Bioluminescence in the Sea

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Abstract

Bioluminescence spans all oceanic dimensions and has evolved many times—from bacteria to fish—to powerfully influence behavioral and ecosystem dynamics. New methods and technology have brought great advances in understanding of the molecular basis of bioluminescence, its physiological control, and its significance in marine communities. Novel tools derived from understanding the chemistry of natural light-producing molecules have led to countless valuable applications, culminating recently in a related Nobel Prize. Marine organisms utilize bioluminescence for vital functions ranging from defense to reproduction. To understand these interactions and the distributions of luminous organisms, new instruments and platforms allow observations on individual to oceanographic scales. This review explores recent advances, including the chemical and molecular, phylogenetic and functional, community and oceanographic aspects of bioluminescence.

OVERVIEW

Bioluminescence: light emission from a living organism

Walking along the beach at night or sailing on a darkened sea, you will often see sparkling lights in the water. This is bioluminescence—the emission of visible light by an organism as a result of a natural chemical reaction. A remarkable diversity of marine animals and microbes are able to produce their own light, and in most of the volume of the ocean, bioluminescence is the primary source of light. Luminescence is nearly absent in freshwater, with the exception of some insect larvae, a freshwater limpet, and unsubstantiated reports from deep in Lake Baikal. On land, fireflies are the most conspicuous examples, but other luminous taxa include other beetles, insects like flies and springtails, fungi, centipedes and millipedes, a snail, and earthworms. This discrepancy between marine and terrestrial luminescence is not fully understood, but several properties of the ocean are especially favorable for the evolution of luminescence: (*a*) comparatively stable environmental conditions prevail, with a long uninterrupted evolutionary history; (*b*) the ocean is optically clear in comparison with rivers and lakes; (*c*) large portions of the habitat receive no more than dim light, or exist in continuous darkness; and (*d*) interactions occur between a huge diversity of taxa, including predator, parasite, and prey.

Given its widespread distribution, bioluminescence is clearly a predominant form of communication in the sea, with important effects on the immense daily vertical migration, predator-prey interactions, and the flow of material through the food web.

This review presents advancements in understanding marine bioluminescence within the last 10 to 15 years, focusing on information that is new and not included in the prior reviews on general bioluminescence (Morin 1983, Herring et al. 1990, Herring & Widder 2001), chemistry (Hastings 1983, 1995; Wilson & Hastings 1998; Shimomura 2006), vision (Warrant & Locket 2004), and reproduction (Herring 2007). As a result of this focus, we do not mention some of the seminal papers well served by those reviews, and we strongly recommend them for their coverage of groundbreaking research. Although the rate of publication on biotechnological applications of luminescence outpaces the literature about light emission in the natural environment, we do not address applied topics, instead focusing on ecology, chemistry, the natural history of bioluminescence, and its distribution in the ocean.

Bioluminescent Organisms

Bioluminescence has been found across a broad range of the major groups of organisms from bacteria and protists to squid and fishes, with numerous phyla in between (**Figure 1**). In most of these cases, luminescence is produced by the organisms themselves and not by bacterial symbionts. Some of the few prominent lineages which are not known to be bioluminescent are flowering plants, and terrestrial vertebrates like birds, amphibians, and mammals. Luminescence is generally higher in deep-living and planktonic organisms than in benthic or shallow species.

Supplemental Material

A list of known luminous genera was cataloged by Herring (1987), but there have been additional discoveries of luminous taxa since that time (**Supplemental Table 1**; follow the **Supplemental Material** link from the Annual Reviews home page at **http://www.annualreviews.org**). In some cases, it is hard to establish that a species is nonluminous. Among filter-feeding organisms, reports of luminescence are hard to confirm, because it is difficult, if not impossible, to separate the organism from associated and ingested protists and microbes. Sponges, bryozoans, and *Cyclosalpa* species have all been reported as luminous at times, but we, like Herring (1987), consider these to be doubtful. Many of the pharmacologically interesting compounds isolated from sponges have turned out to be bacterial in origin (Schmidt et al. 2000, Taylor et al. 2007).

The distribution of bioluminescence across the major taxonomic groups does not appear to follow any obvious phylogenetic or oceanographic constraint. Each lineage shown in blue or green

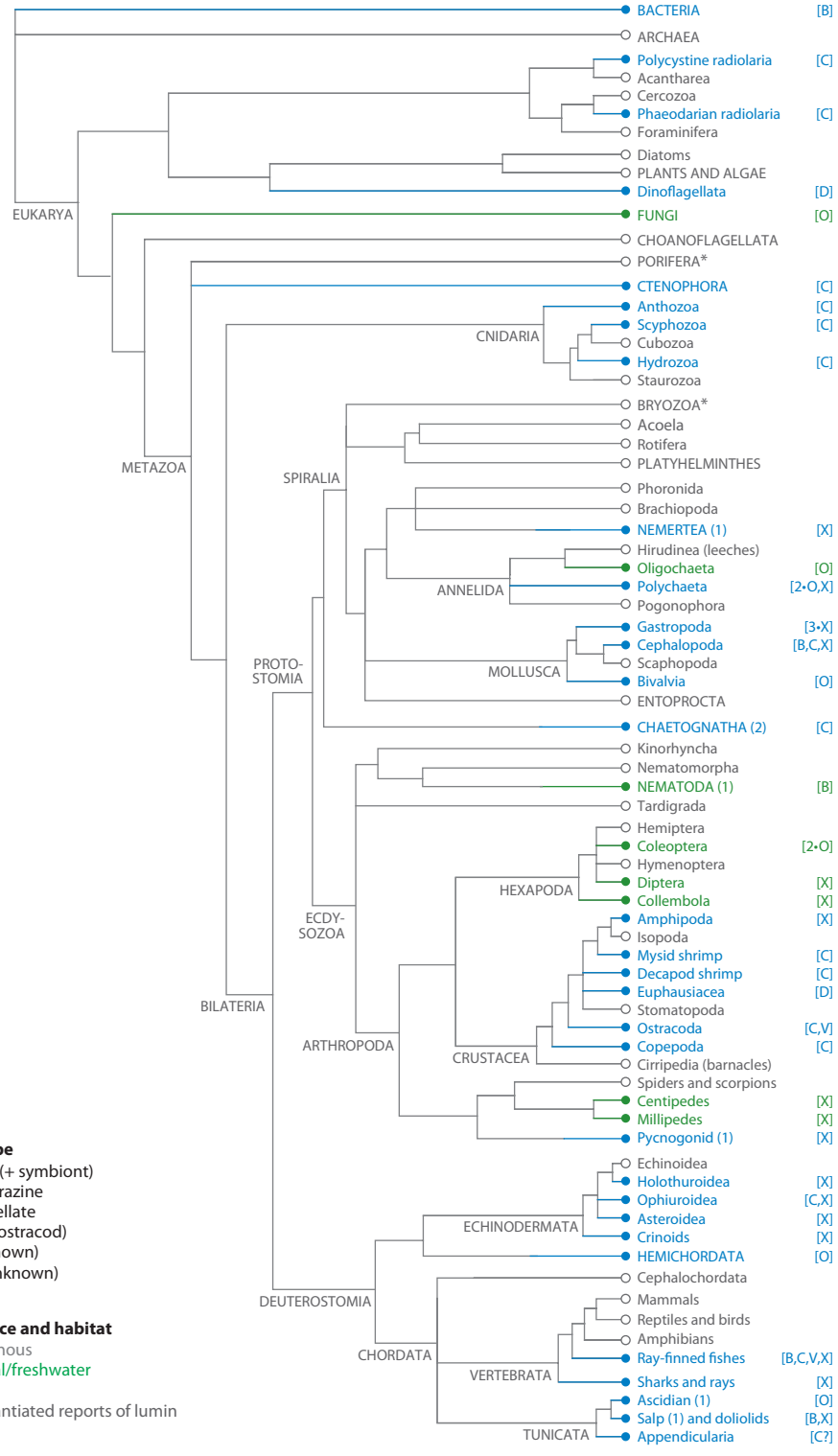


Figure 1

A bioluminescence tree of life. Marine (blue) and terrestrial/freshwater (green) bioluminescence is spread throughout the tree relative to the nonluminous phyla (gray). Many of the luminous taxa use two or more luciferins, denoted within brackets to the right of the taxon names. Tree structure was compiled from taxon-specific sources, with the backbone based on Dunn et al. (2008). Names in capital letters represent "phylum-level" groups or broader.

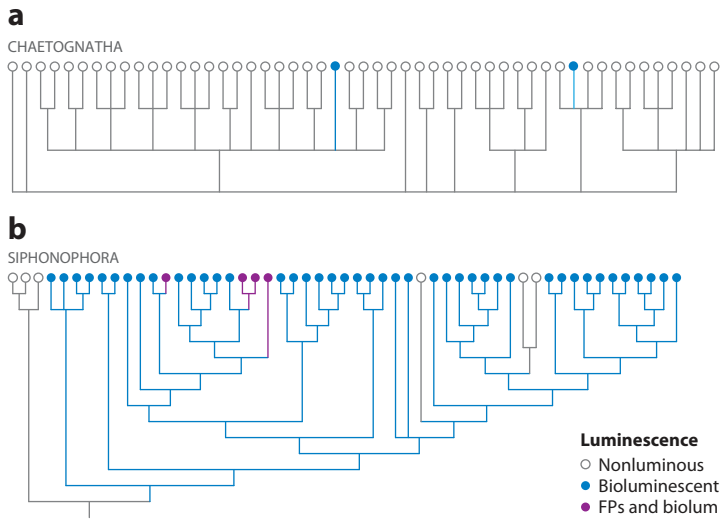


Figure 2

Taxa where bioluminescence is the exception . . . or the rule. (*a*) Nearly all chaetognaths (arrow worms) are nonluminous, but luminescence has been found in two distantly related genera. (*b*) Most siphonophores are luminous except for some cystonectae, benthic rhodaliid species, and two physonect genera. Similar unpredictable patterns are found within many phyla. Chaetognath tree based on current taxonomic classification of the phylum; siphonophore tree based on molecular phylogeny by Dunn et al. (2005). Purple circles represent organisms containing both fluorescent proteins (FP) and bioluminescence.

in **Figure 1** has at least one bioluminescent species. Luminescence can be found in protists that are siliceous (two types of "radiolarians") but not in calcareous foraminifera or coccolithophorids. In contrast, it can be absent in siliceous phytoplankton (diatoms) and present in calcareous echinoderms and molluscs. Among cnidarians, holoplanktonic lineages may be almost entirely luminous (narcomedusae, trachymedusae) or totally nonluminous (Cubozoa), and benthic Anthozoan groups can have many luminous taxa (Octocorals) or almost none (anemones and stony corals). One marine group that is overwhelmingly non-bioluminescent are the parasites, with the exception of hyperiid amphipods. Each of the major lineages shown in the tree also contains nested levels of complexity regarding the presence of luminescence. In some of these clades, like chaetognaths (**Figure 2*a***) and ascidians, there may be only one or two luminescent species, and in others like ctenophores and siphonophores (**Figure 2*b***), all except one or two genera may be luminescent.

Evolutionary Origins

Luciferin: the light-emitting compound

Luciferase: the enzyme that triggers the oxidation of the luciferin

Photoprotein: catalyzing protein + luciferin + oxygen bound together

Bioluminescence is typically produced by the oxidation of a light-emitting molecule—generically called the luciferin—in conjunction with a catalyzing enzyme—either a luciferase or photoprotein. Nonsymbiotic luminous organisms possess the gene for at least their luciferase or photoprotein, if not always for the light-emitting luciferin itself. It is difficult to calculate the number of times that bioluminescence has evolved independently, and there is a potential for both over- and underestimation. Part of the difficulty is defining what is meant by an "independent" origin. In the cases of bacterial symbionts, the trait may have evolved only once for the bacteria, but each squid or fish lineage that uses those microbes has to develop specialized light organs to host and maintain the culture. Bioluminescent molluscs alone must have independently arrived at least seven ways to make light, and probably more. To generate a rough estimate, we have summed the number of distinct light-producing chemical mechanisms across the monophyletic lineages (**Figure 1**), to

estimate that bioluminescence has evolved a minimum of 40 times, and likely more than 50 times, among extant organisms.

