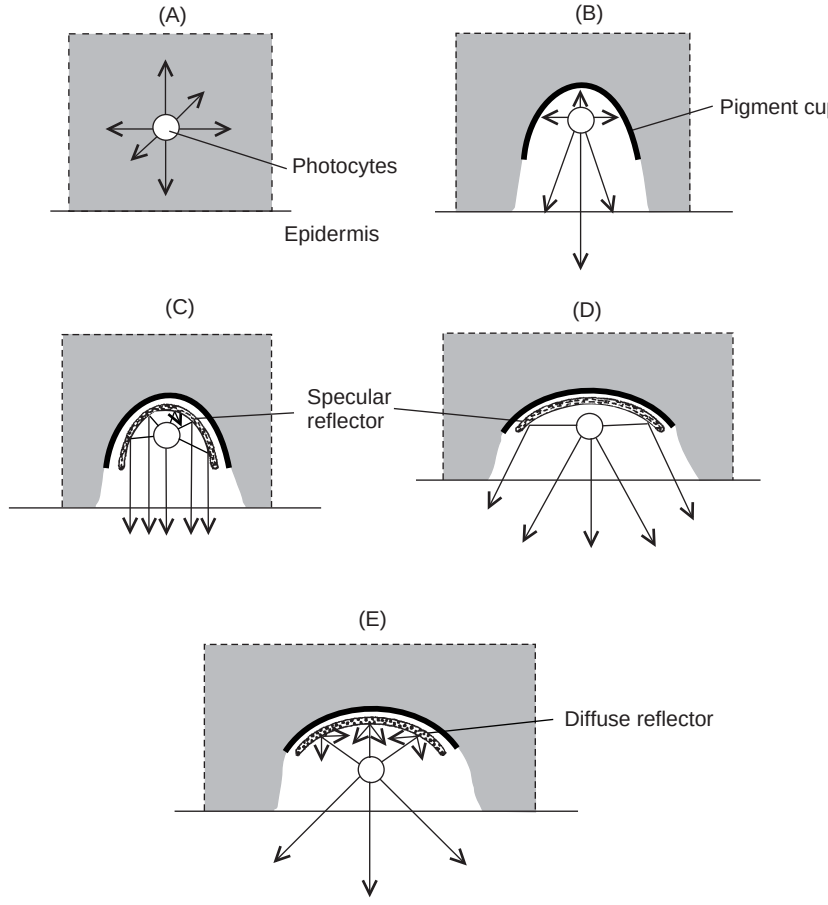

Figure 1 The effects of pigment and reflectors on light emission from photophores: (A) point source emission of a group of photocytes or bacteria is isotropic; (B) pigment cup restricts the solid angle of emission, but absorbs some of the light; (C)–(E) reflectors of different geometries provide a more efficient emission, whether they are specular (C, D) or diffuse (E). Arrows indicate possible ray paths. (From Herring (1985) with permission.)

very elaborate structures. In these animals the photophores are located on the underside of the body and eyestalks and provide a ventral illumination. Predators from below would normally see the shrimp as a silhouette against the dim downwelling daylight but, by emitting light of the same color and intensity as the daylight, the shrimp matches the background, a tactic known as counterillumination camouflage. If the shrimp were to change its orientation in the water, tilting up or down, its luminous output would no longer match the background. All euphausiids and some decapods get over this problem by rotating the photophores in the plane of pitch so that they remain directed vertically downwards and maintain the camouflage.

Many deep-sea decapod shrimps (and the mysid *Gnathophausia*) will squirt an intense cloud of luminescence into the water if they are startled and then disappear into the surrounding darkness. Some of the species living in the upper 1000 m have both squirted luminescence and ventral photophores. The color of light from the two sources is slightly different; the photophores necessarily match the spectral content of daylight, but the squirts are rather bluer and of broader bandwidth.

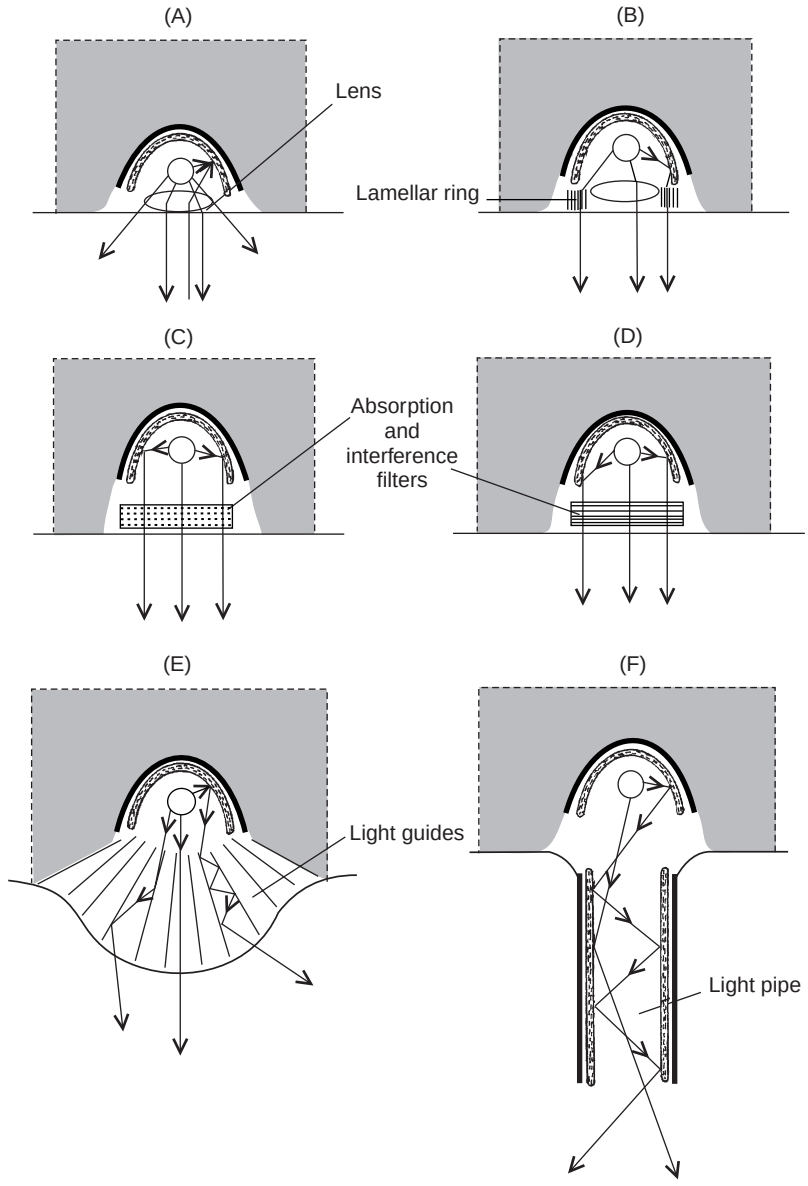

Figure 2 Effects of accessory optical structures in photophores: (A) lens alone; (B) lens and lamellar ring (e.g., euphausiid shrimp); (C) pigment filter; (D) interference filter; (E) light guide diffuser (e.g., some squid); (F) light pipe (e.g., some anglerfishes). (From Herring (1985) with permission.)

Squid and Octopods

At least one squid (*Heteroteuthis*) also produces a squirt of luminescence. It is not luminous ink but material from a special luminous gland. This squid can also produce a steady glow from within the gland. The complexity of photophores in different squid is quite remarkable; a single individual may have several different types on different parts of the body. Many of them are for counterillumination camouflage, being typically located beneath the eye, and sometimes under the liver, two opaque structures that need to be camouflaged. The photophores are able to match the intensity of downwelling light over a considerable range. Other squid have photophores in or on the arms and/or tentacles, sometimes with specialized photophores right at the tips. As they become mature, the females of some squid develop large photophores at the tips of certain arms, presumably as a signal for the males. Females of some pelagic octopods develop an analogous sexual photophore, in the form of a luminous ring round the mouth, as they become ripe, and lose it again when they have spawned. Deep-water octopods may have lights on the arms instead of suckers. Some shallow squids culture luminous bacteria (*Photobacterium fischeri*) in large paired ventral photophores. Bacteria from the female are shed into the water around the egg masses and reinfect the newly hatched larvae, which have special structures for acquiring the symbionts from the water.