Because the ability to make light has evolved many times, this suggests that it is important to organisms, and also that its evolution must be relatively easy. While counterintuitive, this may be partly attributed to readily available light-emitting luciferins in both luminous and nonluminous prey (Shimomura 1987). As a result, a predator need only develop a luciferase as a way to trigger light emission (Warner & Case 1980, Haddock et al. 2001). Bioluminescence can more readily evolve if naturally occurring antioxidant molecules are already present in an organism, and if light production is a by-product of those molecules' chemical activity in the scavenging of reactive oxygen species, as has been hypothesized (Rees et al. 1998, Labas et al. 2001). Dietary linkages also suggest that some extant luminescence is almost certainly a post-Cambrian development, since it had to arise in the predators after the synthesis of luciferins evolved in the prey. To be effective, a community of sighted predators is also required. The fossil record and dates of phylogenetic separation estimated by molecular clocks may help to bracket the dates of luciferins utilized within particular groups, but it is presently difficult to narrow the range within 100 million years. Two, even lineages of ostracod crustaceans (Halocyprida and Myodocopida) that use two different luciferins are thought to have diverged more than 400 mya (Yamaguchi & Endo 2003, Tinn & Oakley 2008), suggesting this as a maximum age for at least one of the known luminescence systems. The fish order Stomiiformes is bioluminescent throughout and is thought to have originated in the Albian age of the early Cretaceous, about 100 mya (Forey & Patterson 2006). The stomiids are certainly well established by the occurrence of a convincing hatchetfish from 12 mya, which appears remarkably like its modern counterparts (Carnevale 2008).

Coelenterazine: the most widely used luciferin in the sea

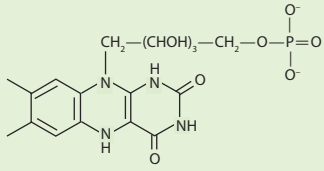
The importance of bioluminescence is also underscored by its widespread distribution throughout the ocean, from the surface to the deep sea, and from the poles to the tropics. In fact, for many marine animals, their primary visual stimulus comes from biologically generated light rather than from sunlight.

CHEMISTRY AND MOLECULAR BIOLOGY

Bioluminescent light is generated as a result of energy released during a chemical reaction (see "Fluorescence and Bioluminescence" sidebar on page 453). In most cases, this reaction is the oxidation of a light-emitting molecule, a luciferin. The reaction rate for the luciferin is controlled by an enzyme, either a luciferase or a photoprotein, which is a luciferase variant in which factors required for light emission (including the luciferin and oxygen) are bound together as one unit. Photoproteins are triggered to produce light upon binding another ion or cofactor, such as Ca^{2+} or Mg^{2+}, which causes a conformational change in the protein. This gives the organism a way to precisely control light emission. Many aspects of bioluminescence chemistry have been collated and reviewed in a book by the 2008 Nobel laureate Osamu Shimomura (2006).

Light-Producing Reactions

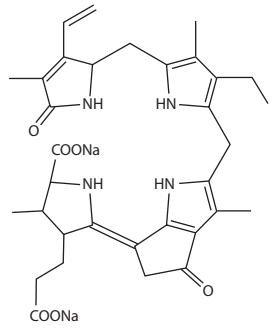
Of the two principal components in a bioluminescent chemical reaction, the luciferins are highly conserved across phyla. Four luciferins are responsible for most light production in the ocean (**Figure 3**), although there are undoubtedly many other light-emitting reactions yet to be discovered. While luciferins are conserved, luciferases and photoproteins are unique and derived from many evolutionary lineages. All Cnidarians, for example, use coelenterazine as the luciferin, but hydrozoans use photoproteins; scyphozoans primarily luciferases; and anthozoans unrelated luciferases, sometimes in conjunction with a luciferin-binding protein. In other words, each luminescent hydrozoan species has one or more genes coding for a photoprotein whose sequence can



Bacterial

Luciferin + Aldehyde + Luciferase

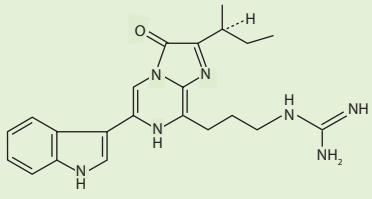
Bacteria
Some fish
Some squid
Pyrosomes?



Dinoflagellate

Luciferin + Luciferase

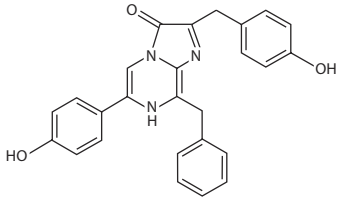
Dinoflagellates
Euphausiid shrimp



Cypridina

Luciferin + Luciferase

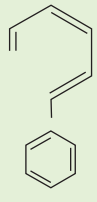
Some ostracods
Midshipman fish
Some other fish



Coelenterazine

Luciferin + Luciferase
Photoprotein

Radiolarians
Ctenophores
Cnidarians
Squid
Some ostracods
Copepods
Decapod shrimp
Mysid shrimp
Some ophiuroids
Chaetognaths
Larvaceans
Some fish



Other or unknown mechanism

Luciferin + Luciferase
Photoprotein
? + ?

Some polychaetes
Bivalves
Hemichordates

Amphipods
Nemertean worms
Tunicates and doliolids
Echinoderms
Other polychaetes

Figure 3

Luciferins used by marine organisms. Shown are the molecular structure, mode of operation, and taxonomic groups known to use them. In the last category, taxa containing unique, characterized luciferins are listed above the dashed line, and those whose luciferins are unknown or poorly understood are listed below the dashed line.

be readily aligned with other hydrozoan photoproteins, but this family of sequences shows little to no correspondence with the luciferases from other cnidarians.

It is curious that a chemically identical luciferin can be the active compound in unrelated organisms. The most striking example of this phenomenon is coelenterazine, which is the light emitter in at least nine phyla, spanning protozoans, jellyfish, crustaceans, molluscs, arrow worms, and vertebrates (**Figures 1**, **3**). The explanation for this convergence is not that these organisms are all synthesizing the same molecule. In some cases luciferin is acquired exogenously through the diet (e.g., Tsuji et al. 1972, Frank et al. 1984, Harper & Case 1999, Haddock et al. 2001). Because luciferins are present in both luminous and nonluminous marine animals (Shimomura et al. 1980, Thomson et al. 1997), they are relatively easy to obtain. But because the complete biosynthesis pathway is not yet known for any marine luciferins, their ultimate origins remain unknown.

Heterotrophic: gains nutrition by ingesting food; contrast with photosynthetic

Bacterial

Bacterial luminescence involves the oxidation of $FMNH_2$ (**Figure 3**) along with a long-chain aldehyde and a two-subunit luciferase. The genetic lux cassettes that are responsible for light production (Meighen 1991) and the conditions required for luminescence are now well understood (reviewed by Dunlap & Kita-Tsukamoto 2006), leading to numerous biotechnological applications (Ripp et al. 2003, Ramanathan et al. 1997, among many others).

Dinoflagellate

The dinoflagellate luciferin is a tetrapyrrole (**Figure 3**), similar to chlorophyll and differing mainly in the metal ions present (Dunlap et al. 1981, Nakamura et al. 1989, Takeuchi et al. 2005). The two compounds may in fact be interconverted on a day-night cycle as the cell alternates between photosynthesis and luminescence on a circadian basis. The structure of the dinoflagellate luciferin is the same as that found in euphausiids (krill) and is another indication of dietary linkages (Nakamura et al. 1989, Shimomura 1995b). Although this connection has not been demonstrated, early studies showed that euphausiids co-occurred simultaneously with large populations of dinoflagellates, and their luminescence ability was greatest in late spring and early summer (Tett 1972), when blooms were present. Some luminous euphausiids, like the large *Thysanopoda* and *Nematobrachion*, feed predominantly on zooplankton rather than phytoplankton (Hu 1978). Because the favored zooplankton species contain coelenterazine, it would be interesting to investigate the chemistry of luminescence in these predatory species and see whether they also use dinoflagellate-type luciferin.

Intracellularly, light emission from dinoflagellates is pH sensitive, owing to two factors. The tertiary structure of the luciferase reveals that a change in H^+ ion concentration causes the luciferase to change conformation, exposing its active site to the luciferin (Schultz et al. 2005). In addition, luciferin can be bound by a pH-sensitive luciferin-binding protein, which holds the luciferin until the pH drops (Mittag et al. 1998), and has also been recently cloned (Lee et al. 1993). The binding protein may also be implicated in the circadian periodicity of dinoflagellate luminescence capability (Morse et al. 1989, Lapointe & Morse 2008).

The dinoflagellate luciferase was originally cloned from *Lingulodinium polyedrum* (=*Gonyaulax polyedra*) (Bae & Hastings 1994), revealing three repeated catalytic domains, each of which is functional (Liu et al. 2004). The luciferase from *Pyrocystis lunula* shares some of the characteristic motifs in each of its corresponding domains, indicating that the duplication event occurred in the luciferase genes before the divergence of these two species (Okamoto et al. 2001). However, when the luciferase was cloned from the heterotrophic dinoflagellate *Noctiluca*, which is thought to be basal, only one of the three domains was present in the luciferase (Liu & Hastings 2007). Surprisingly, this gene also contained a region coding for the dinoflagellate luciferin-binding

protein, which occurs on a separate gene in other dinoflagellate species (Liu & Hastings 2007). Given the assumed relationship between chlorophyll and dinoflagellate luciferin, it will be fascinating to investigate whether some heterotrophic dinoflagellates need to obtain dietary chlorophyll for luminescence, while autotrophic species synthesize luciferin using chlorophyll produced by secondary or tertiary endosymbiotic plastids (Yoon et al. 2002).

Ostracod Luciferin

First examined in the 1950s (Tsuji 1955), the ostracod luciferin (**Figure 3**) was ultimately crystallized and characterized by Shimomura et al. (1957), making it one of the first marine luciferins chemically well understood. Using isotopes of amino acids, Kato et al. (2004, 2007) demonstrated that ostracods synthesize their luciferin from tryptophan, isoleucine, and arginine, but the details of the pathway are not known. This luciferin is found mainly in cypridinid ostracods (*Cypridina*, *Vargula*), and the midshipman fish, where a dietary link has been shown (Warner & Case 1980). It has been somewhat overlooked recently that *Cypridina* luciferin is also used by some fishes (*Pempheris*, *Parapriacanthus*), whose light organ is an extension of their digestive system, rather than a dedicated photophore structure (Sugiyama et al. 1961). The ostracod luciferases were cloned originally from *Vargula hilgendorfi* (Thompson et al. 1989), and more recently from *Cypridina noctiluca* (Nakajima et al. 2004). Curiously, the *Cypridina* luciferin discussed here is only used in the Myodocopid ostracods, while the Halocyprida, including *Conchoecia* (**Figure 4*o***), use coelenterazine (Oba et al. 2004).

Coelenterazine

The two best characterized and most widely used luciferins in marine systems are imidazopyrazinones (a combination of 5- and 6-membered nitrogen-containing rings). This structural motif is shared by coelenterazine (**Figure 3**) (Shimomura & Johnson 1972, 1975) and the *Cypridina* luciferin (**Figure 3**) (Kishi et al. 1966, Hori et al. 1977, Inoue et al. 1977). Coelenterazine was originally named for its presence in the cnidarians *Aequorea* (**Figure 4*c***) and *Renilla* (Shimomura & Johnson 1975), but even early on it was known to occur in many organisms, including the squid *Watasenia* (Inoue et al. 1975) and the shrimp *Oplophorus* (Shimomura & Johnson 1978). It has been found to be the light-emitter in an ever-growing list of bioluminescent species representing nine phyla (denoted by [C] in **Figure 1**) (Haddock & Case 1994, Mallefet & Shimomura 1995, Thomson et al. 1997, Shimomura 2006). Some chemical variants of coelenterazine also occur naturally in squid, including a disulfate version in the firefly squid *Watasenia* (Inoue et al. 1975) and dehydro-coelenterazine in the flying squid *Symplectoteuthis* (e.g., Takahashi & Isobe 1993). Many

Figure 4

Gallery of marine bioluminescent organisms. (*a*) Bioluminescent bacteria grown on a petri dish; (*b*) shallow colonial polycystine radiolarians; (*c*) the hydromedusa *Aequorea victoria*; (*d*) red-tipped tentacles and white stinging cells from the siphonophore *Erenna* sp.; (*e*) pelagic polychaete *Tomopteris*, which emits yellow luminescence; (*f*) planktonic larva of the acorn worm *Ptychodera flava*; (*g*) fluorescence showing the marginal photophores of *Aequorea coerulescens*; (*h*) vampire squid *Vampyroteuthis internalis* with light organs on its arm tips; (*i*) the bioluminescent chaetognath *Caecosagitta macrocephala*; (*j*) ctenophore *Beroe forskalii*, showing a rainbow of structural colors, not bioluminescence; (*k*) bioluminescence emission from light organs of the squid *Abraliopsis* sp.; (*l*) intensified image of luminescent frenzy from *Beroe forskalii*; (*m*) krill *Thysanoessa* sp.; (*n*) live photo of anglerfish *Chaenophryne longiceps*; (*o*) ostracod *Conchoecia* sp. that uses coelenterazine instead of typical ostracod luciferin; (*p*) hatchetfish with an overlay of ventral photophores shown by their blue fluorescence; (*q*) large copepod *Gaussia princeps*; (*r*) myctophid lampfish with species-specific pattern of photophores, and white "sternchaser" organ; (*s*) *Tactostoma* sp., in white light, and (*t*) under fluorescent illumination, showing the red and green photophores. All images show animals illuminated by a white-light strobe except *a*, *k*, and *l*, which record bioluminescent light, and *g*, *p*, and *t*, which use fluorescence illumination to reveal photophore patterns. (Photos: S. Haddock).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organisms, including *Renilla*, store coelenterazine in a stabilized enol-sulfate form (Cormier et al. 1970), which may not be detected in standard assays (Thomson et al. 1997).

Cnidarians appear to be unable to synthesize coelenterazine (Haddock et al. 2001), and its mode of biosynthesis is yet to be determined. Like ostracod luciferin, coelenterazine is thought to derive from cyclization of a tripeptide precursor, in this case, Phe-Tyr-Tyr (Ward et al. 1994). The strongest evidence for its natural origin is from experiments on *Systellaspis debilis*, where isolated eggs showed increasing levels of luciferin despite being dissociated from any potential maternal contribution (Thomson et al. 1995). It also persists in captive copepods (Barnes & Case 1972, Buskey & Stearns 1991), indicating that crustaceans are the most likely, but perhaps not exclusive, source of coelenterazine in the food chain.

Coelenterazine occurs naturally in conjunction with both photoproteins and luciferases. Several luciferases have been cloned from the copepods *Pleuromamma*, *Metridia*, and *Gaussia* (Markova et al. 2004, Takenaka et al. 2008, Szent-Gyorgyi et al. 2003), the decapod shrimp *Oplophorus* (Inouye et al. 2000, Inouye & Sasaki 2007), the sea pen *Ptilosarcus gurneyi*, and two species of *Renilla* (Lorenz et al. 1991, Szent-Gyorgyi et al. 2003). Where it has been examined, scyphozoan jellyfish also use luciferases. The most thoroughly studied is from the coronate *Periphylla* (Shimomura & Flood 1998), but it has not yet been successfully cloned.

Hydrozoans, ctenophores, and radiolarians use coelenterazine in conjunction with photoproteins. The first photoprotein, aequorin, was originally discovered, isolated, and characterized (Shimomura et al. 1962) from the hydromedusa *Aequorea victoria* (**Figure 4*c***) and subsequently cloned (Inouye et al. 1985, Prasher et al. 1986). This is the same species that was the source of the original green fluorescent protein, through a parallel research track (Shimomura 2005). Several other photoproteins have been cloned from hydromedusae, including *Mitrocoma* (Fagan et al. 1993), *Clytia* (Inouye & Tsuji 1993, Inouye & Sasaki 2007), and *Obelia* (Illarionov et al. 1995, Markova et al. 2002). The tertiary structure of these proteins has been solved (Head et al. 2000, Liu et al. 2000), and their properties have been re-engineered for research uses (e.g., Frank et al. 2008, Dikici et al. 2009). A photoprotein from the squid *Symplectoteuthis*, known as symplectin, has also been purified (Fujii et al. 2002, Isobe et al. 2008).

Organisms with a luciferase instead of a photoprotein control light emission by either sequestering the two compounds separately, or by using a luciferin-binding protein to control exposure of the luciferin to oxidation. The coelenterazine-binding protein of the sea pansy has been recently characterized from both *R. reniformis* (Inouye 2007) and *R. mulleri* (Titushin et al. 2008). In these proteins, the coelenterazine is caged within a pocket of helices and escapes through a hole that opens upon the binding of calcium ions (Stepanyuk et al. 2009).

Other and Novel Luciferins

Despite the prevalence of the four major marine luciferins, there are other light emitters known from additional taxa. The light-producing chemistry is well known for the bivalve *Pholas* (Dunstan et al. 2000), and for some polychaetes, including the polynoiid scale worms (Bassot & Nicolas 1995), chaetopterid tube worms, and syllid fireworms (Shimomura 2006). Thanks to the work of Shimomura and colleagues, many of these chemicals have been known for decades, so it is rare for an entirely novel luciferin to be discovered and elucidated. A notable addition to the list of marine luciferins came with the elucidation of the chemistry of the hemichordate *Ptychodera flava* (Kanakubo & Isobe 2005). The hypothesized light emitter, which operates with the involvement of peroxide and riboflavin, has a unique simple symmetrical structure (**Figure 5**). There are many other luciferins still to be discovered, especially among vermiform phyla, echinoderms, and molluscs (denoted by [X] in **Figure 1**).

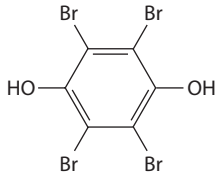

Figure 5

The luciferin of the hemichordate worm *Ptychodera flava*.

FLUORESCENCE AND BIOLUMINESCENCE

The mechanism of light production through a chemical reaction distinguishes bioluminescence from other natural optical phenomena such as fluorescence and phosphorescence. Fluorescent molecules do not produce their own light; they absorb photons, which temporarily excite electrons to a higher energy state. As these electrons rapidly relax to their ground state, they rerelease their energy, usually at a longer wavelength. Because the excitation and relaxation occur almost immediately (within picoseconds to microseconds), fluorescent light is only seen while the specimen is being illuminated. Examples of fluorescent molecules found in nature are chlorophyll, phycobiliproteins, and the green fluorescent proteins (GFPs). The term phosphorescence technically refers to a special case of optically excited light emission in which the relaxation occurs gradually over a long period of time, and photon emission persists for seconds to minutes. This phenomenon is seen naturally in some minerals and photosynthetic systems. In the early literature and for many years thereafter, it was common to use the term "phosphorescence" (perhaps poetically) to describe bioluminescence (Huxley 1898, Darwin 1909).

The technical distinction between bioluminescence and fluorescence is sometimes blurred in a practical context, for several reasons. First, compounds that are bioluminescent may also be autofluorescent, and thus photophores can often be visualized through their fluorescence under short-wavelength or UV illumination (**Figure 4*g,p,t***). Examples are the arm-tip light organs of the vampire squid *Vampyroteuthis infernalis* (Robison et al. 2003), the photophores of hatchetfishes and the midshipman *Porichthys notatus*, the fin photophores of the chaetognath *Caecosagitta macrocephala*, and the "lures" of the siphonophore *Erenna* (Haddock et al. 2005b). Some of these photophores and their associated chemical compounds become fluorescent only after they have reacted to produce light (e.g., Inouye 2004). Another link is that the fluorescence emission spectrum of a molecule may match its luminescence emission spectrum, since the same molecules are participating in the excitation-emission process. Because other natural materials can also be fluorescent (chitin, calcium phosphate), care must be taken when inferring the involvement of bioluminescence from the presence of fluorescence (e.g., Stabili et al. 2008).

One other relationship between bioluminescence and fluorescence is that brightly fluorescent proteins like green fluorescent protein (GFP) may be colocalized with their bioluminescent counterparts. For example, in the hydromedusa *Aequorea victoria* and several other bioluminescent cnidarians, their bioluminescence reaction would normally emit blue light at around 470 nm. Because of the tight association between the light-emitting chemicals and a separate green fluorescent protein, the energy that would be radiated as blue light instead excites the fluorescent pigment and is emitted as green photons (**Figure 6**). As a result of these linkages, it is often possible to learn about the bioluminescence of an organism by examining its fluorescent properties, even though fluorescence does not automatically indicate the presence of luminescence.

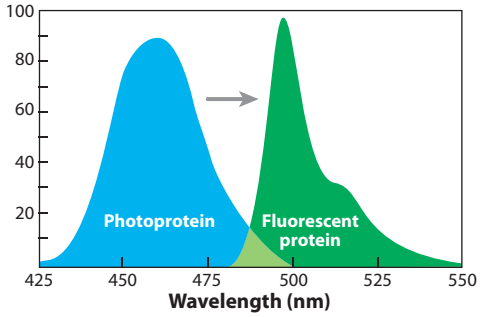

Figure 6
Green fluorescent protein.

Fluorescence: emission of light derived from the energy of an absorbed photon

GFP: green fluorescent protein; its fluorescent chromophore is generated autocatalytically from peptides within the translated protein; can occur in association with bioluminescent proteins

Supplemental Material

DIVERSITY OF BIOLUMINESCENCE

The most comprehensive list of bioluminescent genera was compiled by Herring (1987). **Supplemental Table 1** lists bioluminescent genera discovered since or omitted from that compilation (Follow the **Supplemental Material** link from the Annual Reviews home page at **http://www.annualreviews.org**). Here we detail some of the predominant bioluminescent groups in which there has been recent research.

Bacteria

Bioluminescent bacteria are common in the ocean, especially in temperate to warmer waters (Dunlap & Kita-Tsukamoto 2006). They may be cultured from almost any piece of detritus or tissue found on the beach, and even from uncooked seafood, which has been known to glow after being left for a time. Most bioluminescent animals do not get their luminescence from bacterial symbionts, but this continues to be a persistent misconception (e.g., Sinniger et al. 2008). These mutualistic associations are known mainly from a variety of marine fish and squid species, although the terrestrial pathogen *Photorhabdus* can infect nematode worms (Forst et al. 1997), and even human tissue (Peel et al. 1999). Bacteria are not luminous until they have reached sufficiently high concentrations to initiate quorum sensing (Waters & Bassler 2005, Nealson & Hastings 2006), and once induced, they glow continuously in the presence of oxygen rather than producing discrete flashes. These properties are specific to bacteria, which makes them uniquely suitable as photogenic symbionts and can lead to spectacular marine phenomena such as bioluminescent milky seas (see "Milky Seas" sidebar on page 472).

Among prokaryotes, light production is known only from the so-called eubacteria, specifically Gram-negative γ-proteobacteria, and not from Archaea. Names applied to the genera of luminescent bacteria often vary with the time-period and researchers' preference. The best-studied symbiotic bacteria are in the genus *Vibrio* (**Figure 4*a***), including the predominantly free-living species *V. harveyi* (sometimes called *Beneckea harveyi*), although the genus *Shewanella* also includes a bioluminescent species (Makemson et al. 1997). It was recently shown that many new strains of luminous bacteria, some related to what has traditionally been called *Photobacterium phosphoreum*, are present in the deep sea (Gentile et al. 2008), and many of the current species actually represent diverse assemblages (Dunlap & Ast 2005). Although there are many exceptions, *Vibrio fischeri* (often called *Photobacterium*) is part of the species-complex typically involved in symbiosis with sepiolid and loliginid squid and monocentrid fishes, while *Photobacterium leiognathi* and relatives are primarily symbionts for leiognathid, apogonid, and morid fishes (Kaeding et al. 2007).