Fishes

The variety of photophores in squid is exceeded only by those in fishes. Several groups of fish use luminous bacterial symbionts as their source of light. Shallow-water species (e.g., ponyfish and pinecone fish) utilize bacteria (*Photobacterium leiognathi* and *P. fischeri*, respectively) that grow best at warm temperatures. Deep-sea fishes (e.g., rattails and spookfish) have a different symbiont (*P. phosphoreum*) that does better in colder water. All these fishes have photophores that open into the gut; their symbionts are extracellular and can be grown in laboratory cultures. It is assumed that the symbionts are somehow selected from the normal gut flora. Two particular families of fishes, the shallow-water flashlight fishes and deep-sea anglerfishes, have photophores that do not open to the gut, though, like all the bacterial light organs of squid and other fishes, they do open to the sea water via pores. The bacteria of these two groups of fishes are also extracellular but cannot yet be cultured. They do not belong to any known species, though they are closely related to the other symbionts. It is not known how they are reacquired in each generation. Bacteria glow continually, so these photophores have to be occluded to turn the light off (**Figure 3**).

Most fish do not use bacteria but use their own luciferin/luciferase system. There are a few exceptions, which cannot make the luciferin but have to have it in their diet, like a vitamin. The best-known is the midshipman fish *Porichthys*, which has numerous, complex, ventral photophores. It uses *Vargula* luciferin, and if deprived of dietary Vargula it does not luminesce. The luminescence returns if it is fed either whole *Vargula* or the pure luciferin. Populations of *Porichthys* that have no *Vargula* in their region are nonluminescent, even though they have photophores. The mysid *Gnathophausia* seems to have a similar dietary requirement, in this case for the luciferin coelenterazine.

Other fishes probably synthesize their own luciferin. Their photophores can be extremely elaborate and a single fish may have thousands of tiny

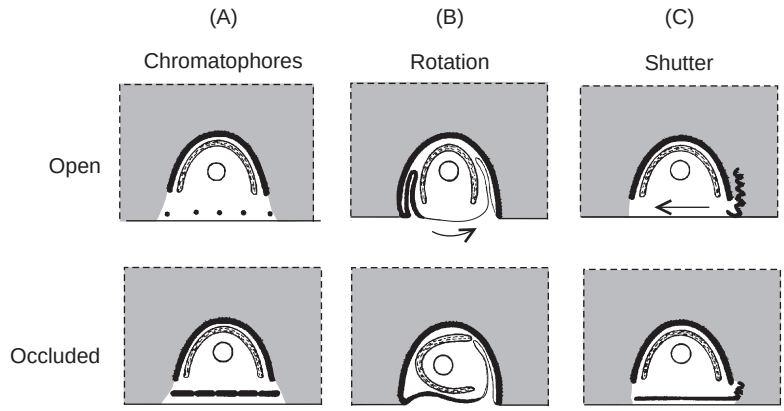

Figure 3 Three means whereby a photophore can be occluded: (A) chromatophores; (B) rotation; (C) shutter. (From Herring (1985) with permission.)

simple photophores, as well as a much smaller number of large complex ones. Most of those fishes in the upper 1500 m have counterillumination camouflage photophores along the ventral surface of the body; the shallower species (e.g., hatchetfishes) cover the whole ventral surface with large photophores; the deeper ones (dragon fishes) have fewer, smaller, ventral photophores. In the large family of lanternfishes shallow-living and deep-living species have equivalent differences in the size and number of their ventral photophores. Many stomiiform fishes have a large postorbital photophore, behind or under each eye, very similar in position to the bacterial photophore of flashlight fishes. Both kinds of fish probably use them to illuminate prey in the surrounding water, and both can hide the white reflective surface of the photophore by rotating it or drawing a fold of black skin over its aperture. Stomiiform males usually have much larger postorbital photophores than females. Male and female lanternfishes have special sexually dimorphic photophores on the tail or head in addition to the ventral camouflage ones. Male anglerfishes have no photophores; the female's bacterial ones can be very complex, with light pipes transmitting the light from the bacterial core to quite distant apertures. The lights are presumed to act as lures, perhaps both for prey and for males. Many stomiiform fishes also have long and complex luminous barbels, whose function is also assumed to be that of a lure, perhaps mimicking particular kinds of luminous plankton.

Almost all of these animals produce blue luminescence, but there are a very few remarkable deep-sea fish that produce both blue and red light (*Malacosteus*, *Pachystomias*, *Aristostomias*). They have the usual complement of body photophores, including a blue-emitting postorbital photophore, but they also have a suborbital red-emitting one. The red-emitting photophores contain large amounts of red fluorescent material and it is presumed that this acts as a fluor, rather like the green fluorescent protein of some jellyfish. The red light will be invisible to most other animals in the deep sea, which have only blue-sensitive visual pigment, but these fishes also have a red-sensitive visual pigment. They have in effect a private wavelength, either for communication or, like a sniperscope, for illuminating prey.

Measurements of Bioluminescence

Some of these organisms are the main contributors to the 'stimulable bioluminescent potential' of the water, i.e., the maximum amount of light that can be produced by turbulence in the water. Stimulated bioluminescence is most obvious in the wakes and bow waves of ships, but measurements of its vertical and horizontal distribution can give a quick indication of the planktonic biomass as well as an indication of the signal a fish shoal or a submarine might produce as it travels through the waters. Oceanographic measurements of bioluminescence were first made in the 1950s when sensitive light meters, lowered into the depths to measure the penetration of sunlight, recorded flashes of luminescence. Later, when it became apparent that it was actually the movement of the light meter that was stimulating the bioluminescence, detector systems known as bathyphotometers were developed. These instruments have taken a variety of forms, with the most common design elements being a light detector viewing a light-tight chamber through which water is drawn either by movement of the bathyphotometer or by a pump (**Figure 4**). Light is stimulated as the bioluminescent organisms in the water experience turbulence, which is generated as the water passes through one or more constrictions or is stirred with a pump impeller. Units of measurements depend on the method of calibration and the residence time of the luminescent organism in the chamber. When residence times are short compared to the duration of the flash, the amount of light measured is a function of the detection chamber volume, so the light measured by the light detector (in photons s^{-1} or watts) is divided by the chamber volume and reported as photons s^{-1} per unit volume or watts per unit volume. On the other hand, when the residence time is long enough for an entire flash to be measured, the light measured is a function of the volumetric flow rate (volume s^{-1}) through the chamber rather than the chamber volume and the light measured must be divided by flow and reported as photons per unit volume.

Bathyphotometers come in a variety of configurations, including profiling systems, towed systems, and moored systems. The 'stimulable bioluminescence potential' measured with a given bathyphotometer will depend on the organisms it samples. Low-flow-rate systems with small inlets will preferentially sample slow swimmers such as dinoflagellates, while higher flow rates and larger inlets will also sample zooplankton such as copepods and ostracods. Bathyphotometer measurements of stimulated bioluminescence have been made in most of the major oceans of the world. These measurements have generally been made in the upper 100 m of the water column at night. There is considerable seasonal variability in the amount of light measured, with average values ranging from approximately 10^9 to 10^{11} photons l^{-1}. There is also a pronounced diel rhythm of stimulable bioluminescence, with the