The participants in the mutualism between bacterium and host were thought to share parallel phylogenies, as might be expected (Nishiguchi et al. 1998). Unexpectedly, however, broader surveys found that light organs include a complement of bacterial populations in both squid (Guerrero-Ferreira & Nishiguchi 2007, Wollenberg & Ruby 2009) and fishes (Dunlap et al. 2007). So the evolutionary dynamics are relatively fluid and opportunistic, and several strains make suitable symbionts for light-organ colonization. Nonetheless, there are close evolutionary ties, and in the best-studied mutualism, that between the bobtail squid *Euprymna scolopes* and *Vibrio fischeri*, the presence of the bacteria actually induces the morphological development of the squid light organ (McFall-Ngai & Ruby 1998). The host squid also monitors the luminescent performance of the symbionts and strains that fail to maintain adequate light production are rejected by a yet unknown mechanism (Visick et al. 2000, Nyholm et al. 2004). A whole-genome sequence of *V. fischeri* provides robust support for the idea that the same mechanisms that allow disease-causing enteric Vibrionaceae to infect human hosts (e.g., *V. cholerae*, *V. parahaemolyticus*) may be at work in establishing beneficial symbioses with marine species (Ruby et al. 2005). In fact, one researcher is said to have infected himself for a period of months when working with luminous *Photobacterium leiognathi* (Campbell 2008).

Dinoflagellates

Next to fireflies, dinoflagellates are the most commonly encountered bioluminescent organism. They typically cause the sparkling lights in the water seen by sailors, swimmers, and beachgoers, and they produce the "bioluminescent bays" which are tourist destinations in Puerto Rico and Jamaica. These protists can be autotrophic (photosynthetic) or heterotrophic, feeding on other phytoplankton and prey. In large numbers, some species may form potentially toxic red tides, typically during a stratified calm period after an influx of nutrients (discussed below). There are at least 18 luminous genera (Baker et al. 2008), including *Gonyaulax* (=*Lingulodinium*), *Noctiluca*, *Protoperidinium*, and *Pyrocystis*. Dinoflagellates invest heavily in their ability to luminesce, and allocate energy to bioluminescence before growth, although luminescence comes second to the ability to swim (Latz & Jeong 1996).

Radiolarians

Radiolarians are ameboid protists whose skeletal elements, when present, are made from amorphous silica. The classification of this nominal group in the sense of Haeckel (1887) is in a state of flux, and phylogenetic studies have shown it to include several independent lineages, primarily the Polycystinea (**Figure 4*b***) and Phaeodarea (Polet et al. 2004, Kunitomo et al. 2006). Within the polycystines, one order, the shallow-living Collodaria, is known to be bioluminescent. It contains the genera *Collozoum* and *Thalassicola*, which use coelenterazine bound to calcium-activated photoproteins (Herring 1979, Latz et al. 1991). It might seem that, as protists, radiolarians would be unlikely to have a way to acquire coelenterazine through their diet, but many of them actually consume or digest larger prey. The other major lineage of radiolarians lies within the Cercozoa and does not form a monophyletic group with the polycystines in general, nor the Collodaria in particular (Polet et al. 2004, Yuasa et al. 2006). Nonetheless, members of this predominantly deep-sea group, including *Aulosphaera* spp. and *Tuscaridium cygneum*, are also bioluminescent (Ling & Haddock 1997).

Ctenophores

Bioluminescence is very well represented in the comb jellies, where more than 90% of planktonic genera (and none of the benthic species) are known to produce light (Haddock & Case 1995).

Ctenophores use calcium-activated proteins and coelenterazine, some of which have been recently cloned (S.V. Markova, unpublished data; S.H.D. Haddock, unpublished data). Their luminescence can be internally expressed, sometimes in cascading waves as with *Beroe forskalii* (**Figure 4*i,l***), but some species like *Euplokamis stationis*, *Mertensia ovum*, and *Eurhamphaea vexilligera* also emit glowing particles as part of an escape response (e.g., Widder et al. 1992). At least one species of bioluminescent ctenophore also contains a green fluorescent protein (S.H.D. Haddock and N. Mastroianni, unpublished paper).

Cnidarians

Bioluminescence is found in both benthic and planktonic cnidarians, the group that includes corals, anemones, hydroids, medusae, and siphonophores. As far as is known, the luminous species all use coelenterazine as their light-emitting substrate.

Luminous hydrozoans include both hydromedusae and siphonophores. Most of the planktonic forms are bioluminescent, including 91% of planktonic siphonophore genera (**Figure 2*b***), while for unknown reasons it is rare among certain other groups, like the species of benthic hydroids that do not produce medusae. Most famous of the luminescent hydrozoans, and arguably of all bioluminescent invertebrates, is the shallow-living hydromedusa *Aequorea victoria* (**Figure 4*c,g***), which provided the original source material for research on photoproteins and the Nobel Prize–winning GFP (Prasher et al. 1985, 1992; Shimomura 2005). Most hydrozoans likely use bioluminescence for defensive or warning purposes, but siphonophores also use luminescence (Haddock et al. 2005b) and fluorescence (Pugh & Haddock 2009) to attract prey directly to their stinging tentacles (**Figure 4*d***).

Two orders of scyphozoans contain luminous members, including nearly all of the deep-sea coronates such as *Atolla* spp. and *Periphylla periphylla*, and some of the semaeostomes such as *Pelagia noctiluca*, *Phacellophora*, and the deep-sea *Poralia* (Haddock & Case 1999). Rhizostome species are not known to be luminescent. Scyphozoans were among the first bioluminescent animals recorded in the literature, dating back to Pliny the Elder in the first century A.D. *Periphylla*, *Atolla*, and other coronates produce cascading waves of light and can also exude luminous particles (Herring & Widder 2004).

Several luminous anthozoans are found within the octocorals (Alcyonaria), including sea pens and sea pansies. The first luminous soft coral *Eleutherobia grayi* was only recently discovered in the South Pacific (Williams 2001). There are many luminous octocorals found in shallow sandy bottoms (*Renilla*, *Ptilosarcus*), and in the deep sea (*Stylatula*, *Halipterus*, *Anthomastus*). Although the hard corals and anemones (Hexacorallia) are now famous for the possession of fluorescent proteins (e.g., Shagin et al. 2004), they are not usually bioluminescent. Among the hexacorals, one prominent luminous species is the epibiotic parasite *Parazoanthus*, which is unique in that its zooids form colonies growing over sea fans and sponges. Deep-living bamboo corals (Isidids) are also well known for their luminescence, and new species continue to be discovered (Etnoyer 2008).

Annelids

There are several different bioluminescent lineages among marine polychaetes, yet the chemical mechanisms of light production have not been fully determined for most species. Shimomura (2006) summarizes what is known in this regard. Some of the terrestrial annelids have been chemically characterized (e.g., Petushkov & Rodionova 2007), but there do not seem to be many parallels between the groups, and luminescence has several independent origins just within the annelids. The life cycles of the famous syllid fireworms, including *Odontosyllis*, have been thoroughly studied

through the years (Fischer & Fischer 1995). This normally benthic species produces a spawning stage near the time of the full moon. Females produce luminescent secretions that attract the males to swarm around them. Although these polychaetes use bioluminescence during spawning, like most organisms they will also produce internal luminescence in response to physical disturbance (Fischer & Fischer 1995, Deheyn & Latz 2009). In *Eusyllis*, fragments can continue luminescing for weeks, even without the head attached (Zörner & Fischer 2007). Such defensive responses are also common in other polychaete lineages, where there is no evidence of a function during mating.

Pelagic: living in the water column, as opposed to benthic

Although luminescence is often expressed by planktonic species or life-history stages, there are several benthic scale-worms (Polynoidae) that emit light using a protein triggered with superoxide radicals (Bassot & Nicolas 1995). The scales in Polynoidae are shed into the water where, released from nervous inhibition, they can glow and flash as a distractive decoy for minutes. In other benthic species, the function of luminescence is not as clear. The tube-dwelling chaetopterid *Chaetopterus* and the terebellid *Polycirrus* both produce light at around 440 nm (Huber et al. 1989). Glowing particles are exuded from their tubes when the worms are disturbed. It has been suggested that short-wavelength luminescence is an aposematic signal advertising distastefulness, or that light production drives off commensals that would otherwise take up residence in the worms' tubes (Morin 1983), although no experiments have been conducted to test this. Benthic *Chaetopterus* make light using a unique photoprotein (Shimomura 2006) five times as large as cnidarian photoproteins. Luminescence is also present in a recently discovered planktonic species of *Chaetopterus* (Osborn & Rouse 2008).

While terebellids fall at the short-wavelength end of bioluminescence spectra, another polychaete emits at the other extreme, with long-wavelength luminescence. Among the planktonic polychaetes, species of *Tomopteris* (**Figure 4*e***) produce a golden yellow light with unknown chemistry. Many planktonic members of the Flabelligeridae, including *Poeobius meseres* and *Flota vitjasi*, are luminescent (S.H.D. Haddock, unpublished data), and a newly discovered group of deep-sea polychaetes carries luminescent "bombs" that it drops when disturbed (Osborn et al. 2009). These are families in which planktonic existence is a derived trait (Osborn & Rouse 2008), suggesting another independent origin of luminescence correlated with animals moving up into the water column.

Other Worms

Bioluminescence makes scattered appearances among the many other wormlike phyla. Several species of acorn worms (Hemichordata) are luminescent, including *Balanoglossus* and the planktonic tornaria larvae of *Ptychodera flava* (**Figure 4*f***), whose luciferin was recently characterized (Kanakubo & Isobe 2005).

In the ribbon worms (Phylum Nemertea), there is only one known luminous species (Kanda 1939), but there are many deep-sea pelagic species that have only been examined preliminarily (J.L. Norenburg & P. Roe, pers. comm.). In 1939, Nemertea was the last phylum found to be luminescent until the discovery of the first bioluminescent chaetognath (**Figure 4*b***) (Haddock & Case 1994). Chaetognaths (arrow worms) use a luciferase+coelenterazine chemistry and shed a cloud of glowing particles in conjunction with an escape response.

Molluscs

Luminous marine molluscs include a few unusual gastropods like the whelk *Planaxis* and the spectacular pelagic nudibranch *Phylliroe*. One of the longest-known and best studied luminous molluscs is the bivalve *Pholas*. It seems somewhat unexpected for a clam to be luminous, but this

was the species used in pioneering experiments by Dubois in 1887 that established the existence of a luciferin+luciferase reaction. More than 100 years later, the photoprotein pholasin was cloned and characterized (Dunstan et al. 2000).

The most prominent of the bioluminescent marine molluscs are the cephalopods. Among the squids alone, there are at least 70 luminous genera (Herring 1977). Bacterial symbionts produce luminescence for several genera in the families Sepiolidae and Loliginidae (Ruby & McFall-Ngai 1992; Jones & Nishiguchi 2004; Nyholm et al. 2004, 2009). The rest of the squids, though, have intrinsic bioluminescence, using a luciferin along with their individual luciferase. Some of these have been chemically characterized. For example, *Symplectoteuthis* has a photoprotein that operates with dehydro-coelenterazine (Takahashi & Isobe 1994, Isobe et al. 2008). In *Watasenia scintillans*, the luciferase reacts with coelenterazine-disulfate and also has a requirement for ATP and Mg^{2+} as cofactors, which is unusual for coelenterazine-based luminescence (Tsuji 2002, 2005). Known in Japan as *hotaru-ika* or the firefly squid, *Watasenia* is the subject of a popular festival each spring. Light organs cover the ventral mantle with bright organs near the eyes and at the tips of the arms—typical for many other kinds of squids. Cranchiids also have well-developed ocular photophores, and many squid combine their complex iridescent reflectors with their light-emitting apparatus (Herring et al. 2002).

Squids can produce an impressive variety of luminescent displays. Many use their ventral photophores for counterillumination (**Figure 4*k***) (Herring et al. 1992). The deep-sea vampire squid *Vampyroteuthis* (**Figure 4*j***) is sufficiently distinct to have been classified in its own order. In addition to two large mantle photophores, and small light organs scattered across its body, it can release glowing particles from special light organs on its arm tips, apparently to distract predators (Robison et al. 2003). *Octopoteuthis* takes on a variety of coloration patterns, and will drop its arms when disturbed, leaving the glowing arm tips as decoys (Bush et al. 2009). Another cephalopod with light organs at its arm tips is *Taningia danae*. This highly active squid has clawlike hooks instead of suckers, and large (up to 2 cm) light organs at its arm tips. They are thought to use luminescence both for intraspecific communication and potentially to stun prey. Using high-definition cameras deployed in combination with bait and glowing lights, Kubodera et al. (2007) obtained incredible in situ video (available at doi:10.1098/rspb.2006.0236) of *Taningia* seemingly signaling to the artificial light sources using long glows. It also produced short, bright flashes from its arm-tip photophores as it attacked the bait.