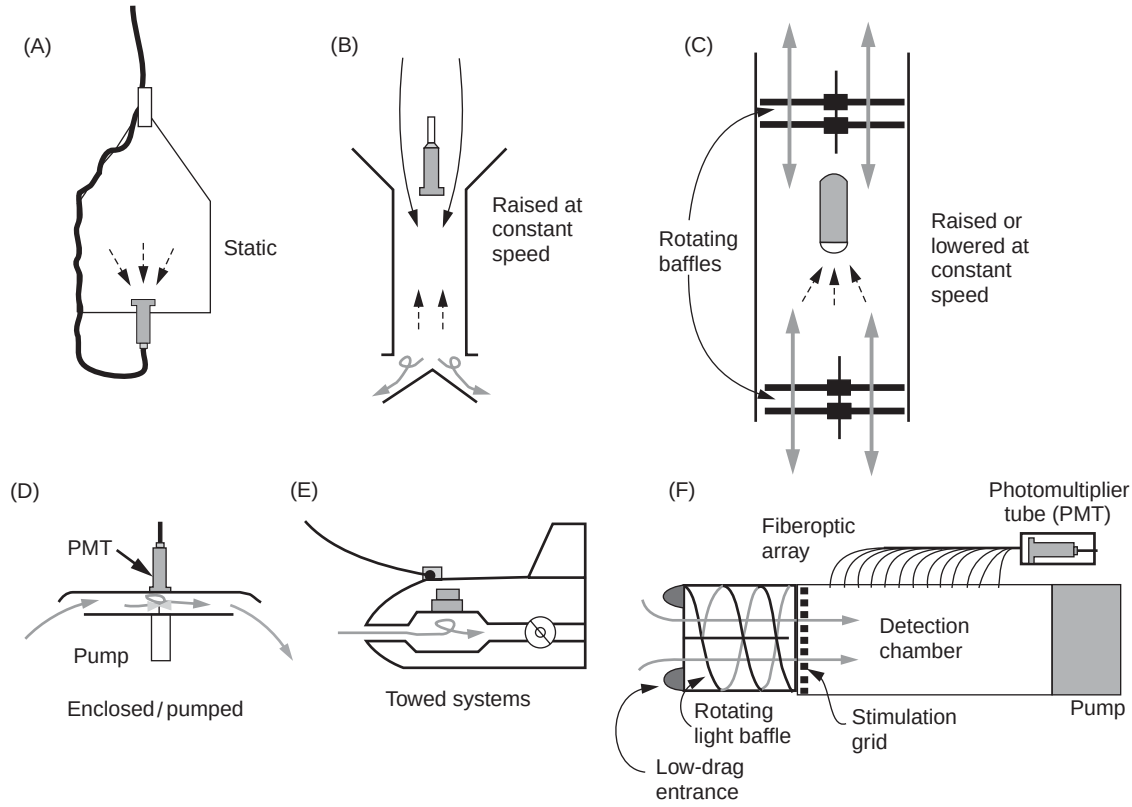

Figure 4 Various bioluminescence bathyphotometer designs. (A) Open field detectors designed to measure downwelling irradiance also measure bioluminescence stimulated by motion of the detector system. (B) An early sounding bathyphotometer that was raised at constant speed. Water was entrained by the upper funnel and bioluminescence was primarily triggered by turbulent flow at the exit baffle. (C) A refinement of the device in (B), equipped with entry and exit baffles that also provide excitation as water is entrained by raising or lowering. (D) Generic sketch of a low-volume enclosed and pumped bathyphotometer in which excitation is provided by pump impeller. Detector chamber volume about is 50 ml with indeterminate flow path and maximum flow rate of 1 liter s^{-1}. This device could be used in either a moored or profiling configuration. (E) Generic towed system with excitation provided by entry baffle and flow provided either by forward motion or pump downstream from detector chamber. (F) More recent design of a high-flow-rate (up to 44 ls^{-1}), large inlet bathyphotometer (12 cm ID) with a large volume detection chamber ($>$ 11 litres) and hydrodynamically defined excitation using a grid at the inlet. (Adapted with permission from Case JF, Widder EA, Bernstein SA *et al.* (1993) Assessment of marine bioluminescence. *Naval Research Reviews* 45: 31–41.)

photon flux measured in surface waters being greatly reduced or absent during the day. This is a consequence of the circadian rhythm of stimulable bioluminescence found in many dinoflagellates, as well as of diel vertical migration, which results in many luminescent species of plankton and nekton moving into surface waters only at night.