Females of the pelagic deep-sea octopods *Japetella* and *Eledonella* have a greenish-yellow ring around their mouth which is only periodically luminous (Robison & Young 1981), indicating a potential role in reproduction (Herring 2007). *Stauroteuthis* and other genera of deep-sea cirrate octopods were long suspected to have glowing suckers (Chun 1910), but this was only recently confirmed to be bioluminescence (Johnsen et al. 1999). The lights lining the arms are thought to attract prey within the webbed canopy characteristic of this slow-moving cephalopod group.

Given the diversity of ways that cephalopods produce bioluminescence, it is likely that the number of independent evolutionary origins in this group, and in Mollusca generally, is much higher than estimated.

Crustaceans

Many types of planktonic crustaceans are bioluminescent, and they use species-specific luciferases with at least three different types of luciferins. With regard to the number of times they have reinvented bioluminescence, crustaceans rival molluscs and polychaetes. Euphausiids, or krill (**Figure 4*m***), use the same luciferin as dinoflagellates (Nakamura et al. 1989, Shimomura 1995b),

strongly suggesting a dietary connection. They have light organs along the lower surface of their body, which they use for counterillumination, and some species also have two small light organs on their eyestalks. These might serve as feedback mechanisms for determining how well their ventral photophores are matching background light. Like most photophores, these are under nervous control, involving serotonin moderated by nitric oxide (Krönström et al. 2007). Krill also use physical mechanisms to contract and dilate photophores to regulate light production (Krönström et al. 2009).

In shallow reefs of the tropical Atlantic, dramatic displays of luminescence at dusk are often attributable to ostracods (**Figure 4*o***). Ostracods can eject luciferin and luciferase through nozzles near their mouth, leaving discrete puffs of light in the water. Cypridinids provide the best marine examples of complex use of luminescence during mating, analogous in complexity and subtlety to the situation seen in fireflies (e.g., Buck & Case 2002). Shallow Caribbean ostracods, including many new species, have been extensively studied by Morin and colleagues (Cohen & Morin 1990; Morin & Cohen 2010; Torres & Cohen 2005; Rivers & Morin 2008, 2009).

Copepods, as one of the most abundant marine invertebrates, are also one of the most abundant bioluminescent groups in the sea, although the widespread genus *Calanus* is not luminescent. Common luminous genera include *Pleuromamma*, *Metridia*, *Oncaea*, and *Gaussia*. Bioluminescence involves coelenterazine, exhibited either as intracellular flashes or emitted into the water as part of an escape response (Widder et al. 1999). The giant (1 cm) deep-sea copepod *Gaussia princeps* (**Figure 4*q***) is a particularly good model for laboratory study of bioluminescence, behavior, and neurobiology (Bowlby & Case 1991, Weatherby et al. 2000, Fields et al. 2002). GFP-like fluorescent proteins have been cloned from copepods (Shagin et al. 2004, Masuda et al. 2006), but surprisingly they have only been found in nonluminous species. Many of the bioluminescent copepods are predatory and live moderately deep, although the tiny Poecilostomatoid copepod *Oncaea* is one example that is shallow and pseudoplanktonic (Bottger-Schnack & Schnack 2005). It occurs in the water column in association with larvacean houses (Ohtsuka et al. 1996), marine snow (Green & Dagg 1997), and other organisms (Gasca et al. 2007).

Decapod shrimp use light in several ways: Sergestids counterilluminate with photophores that tilt to maintain their downward orientation no matter which way the animal is swimming (Latz 1995). Oplophorids, including the genera *Systellaspis*, *Acanthephyra*, and *Oplophorus*, can disgorge large volumes of luminous fluid (Inouye et al. 2000) as part of a distress response. The visual systems of many of these crustaceans have been recently investigated in relation to their bioluminescent ability and their vertical migration behaviors. In both temporal and spectral properties, the visual systems of adults are tuned to detect bioluminescence (Frank & Widder 1999, Frank 1999), while juveniles may also be attuned to shorter wavelengths related to the detection of downwelling surface light (Frank et al. 2009).

Although many amphipods living in the water column are parasites on gelatinous plankton, several of these are nonetheless bioluminescent. *Scina* is a genus that emits uniquely short-wavelength luminescence ($\lambda_{max} \sim 440$ nm) from its antennae and legs (Bowlby & Case 1991). The visual system of this species, however, is not especially sensitive to those wavelengths (Cohen & Frank 2007), and the function of the luminescence is not known. Nonluminous amphipods will track blue light sources (Land et al. 1995), and it is suggested that they use this in hunting for the bioluminescent jellies they parasitize. Although the group that includes *Scina* and *Proscina* is not usually thought to be parasitic, examples of associations between *Proscina* and gelatinous hosts have been found (Gasca et al. 2007). In addition to producing typical blue-green light, some individuals of *Cyphocaris*, a genus of gammarid, can emit orange light (595 nm) through an unknown mechanism (Bowlby & Case 1991).

Echinoderms

Bioluminescence is found in most of the major groups of echinoderms: brittle stars (Ophiuroidea), sea stars (Asteroidea), sea cucumbers (Holothuroidea), and even crinoid sea lilies (reviewed by Herring & Cope 2005). Much of the recent work on echinoderms has focused on ophiuroid (brittle star) behavior and neurophysiology (e.g., Deheyn et al. 2000, Dewael & Mallefet 2002). A complex system of neurotransmitters modulates light output in these groups, and light originates from both an unknown photoprotein and a coelenterazine+luciferase reaction, depending on the species (Shimomura 2006).

In echinoderms other than brittle stars, luminescence is more common among deep-sea taxa (Brisingidae and Paxillosida for sea stars, *Pannychia*, *Peniagone*, and *Scotoanassa* for the holothurians, and *Thaumatocrinus* and *Annacrinus* among crinoids). As is typical for bioluminescence, it is also disproportionately represented in the pelagic holothurians such as *Enypniastes eximia* (Robison 1992) and *Pelagothuria*. New luminous ophiuroid species continue to be discovered (Mallefet et al. 2004), and undoubtedly the diversity of bioluminescent echinoderms as a whole will continue to increase as more deep-sea species are examined in good condition.

Tunicates

Bioluminescence is not as prevalent in planktonic colonial tunicates (thaliaceans: salps and doliolids) as in other plantonic groups. Although the colonial salp *Pyrosoma* has been renowned for its bioluminescence for centuries, other salps have not been confirmed as bioluminescent. Pyrosome luminescence has two unusual properties: It comes as a long, steady glow, and it can be induced upon illumination by light. The duration of the glow and the presence of bacteria-like particles suggest that bacteria are involved (Haygood & Prince 1993), but this is still the subject of a long-running debate (Godeaux et al. 1998).

Two other urochordate groups, long thought to be nonluminous, have been found to have luminous members. Doliolids are similar to salps, and nearly all species are not luminescent. However, a deep-sea bioluminescent doliolid was recently described (Robison et al. 2005), and bioluminescence has also been seen in *Paradoliopsis harbisoni* and *Pseudusa bostigrinus* (S.H.D. Haddock, unpublished data). Although most benthic tunicates are not luminescent, intrinsic bioluminescence was discovered in the shallow-living benthic ascidian *Clavelina miniata* (Aoki et al. 1989). This species produces light of 535 nm from phagocytes in the tunic (Chiba et al. 1998), and the glow may persist for 10 to 30 seconds (Hirose 2009).

Bioluminescence is well represented in the planktonic larvaceans (Appendicularia). Most known genera have bioluminescence, including *Mesochordaeus* (Renaux & Youngbluth 1990, Hopcroft & Robison 1999), *Bathochordaeus* (Hamner & Robison 1992), and about half of the *Oikopleura* species (Galt & Flood 1998). Larvaceans secrete luminous inclusions into their mucus and cellulose feeding filters (Galt & Sykes 1983) and can leave behind many bioluminescent "houses" each day with the potential to contribute a disproportionately large amount of luminescence (10^{14} to 10^{16} photons $\cdot$ m^{-3}) to the water column (Galt & Flood 1998). *Oikopleura labradoriensis* uses a coelenterazine+luciferase system (Galt & Flood 1998), which is curious since their diet is unlikely to include crustaceans and thus suggests another potential source for coelenterazine.

Fish

Bioluminescence is found in at least 42 families across 11 orders of bony fishes (compiled from Suntsov et al. 2008), in addition to one family of sharks. In contrast with invertebrate taxa,

several of these groups use bacterial symbionts for light production, including the well-known anglerfishes (**Figure 4*n***) (Munk 1999, Pietsch 2009), flashlight fish like *Photoblepharon* spp. (Haygood & Distel 1993), and shallow ponyfishes like *Leiognathus* spp. (Wada et al. 1999, Ikejima et al. 2008). The other luminous fishes have intrinsic luminescence using either coelenterazine (Mallefet & Shimomura 1995), ostracod luciferin, or some other uncharacterized light-emitter. Fish photophores are often highly modified and adapted to control not only the intensity of light but its angular distribution, according to their particular function (Cavallaro et al. 2004).

Intrinsic luminescence: luminescence caused by chemicals within the organism, not due to symbionts

Myctophids, or lanternfishes (**Figure 4*r***), are extremely abundant in the midwater, migrating near the surface at night. They have small photophores pointed downward and to the side, as well as large photophores on the tail, which can produce bright, fast (1×10^{11} photons s^{-1} for <400 ms) flashes (Mensinger & Case 1990). The genus *Diaphus*, which feeds actively on copepods and amphipods (Suntsov & Brodeur 2008), has prominent forward-facing photophores, which may be used to illuminate or induce fluorescence in their prey. If they use these headlights for hunting, it may also make them susceptible to visual attraction, as this genus was the most abundant in the diet of stomiid dragonfish (Sutton & Hopkins 1996).

The order Stomiiformes (e.g., hatchetfishes, dragonfishes) (**Figure 4*p,s,t***) includes some of the most elaborate arrangements of photophores, including barbels, ventral arrays, and red and blue suborbital photophores (Herring & Cope 2005). Within the family Stomiidae, there are several new species, which are distinguished partly on the basis of their barbel and light-organ morphology (Sutton & Hartel 2004; Kenaley & Hartel 2005; Kenaley 2008, 2009). Their diversification could be tied to feeding ecology, since stomiid species have a fairly high degree of prey specificity, and the favored prey of various species span copepods, euphausiids, decapod shrimps, fishes, and squid (Sutton 2005). Among the most interesting members of this group are the Malacosteinae, which are well known for having the unique ability to produce and detect long-wavelength red light (Partridge & Douglas 1995, Douglas et al. 2000, Herring & Cope 2005). What is curious about this group is that *Aristostomias* and *Pachystomias* eat fish, as expected, but *Malacosteus*, despite its large teeth, few gill-rakers, and no floor to its mouth, feeds frequently on copepods with only occasional meals of large fish (Sutton 2005). Although the three genera share unique visual and bioluminescence abilities, *Malacosteus* also differs in achieving its long-wavelength sensitivity by a distinct mechanism requiring chlorophyll as a sensitizer (Douglas et al. 1998, 1999). Because vertebrates cannot synthesize chlorophyll, *Malacosteus* gains its visual abilities through its diet of copepods, which contain phytoplankton-derived pigments in their guts. The ability to produce long-wavelength light may turn out to be more widespread than originally thought, since other stomiids have red suborbital photophores that appear morphologically similar to those of the Malacosteinae (**Figure 4*s,t***) (S.H.D. Haddock, unpublished data).

In the order Chondrichthyes, the Squalidae are a family of luminous lantern sharks that use ventral countershading for both defensive and offensive purposes (see the section on Functions below).

ECOLOGY, BEHAVIOR AND PHYSIOLOGY

Bioluminescence and Vision

Despite the taxonomic diversity of bioluminescence in the sea, its spectral properties are largely constrained to blue-green wavelengths, centered around 470 nm, with some exceptions highlighted above. In some cases, the default emission of the luminescent reaction is modified by the presence of fluorescent proteins or other fluorescent compounds (Denton et al. 1970, Shimomura 1995a, Haddock et al. 2005b, Herring & Cope 2005). These spectral properties are closely linked to

the visual systems of marine animals, both driving the adaptation of color sensitivity (Douglas & Partridge 1997, Frank & Widder 1999, Cohen & Frank 2007, Frank et al. 2009) and being driven by the qualities of the marine environment (Johnsen & Widder 1998, 1999; Cummings & Partridge 2001; Johnsen et al. 2004). In planktonic cnidarians and ctenophores, bioluminescence spectra tend to be shifted to shorter wavelengths as the species' depth of occurrence increases (Haddock & Case 1999), and this corresponds to the trend seen in fish visual pigments (Douglas et al. 1995). Most of the species that use green fluorescent protein as part of their luminescence system are found at shallow depths, and this modification is only occasionally present among deeper-living species (Haddock et al. 2005a).

Although yellow to red light is rare in the ocean, and most deep-sea fish have monochromatic color sensitivity centered about the blue-green wavelengths (e.g., Douglas & Partridge 1997), there are several indications that some fishes, besides those that emit red light themselves (Douglas et al. 1998, 2000), can detect longer wavelengths than just blue or green light (Douglas et al. 2002, Widder et al. 2005, Turner et al. 2009). Squids can also have chromatic vision through the presence of multiple visual pigments (Matsui et al. 1988, Seidou et al. 1990), and some, in particular *Vampyroteuthis infernalis*, have lenses capable of acute vision (Sweeney et al. 2007), which would lend themselves to discriminating bioluminescent sources against a dim or dark background. The eyes of the copepod *Cephalophanes* (Nishida et al. 2002) and the ostracod *Gigantocypris* (Warrant & Locket 2004) have semiparabolic reflectors thought to be adapted to the detection of bioluminescence. In the case of the copepods, it is hypothesized that they detect and feed on the luminous carcasses of other copepods that became luminous due to bacterial infections (Nishida et al. 2002).

In the evolutionary jockeying for selective advantage that occurs between animals that emit and those that detect bioluminescent light, fish and squid have developed additional ways to improve their perception. Some species have modified yellow lenses (Robison & Reisenbichler 2008) thought to act as long-pass filters, enhancing spectral differences and allowing fish to take advantage of the slightest mismatch between the color of bioluminescence and ambient light (Warrant & Locket 2004).

Excitation Mechanisms

As observers, we typically encounter bioluminescence in organisms that have been induced to flash by a physical disturbance. In a natural context, however, the emission of light is closely controlled by chemical and neurological mechanisms. Animals can turn their photophores on and off, but they can also modulate the intensity, color, and even angular distribution of light. These control mechanisms often involve calcium ions and other standard neurotransmitters. In dinoflagellates, control over light emission begins with a physical stressor that deforms the membrane (Latz & Rohr 1999), and involves a cascading series of triggers, including G-protein-coupled receptors (Chen et al. 2007), calcium ions (von Dassow & Latz 2002), and ultimately H^+, which triggers the release of luciferin from its binding protein, as discussed above. This sequence of events occurs with less than 12 ms latency, as measured with great precision on single cells using a microfluidics setup (Latz et al. 2008).

Because bioluminescence in many organisms is under nervous control, it can provide a visual map of the conduction velocities of the nervous system. The tradition of this method dates back to Panceri (1872) with his experiments on scyphozoans, and it has continued with application to the nerve net of the sea pansy *Renilla*, and to the epithelial conduction of hydrozoans (e.g., Mackie 1991). This is a natural analog to the ways that calcium-activated photoproteins currently are used in research to create biooptical sensors and to illuminate cellular processes (e.g., Daunert & Deo 2006, Manjarrés et al. 2008).

Dinoflagellate luminescence and the light from other organisms can be tied to a circadian rhythm, in which the luciferins are oxidized and rebuilt with each day/night cycle (Bode et al. 1963, Lapointe & Morse 2008). Other bioluminescent organisms living in illuminated environments may also require a period of dark acclimation before they will begin to luminesce; in the case of ctenophores, this is due to direct photodegradation of their photoproteins (Ward & Seliger 1974). In most deep-sea animals, however, the ability to produce light is essentially always present.

Energetics of Bioluminescence

Bioluminescence is an extremely effective way for invertebrates to communicate to organisms much larger and potentially far away and this may help explain its prevalence. Depending on the conditions, a bioluminescent flash can be seen from tens to hundreds of meters away (Warrant & Locket 2004, Turner et al. 2009). Even a single-celled dinoflagellate 0.5 mm long can send a signal to a large fish 5 m away—the equivalent of a 2 m tall human being able to communicate over a distance of 20 km. Chemical cues, while certainly playing important and overlooked roles in the sea (e.g., Moore et al. 1999, Woodson et al. 2007), perform a different set of functions than optical or acoustical signals; they do not diffuse rapidly enough to send the acute signals across distances that are possible through bioluminescence. Chemicals do have the advantage, however, of operating between nonvisual organisms, where bioluminescence is ineffective. Acoustical signals are transmitted extremely effectively in the sea (Medwin 2005), but they have the drawback of being relatively nondirectional, and many planktonic organisms lack the hard (or at least firm) body parts or gas bladders required to generate sounds (Moulton 1957, Patek 2001, Henninger & Watson 2005). Thus bioluminescence is one of the most effective ways for a small organism to communicate efficiently to a much larger organism in the sea.

FUNCTIONS OF BIOLUMINESCENCE

Bioluminescence serves many functions for marine organisms, and it frequently serves multiple roles for a single organism (**Figure 7**). One of the caveats in interpreting the ecological roles of bioluminescence is that types of light emission seen during laboratory stimulation may not reflect how they appear in nature, any more than one would conclude that human vocalization is an antipredatory response because we cry out when poked. Luminescence may be important at a particular developmental state—the temporarily planktonic larva of a benthic worm, or the medusa stage of a hydroid—or it may only be expressed during a particular reproductive period, as with the female octopod *Japetella*. Even if the correct developmental stage is available and the animal is in good condition, it is difficult to reproduce controlled, darkened conditions and then observe natural behaviors. Nonetheless, there have been some elegant recent studies of the functions of marine bioluminescence, and this continues to be one of the most promising arenas for future discoveries.

In the most general sense, bioluminescent glows are thought to function as attractant signals, and sudden flashes are thought to be repellent. The space over which this operates is important to consider, since a flash directed at short range can nonetheless attract attention from afar. Within the basic categories of defense, offense, and communication lie a variety of hypothesized functions.

Defense

There are more examples known of defensive functions of bioluminescence (**Figure 7**, blue area) than offensive (**Figure 7**, magenta area). When a bright flash is evoked at close range,

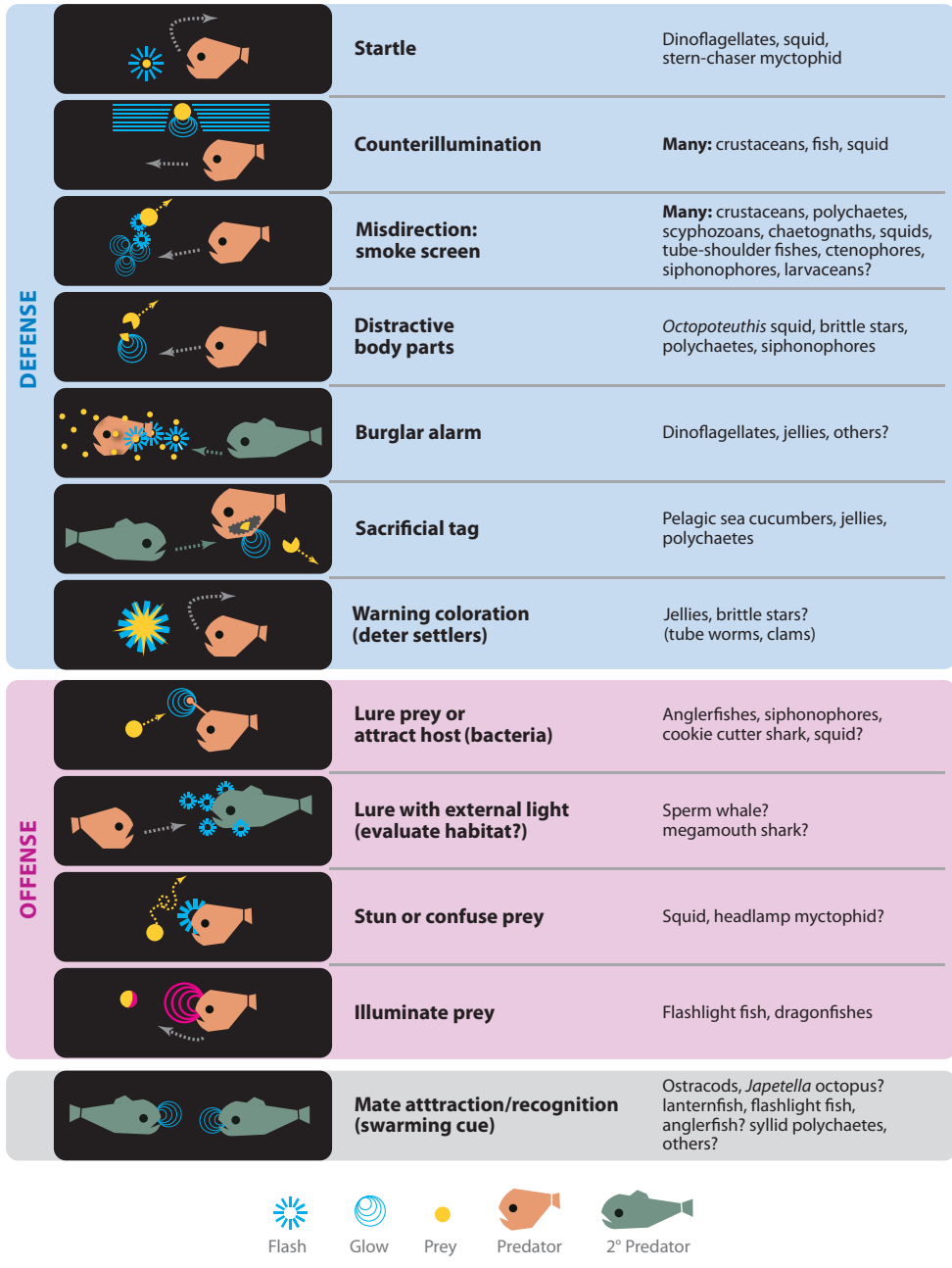

Figure 7

Schematic diagram showing the functions of bioluminescence. Marine luminescence can be used for defense (blue), offense (magenta), and intraspecific communication (gray). The organisms thought to benefit from these functions are listed to the right. Some animals are known to use their luminescence in two, three, or even four different roles.

bioluminescence is assumed to startle predators, causing them to hesitate, in a form of predator intimidation analogous to the peacock butterfly (Vallin et al. 2006). When exuded or secreted, the display may take the role of a smoke screen—a cloud of sparks or glowing fluid that makes it difficult for the predator to track the location of its escaping prey. This behavior is seen in many animals, including copepods, shrimp, tube-shoulder searsiid fishes, ctenophores and siphonophores (Haddock & Case 1999), a chaetognath (Haddock & Case 1994), and the vampire squid, which lacks an ink sac but instead emits a cloud of luminous secretions from its arm tips (Robison et al. 2003). Organisms like the deep-sea squid *Octopoteuthis deletron* may autotomize luminous body parts (Bush et al. 2009), which then continue to move and flash to draw away the attention of predators.

Apparently more common, but observed only anecdotally, is the application of a sacrificial tag. In this situation, an organism may lose part of its body to a predatory encounter. These lost tissues can continue to glow for hours afterward (Robison 1992, Herring & Widder 2004), even within the predator's stomach (pers. obs.). In the deep sea, where transparency is paramount (Johnsen & Widder 1998), the glowing tissue can draw attention to the predator, making it risky to consume bioluminescent prey. This is thought to be the selective force driving the presence of so many black- or red-pigment guts in otherwise transparent animals (Johnsen 2005), since most red and orange pigments absorb blue light. Many invertebrates also have excellent powers of regeneration and may be able to regrow the missing appendage while their predator suffers from having taken in the "Trojan horse." This phenomenon could be at work in nearly any bioluminescent organism large enough to recover from loss of tissue or skin during an attack.