In most cases where the organisms responsible for the stimulable bioluminescence potential have been sampled, they have been found to be primarily dinoflagellates, copepods, and ostracods. Euphausiids too may be significant sources of bioluminescence in the water column but will only be sampled by very high-flow-rate systems. Gelatinous zooplankton, such as siphonophores and ctenophores, represent another potentially significant source of bioluminescence but are often overlooked because they are destroyed by the nets and pumps that oceanographers generally depend on for sampling the water column. All these organisms represent significant secondary producers and measurement of their bioluminescence provides a rapid means of assessing their distribution patterns, in the same way that fluorescence measurements have provided valuable information on the fine-scale distribution patterns of primary producers. As with fluorescence measurements, the primary method used to determine which organisms are responsible for the light emissions has been to collect samples from regions of interest with nets or pumps.

More recently there has also been some progress in developing computer image recognition programs that can identify luminescent organisms by their unique bioluminescent 'signatures.' Potential identifying properties of the light emissions include intensity, kinetics, spatial pattern, and spectral

distribution. Flash intensities are highly variable; while a single bacterium may emit only 10^4 photons s^{-1} a single dinoflagellate can emit more than 10^{11} photons s^{-1} at the peak of a flash (approximately 0.1 mW). Some of the brightest sources of luminescence are found among the jellies; some comb jellies, for example, have been found to emit more than 10^{12} photons s^{-1}. Flash durations are also highly variable and can be tens of milliseconds (e.g., the flash from the 'stern chaser' light organs on the tail of a lantern fish) to many seconds (e.g., in many jellyfish). The vast majority of planktonic organisms such as dinoflagellates, copepods, and ostracods, have flash durations of between 0.1 and 1 s. The number of flashes that a single organism can produce depends on the amount of luminescent material that is stored and the manner and rate of excitation. While some organisms produce only a flash or two in response to prolonged stimulation, others may respond with tens to hundreds of flashes until their luminescent chemical stores are exhausted and/or their excitation pathways are fatigued. Full recovery of luminescent capacity can occur in a matter of hours to days depending on the availability of substrates for resynthesis of the luminescent chemicals. Spatial patterns of bioluminescence vary from essentially point sources for the smaller plankton to highly identifiable outlines and/or species-specific photophore patterns for many of the nekton. As indicated earlier, most marine bioluminescence is blue; however, there are often subtle differences in spectral distributions that could aid in identifications.

Bioluminescent Phenomena

Sometimes the bioluminescent plankton are responsible for dramatic surface phenomena. Luminescent wave crests have already been noted, but occasionally the sea may appear to be glowing uniformly. This 'milky sea' phenomenon has been described as like 'sailing through a field of snow' and is particularly common in the north-west Indian Ocean at the time of the south-west monsoon. It is probably the result of luminous bacteria growing on an oily surface scum. Other luminous phenomena include erupting balls of light exploding at the surface (probably fish schools coming up through dense luminous plankton and scattering at the surface) and, most dramatic of all, 'phosphorescent wheels.' These appear first as parallel bands of light racing across the sea surface and then change to become vast rotating wheels whose spokes may appear to extend to the horizon and which travel past the vessel at 50–100 km h^{-1}! They occur only in less than 200 m of water and are most frequent in the Arabian Gulf. Explanations invoke stimulation of the surface bioluminescent plankton either by the ships engines or by seismic activity in the region. Neither alternative is wholly convincing.