Counterillumination

One type of bioluminescent defense that has been well studied in the laboratory is counterillumination, which is common among crustaceans, cephalopods, and fishes. This form of camouflage involves using ventral (lower) photophores (**Figure 4*k***) to match the dim light coming from the surface, thus making a potential shadow disappear. Counterillumination can be achieved either through a uniform match to the light field or by sufficiently disrupting the silhouette (Johnsen et al. 2004). Under controlled conditions, sergestiid shrimp (Latz 1995), deep and shallow squid (e.g., Young & Mencher 1980, Herring et al. 1992, Jones and Nishiguchi 2004), and the midshipman fish (Harper & Case 1999) have been shown to match the intensity, angular distribution, or color of downwelling light. In the midshipman experiments, the counterillumination behavior occurred even in naïve fish raised without dietary luciferin. Upon being fed with ostracods, the juveniles immediately demonstrated the appropriate illumination response (Harper & Case 1999). Many predators in the midwater have upwardly directed eyes, sometimes tinted yellow, to search for silhouettes. In *Macropinna microstoma*, the eyes can tilt between upward- and forward-looking positions (Robison & Reisenbichler 2008), while the spookfish, *Dolichopteryx longipes*, has evolved two fields of view in each eye, one focusing upward with a lens and one looking sideways with a mirror, so it can hunt while keeping an eye on what is happening below (Wagner et al. 2009). A variation of counterillumination where it might be used for offensive purposes is discussed below under Prey Attraction.

Burglar Alarm

Similar to the idea of a sacrificial tag described above, the burglar alarm is an indirect effect of an organism's bioluminescence, whereby its predators become vulnerable to attack from higher order predators. Often invoked as a function of bioluminescence, it is difficult to test. A key laboratory experiment showing this effect was conducted using dinoflagellates as the luminescent prey, mysid

shrimp as the nonluminous predator, and the midshipman fish *Porichthys notatus* as the secondary predator (Mensinger & Case 1992) and it was later replicated with some success using cephalopods as the top predators (Fleisher & Case 1995). In these situations, the top predators used the trail of bioluminescence to track the path of their prey, but the burglar alarm also operates in situations where a flash of light merely draws attention to the bioluminescent organism's predator.

Aposematism

On land, it is widely accepted that bright coloration can advertise toxicity or unpalatability, and this has been shown to apply to terrestrial bioluminescence as well (De Cock & Matthysen 1999, 2003). A similar mechanism has been suggested for many marine organisms, including scale worms, jellyfish, and brittle stars (Grober 1988, Bassot & Nicolas 1995, Herring & Widder 2004), although none has yet been convincingly demonstrated (see Guilford & Cuthill 1989). It would be particularly suitable for cnidarian bioluminescence to function this way; they are fragile yet potentially deadly, and it is to their advantage and advantageous to other organisms to avoid physical encounters.

Offense: Prey Attraction

Anyone who has seen moths drawn to a light can appreciate the possibility of using a glowing light as a lure. This is most prominent in fish, especially the diverse anglerfishes, which use bacteria to produce a long glow controlled by altering the conditions in the light organ where the bacteria are cultured (Pietsch 2009). Many types of stomiid dragonfish also have luminous barbels, although not involving bacteria; in fact, there are only two scaleless stomiids without barbels out of 25 genera (see Kenaley & Hartel 2005). One is *Malacosteus*, which feeds on copepods and has red suborbital photophores, thus suggesting a different strategy for capturing prey.

Attraction through bioluminescence has often been suggested for other taxa as well. In particular, the squid *Chiroteuthis* has special light organs thought to serve as lures that dangle at the end of long tentacles hanging down like fishing lines (Voss 1967, Robison et al. 2003). The octopus *Stauroteuthis* may use its luminous suckers to attract planktonic prey in a similar manner (Johnsen et al. 1999). Siphonophores, ropelike planktonic hydrozoans, have been previously suggested to use visual mimicry to attract prey (Purcell 1980), and some species of *Erenna* in the deep-sea have highly modified tentacles with bioluminescent lures that flick up and down next to their stinging cells. In one species, the bioluminescent lure is surrounded by a red fluorescent coating (Haddock et al. 2005b), raising the possibility that this species preys particularly on fishes with unexpectedly long-wavelength sensitivity (Douglas et al. 2002, Turner et al. 2009).

A variation combining both counterillumination and prey attraction has been suggested for the cookie-cutter shark *Isistius brasiliensis* (Widder 1998). This relatively small species feeds by taking bites out of the bodies of much larger fish, cetaceans, and squid, and it has been unclear how it might get close enough to attack these fast-moving prey. Widder (1998) hypothesizes that an optical "flaw" in the counterillumination pattern—a dark band below the mouth—looks like the silhouette of the prey of one of these larger species. When the fish or squid draws near to attack this apparent prey, it is instead attacked by the shark. This application of bioluminescence occurs only after the shark is grown, because the ventral pattern of light of another squaloid shark appears to serve a normal counterillumination role in juveniles, at least until they are fully developed (Claes & Mallefet 2008).

Animals may not have to make their own light to gain a predatory advantage from the existence of bioluminescence. Some nonluminous top predators may initiate a burglar alarm response

themselves, and actively use bioluminescence in their environment to attract or reveal their prey. Elephant seals (*Mirounga* spp.) dive to mesopelagic depths (Le Boeuf et al. 2000) and feed on fish and squid (Sinclair 1994), including fast-swimming and deep-water species (Rodhouse et al. 1992). Campagna et al. (2001) added light sensors to their normal time-depth recorders and deployed them on southern elephant seals off Península Valdés, Argentina. They found that during their dives the seals consistently encountered bioluminescence, which increased when they approached the area that includes the productive Malvinas Current. This light may aid the seals in finding their prey, or in evaluating the potential prey density of their environment (described in Case et al. 1994). Ocean sunfish and leatherback turtles both subsist largely on jellies (e.g., Hays et al. 2009), and it has been suggested that they use luminescence to help in their search for prey (e.g., Davenport 1988, Davenport & Balazs 1991, but see Houghton et al. 2008). A more proactive use of bioluminescence has been suggested for sperm whales by Fristrup & Harbison (2002). They examine the hypothesis that to gain an advantage while hunting squid in dark or twilight depths, the whales intentionally stimulate bioluminescence, which is made more pronounced by the white lining of their mouth. Squid, demonstrably attracted to light, would be drawn to the whale, which would otherwise have a difficult time finding them in sufficient numbers. The megamouth shark could also use indirect bioluminescence as it vertically migrates along with its planktonic prey (Nelson et al. 1997). Although the shark is not known to be bioluminescent (Herring 1985), it has a white pigmented band along its upper jaw that may reflect luminescence or downwelling light to draw plankton closer (Takahashi 2001).

Illumination

Other predatory applications include the use of bright light by a predator to stun or confuse prey. Videos of the squid *Taningia* flashing its tentacles while attacking bait (Kubodera et al. 2007) support this hypothesis, but there is little to no experimental evidence for this. The bright forward-pointing "headlamps" of the myctophid *Diaphus* might operate in this way, although they could also be used to illuminate or to induce fluorescence in prey. The scaleless dragonfishes are thought to use bioluminescence to aid in visual searching, including those with red suborbital photophores discussed above.

Intraspecific Communication

Communication within species is a well-known function of bioluminescence in terrestrial firefly courtship (e.g., Lall et al. 1980, Buck & Case 2002, Woods Jr et al. 2007), but these types of communication are less well known for the sea. Sexual dimorphism and the use of bioluminescence for mating have been reviewed by Herring (2000, 2007). The best-studied marine mating system is that of the Caribbean ostracods (Morin 1986, Morin & Cohen 2010). Ostracods show species-specific patterns of signaling, complex three-dimensional mate-following behavior (Rivers & Morin 2008), and even so-called sneaker males that follow along with displaying males and attempt to benefit from the surrounding displays while not producing luminescence of their own (Rivers & Morin 2009). Other examples of organisms thought to use bioluminescence for reproduction-related communication are fireworms, the pelagic octopods *Japetella* and *Eledonella*, and the ponyfishes, which produce synchronized group displays (Woodland 2002) and have evolved luminescent-based sexual dimorphism (Ikejima et al. 2004). In addition to mating displays, the shallow flashlight fish *Photoblepharon* has been suggested to use its large suborbital light organ for everything from finding prey, confusing predators, and interspecific communication (Morin et al.

1975). The lures of anglerfish might also be employed for mate-finding purposes in addition to prey attraction (Herring 2007).

Bathyphotometer: an instrument to quantify stimulated light present in the water

Light emission or visual sensitivity at unusually long or short wavelengths (as is the case with *Japetella* and the firefly squid *Watasenia*) may indicate that bioluminescence is being used as a private communication channel, rather than for one of the interspecific predator-prey functions described above. The presence of species-specific photophore patterns and sexual dimorphism suggests that the organisms use these features to distinguish each other, just as biologists do, but demonstrating this effect is difficult in the deep-sea where many of the organisms are found (Herring 2007).

Metabolic Byproduct?

It is relatively easy to speculate on functions of luminescence in metazoans and even protists, but for bacteria it has been suggested that light emission came first as a by-product of oxidation reactions that were already occurring in the cells (Rees et al. 1998). Luciferins often have strong antioxidant properties and may help scavenge free radicals to the benefit of cells (Devillers et al. 1999). Under these conditions, the presence of light-emitting compounds (luciferins) could have been useful for organisms before their eventual (and sophisticated) functions arose. Luminous marine bacteria derive from enteric genera for which the intestine of a fish is a favorable environment, thus the now-classic suggestion (Robison et al. 1977) that the glow of bacteria ultimately served to attract organisms to ingest them. Bacteria can be induced to produce light upon reaching the high concentrations found on a marine snow particle or fecal pellet, and would therefore be of sufficient size to be consumed. Luminous bacteria are readily cultured from fish intestines and a variety of habitats (Ruby & Morin 1979), and the fecal pellets of eelpouts (Zoarcidae) and discarded molts of crustaceans have been found to be brightly and visibly luminous (S.H.D. Haddock & R.D. Harper, unpublished data).

OCEANOGRAPHIC DISTRIBUTION AND POPULATION DYNAMICS

Most bioluminescent organisms in the marine environment generate light in response to mechanical stimulation, which often leads to brilliant displays in the wakes of ships, in breaking waves, or even around the bodies of rapidly moving dolphins (Rohr et al. 1998). Early research on bioluminescence in the sea was driven primarily by the desire to understand the chemical and physiological mechanisms, as well as the ecological advantage that bioluminescence affords marine organisms.

The flash kinetics of mechanically stimulated bioluminescence also accommodate an understanding of the distribution of organisms in time and space. Mechanically stimulated bioluminescence, or bioluminescence potential, generally refers to the flash potential from a single stimulus event measured in a chambered pump-through bathyphotometer (Seliger et al. 1969) or across a mesh screen (Widder et al. 1993, Widder 2002, Priede et al. 2006). Early systems provided qualitative distributions of bioluminescent organisms, because the mechanical stimulus was not defined. Over the last two decades, a significant body of literature has developed establishing shear-stress dependency of flow-stimulated bioluminescence (Maldonado & Latz 2007, Latz et al. 2008) and defining the shear thresholds for stimulation (Latz & Rohr 1999, Latz 2004) in a number of dinoflagellate species. This has led to the development of a series of bathyphotometers designed to enable comparable and quantitative assessment of light production (Widder et al. 1993, Herren et al. 2005).

In the following sections, the distribution of bioluminescence in the open ocean and coastal regions will be highlighted, with examples of applied uses of bioluminescence measurements.

The measures highlight organismal diversity and may afford the oceanographic community a complementary tool to observe and understand planktonic communities in the ocean.