Applications of Bioluminescence

Bioluminescence plays a major role in the ecology of the ocean at all depths. Its quantification and distribution can provide oceanographers with a rapid biological marker for the proximity of physical features such as fronts and eddies, as well as an indication of the presence of particular species in the zooplankton and nekton communities. Aerial surveys with intensified videocameras have been used to find near-surface shoals of commercial fishes in several parts of the world, and in time of war (hot or cold) can monitor the night-time movements of surface vessels, torpedoes and submarines. More profitably, the use of bioluminescence has extended well beyond the oceans and into less obvious fields such as biomedical assays, pollution monitoring, and neuromuscular and developmental physiology. Bioluminescent systems extracted from marine organisms are now used widely as intracellular markers whose light emission signals a particular biochemical event or the presence of potentially damaging radicals such as active oxygen. Photoproteins extracted from jellyfish have provided much of the information on the role of intracellular calcium. The green fluorescent protein, also from jellyfish, is widely used as an intracellular marker. These systems have been cloned and manipulated genetically to extend their biomedical usefulness. The genes controlling the bioluminescence of marine bacteria have also been identified and cloned. They and the jellyfish genes can be inserted into other organisms as 'reporter' genes. These 'report' on the activation of other genes, to which they are attached, by causing light emission that can easily be monitored. Changes in the light emission of cultures of bioluminescent marine bacteria or dinoflagellates are also used to monitor a wide range of toxic pollutants. The bioluminescence that plays such an important part in the ecology of the oceans now has a plethora of other uses in the terrestrial world.

See also

Cephalopods. Copepods. Crustacean Fisheries. Deep-sea Fishes. Fish Migration, Vertical. Fish Larvae. Gelatinous Zooplankton. Krill. Mesopelagic Fishes. Plankton Viruses. Protozoa, Planktonic Foraminifera. Protozoa, Radiolarians.

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BIO-OPTICAL MODELS

A. Morel, Université Pierre et Marie Curie, Villefranche-sur-mer, France

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Introduction

The expression 'bio-optical state of ocean waters' was coined, in 1978, to acknowledge the fact that in many oceanic environments, the optical properties of water bodies are essentially subordinated to the biological activity, and ultimately to phytoplankton and their derivatives. More recently the adjective bio-optical has been associated with nouns like model or algorithms. At least two meanings can be distinguished under the term 'bio-optical model.'

A bio-optical model can designate a tool used to analyze, and then to predict, the optical properties of biological materials, such as phytoplanktonic or heterotrophic unicellular organisms, the most abundant living organisms in the ocean. Such models are based on various fundamental theories of optics which apply to a single particle, and make use of a set of rigorous equations. The optical properties which can be 'modeled' belong to the category of the inherent optical properties (IOP, *see* **Radiative Transfer in the Ocean**). Defined at the level of a single cell, the extension of IOPs to a collection of cells (a population) or to an assemblage of populations is straightforward from conceptual and numerical viewpoints. The computation of IOPs are carried out by using some physical characteristics of the organisms, or of the population (such as cell size, size distribution, chemical composition which governs the complex index of refraction).

Bio-optical models can also refer to various ways of describing and forecasting the 'bio-optical state' of the ocean, namely the optical properties of a water body as a function of the biological activity within this water. Both the IOPs and the apparent optical properties (AOPs) of the water are aimed at in such approaches. In contrast to the first kind of theoretical models, these models are essentially empirical, descriptive, and actually derived from field measurements. They initially rest on observations of some regular variations in the oceanic optical properties along with its algal content in 'Case 1 waters' (see **Table 1**). The chlorophyll concentration, [Chl], is commonly used as an index to quantify the algal content, and more generally the bio-optical state of ocean water. Once identified, and if recognized as statistically significant, such empirical relationships (between optical properties and [Chl] can be inverted, and thereafter used as predictive tools or model.

It is worth remarking that regular trends generally vanish in so-called Case 2 waters (**Table 1**). Indeed, in these waters the optical properties are no longer influenced just by phytoplankton and related particles, as they are in Case 1 waters. They are also, and independently, determined by other substances of terrestrial origin, notably by sediments and colored dissolved (organic) matter, carried from land into coastal zones and not correlated to [Chl]. Therefore, bio-geo-optical models, that might be developed and locally useful in such areas, are not of general applicability.

The two kinds of models are not disconnected. To the extent that the IOPs at the level of particles are additive, the first models, in principle, may be utilized to reconstruct the IOPs of a water body containing any assemblage of organisms and other (living