Ocean Basin Distributions

In shallow sunlit regions of the oceans, biomass and organic compounds are required to support large accumulations of autotrophic, mixotrophic, and heterotrophic organisms. These materials are found in areas of elevated nutrient concentrations and of physical aggregation, where they cause increased primary production and frequently higher autotrophic biomass concentrations, as reflected in the accumulation of chlorophyll *a* (Chl *a*). This can lead to a direct relationship between Chl *a* and bioluminescence as seen in many different locations (Lieberman et al. 1987, Lapota 1998, Cussatlegras & Geistdoerfer 2001). In addition, some late-stage phytoplankton blooms may yield a successional accumulation of autotrophic dinoflagellates that may include bioluminescent species, e.g., *Lingulodinium* sp. or *Ceratium fucus*, which may also contribute to a positive relationship between Chl *a* and bioluminescence (Swift et al. 1995, Lapota 1998). Large-scale surveys in the Black Sea and Eastern Mediterranean Sea found correlations between bioluminescence and both Chl *a* and dinoflagellate cell counts (Piontkovski et al. 2003). Higher autotrophic biomass in turn leads to an increase in associated mixotrophic and heterotrophic biomass. As a result, studies have also found strong relationships between bioluminescence and heterotrophic biomass. In the Black Sea and Ionian Sea, over horizontal scales of meters to kilometers, the heterogeneity of bioluminescence matched that of both zooplankton biomass and physical temperature fields (Tokarev et al. 1998, 1999). The fact that bioluminescent organisms are autotrophic, mixotrophic, and heterotrophic makes quantitative relationships between bioluminescence and ecological parameters over large spatial domains difficult to obtain. However, as bioluminescent organisms represent a fraction (~1–2%) of the total number of organisms in the surface ocean (Morin 1983), bioluminescence potential in the epipelagic zone is directly related (with a large variance) to total biomass loads of the water column (Lapota 1998).

There are few studies available that provide an ocean-scale perspective of bioluminescence distributions. For those that exist though, there is generally good agreement between bioluminescence intensity and total biomass. This is true for a large data set collected during cruises of the former Soviet Union from 1963 to 1989 and the British Atlantic meridional transect program from 1995 to 1999 in the equatorial and the anticyclonic gyre of the South Atlantic Ocean (Piontkovski et al. 1997, 2003). Here, almost 3000 individual vertical casts of bioluminescence potential were compiled to provide an integrated view of the Equatorial and South Atlantic Ocean (**Figure 8*a***). What is most striking about this distribution is the similarity to the integrated Chl *a* (**Figure 8*b***), mapped from an independent remote-sensing data set (Acker & Leptoukh 2007). The correspondence is especially strong in the upwelling zones of the North Equatorial Current, the South Equatorial Current, and the Benguela Current. There is even a decrease associated with the eastbound Guinea Current. On the western portion of the Atlantic basin, the prevailing downwelling conditions and along-shore flow of the Brazil and North Brazil Currents prevent high biomass accumulation and bioluminescence potential offshore. Correlated with the bioluminescence intensity with depth across this survey domain were the distributions of in situ Chl *a*, phosphate, salinity, and copepod diversity, especially associated with the isopycnals along the north and eastern boundaries of the South Atlantic Gyre (Piontkovski et al. 1997, 2003).

Other large-scale attempts to relate physical oceanography to the bioluminescence variability of the water column include the Biowatt and Marine Light-Mixed Layer (MLML) programs (Marra and Hartwig 1984, Marra et al. 1995). Biowatt and MLML demonstrated a seasonal fluctuation of bioluminescence and that heterotrophic dinoflagellates were the dominant source of

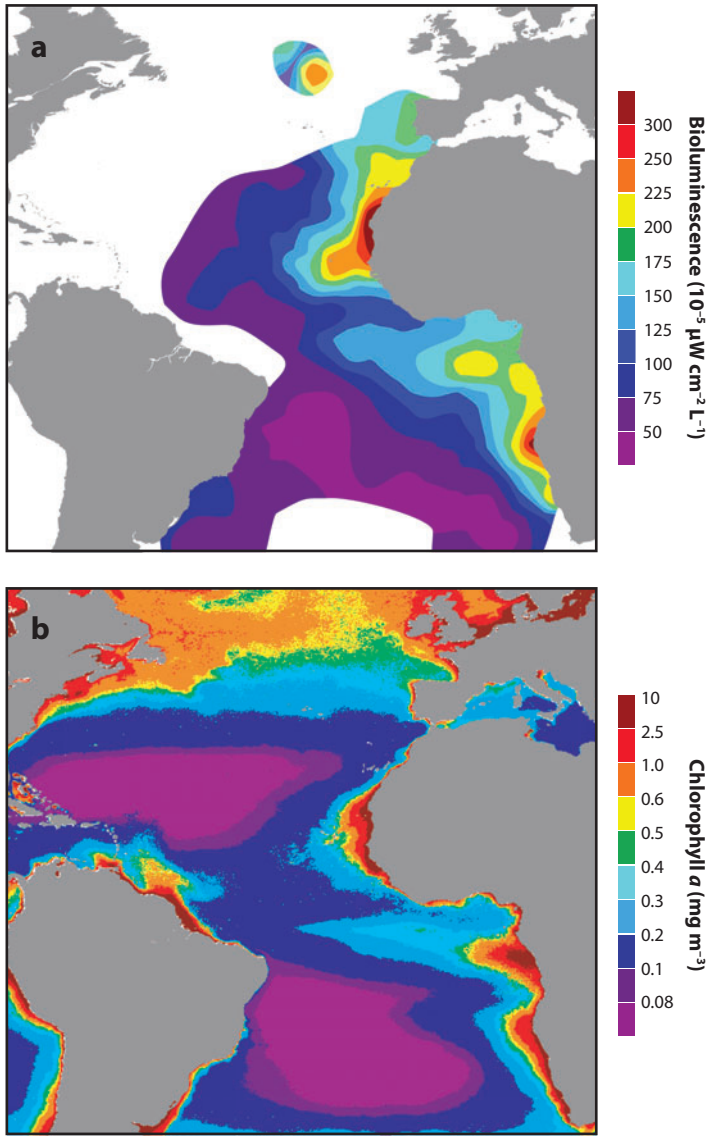

Figure 8

Oceanic-scale distributions of (*a*) bioluminescence and (*b*) chlorophyll *a* in the Atlantic. The distribution of bioluminescence is drawn from data in Piontkovski et al. (1997) and represents a 20-year data set of the mean bioluminescence from 0 to 100 m. The satellite retrieval represents the mean field of chlorophyll *a* from the combined SeaWiFS and MODIS-Aqua ocean color sensors for the period between September 1997 and February 2009. Data for the chlorophyll map in (*b*) were retrieved from the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences (GES) Data and Information Services Center (DISC).

bioluminescence in the North Atlantic, south of Iceland (Swift et al. 1995). One of the more interesting results from these programs was to demonstrate that high-frequency variations in temperature, salinity, fluorescence, downwelling light, and bioluminescence were coupled, in part, to high-frequency variations in physical forcing. This discovery of coupling between the distribution of bioluminescent organisms and the physical dynamics was found to translate to all scales of oceanographic observations from ocean-basin scale, to coastal dynamics, to fine-scale vertical structure.

Deep-Sea Distributions

Deep-sea bioluminescence has been known since the days of the *Challenger* expedition (Tizard et al. 1885) and Beebe's bathyscaphe dives (Beebe et al. 1934), but improved technologies have given the ability to quantify these sources. As with the occurrence of bioluminescence in the epipelagic zone of the oceans, the distribution of bioluminescent organisms in deeper other waters correlates with overall biomass and varies regionally based on differences in physical forcing. Much of the literature describes the distribution of bioluminescence in the midwater and deep-ocean environments as the number of sources per m^3 that are imaged when passing through a screen (e.g., Priede et al. 2006, based on the methods of Widder et al. 1999). While not quantitative in terms of light production, these accounts do provide quantitative counts of bioluminescent organisms and a perspective on their three-dimensional distribution in the water column. Over the Mid-Atlantic Ridge, luminous sources measured by free-falling profilers decreased asymptotically from 46 m^{-3} at 300–500 m to 6 m^{-3} between 1500 m and the seafloor (Heger et al. 2008). However, in regions where the water column was influenced by topography, such as the Azores and the Faraday Seamount, the number of sources in the midwater doubled relative to shallower depths. High abundances of deep-sea bioluminescent sources have been found correlated with biomass in eddies of the Subpolar Front (Heger et al. 2008) and around South Atlantic seamounts (Tokarev et al. 2003). Other surveys, covering hundreds of kilometers, detected a seasonal signal around Porcupine Seabight, with fourfold variation related to the spring peak of primary production in the surface layers (Gillibrand et al. 2007b). The abundance of luminous animals in the deep water column means that any organism or equipment moving through that environment, including trawling gear, stimulates large amounts of light (Jamieson et al. 2006).

Another indirect method of examining bioluminescence in the midwater and deep oceans is the use of bottom-mounted neutrino observatories, which consist of arrays of low-light sensors suspended in the water column. Physicists, interested in detecting Čerenkov radiation, work to minimize the "noise" of biologically generated light from their measurements (Widder 2007), although it is inescapable even at great depths (Clarke & Hubbard 1959). Wilkes (1994) showed that bioluminescence was detected by the DUMAND (Deep Underwater Muon and Neutrino Detector) off the coast of Hawaii and contrasted that to the AMANDA (Antarctic Muon and Neutrino Detector Array), under Antarctic ice, where there was no bioluminescence. For the NESTOR (Neutrino Extended Submarine Telescope with Oceanographic Research), deployed off of Greece, bioluminescent activity was found to be present ~1% of the active time, although more recent observatories, such as ANTARES (Astronomy with a Neutrino Telescope and Abyss environmental RESearch) off France, have shown bioluminescence to influence up to 30% of the active time (Katz 2004, Aguilar et al. 2006). Based on its kinetics, this light is clearly produced by metazoan flashes and glows and is not of microbial origin (Bradner et al. 1987, Webster et al. 1991). These bioluminescent signals were found to correlate with current speed and shear (Amram 2000), as more organisms flowed past and encountered the detector array. This finding influenced modifications to the existing detector and to future detectors (Katz 2006). Based on an intense

MILKY SEAS

A large-scale bioluminescent surface phenomenon, known as milky seas, is the result of high concentrations of luminous bacteria (Herring & Watson 1993). Bacteria emit a relatively faint glow per cell, but light production is continuous, so their luminescence can be visually distinguished from blooms of dinoflagellates, for example. Bacteria can form large slicks lasting days under appropriate conditions (Lapota et al. 1988). It is suggested that occurrence of these large light-emitting surface slicks may be facilitated by substrates produced by a previous or concurrent phytoplankton bloom (Miller et al. 2005, Nealson & Hastings 2006). As conditions required for these events are highly unpredictable, most documented accounts have been from merchant ship logs, with the exception of a single research study (Lapota et al. 1988). Miller et al. (2005, 2006) demonstrated the use of satellite remote sensing as a means of detecting milky seas for the first time, showing an affected area of 15–17,000 km^2 off the Horn of Africa (**Figure 9**). The counterclockwise motion of the northern portion of the slick tracked over three days was consistent with presence of a cold-core ring (Miller et al. 2006). Future studies of this elusive phenomenon may be guided by the use of existing and planned low-light satellite sensors, trained on the northeastern portion of the Indian Ocean and Arabian Sea where more than 70% of milky seas events have occurred (Herring & Watson 1993). This area may be the site of so many events because of an unusual combination of warm surface temperatures (favorable to microbial growth) yet high productivity due to upwelling.

sampling effort around two of the detectors, Priede et al. (2008) found that the potential for interference at ANTARES and NESTOR matches the biomass distribution for each area, with the area off southern France sixfold higher than off the east coast of Greece.

In addition to water-column distributions of bioluminescence, a number of studies have examined bioluminescence on the seafloor using a series of free-falling landers outfitted with low-light imaging systems (Bailey et al. 2007), which appear to sample the bioluminescent organisms at great depths better than traditional shipboard profiling (Webster et al. 1991). These studies have used bait to attract organisms for assessment, because the rate of flashing in nonbaited systems has proved too low to be detected (Priede et al. 2006, Gillibrand et al. 2007a). The response to bait has been relatively rapid (~0.5 hr), with subsequently consistent bioluminescent events on the order of 2 min^{-1}. Concentrations were inversely related to seafloor depth, with enhancement near shelf areas (Gillibrand et al. 2007a). Exceptional bioluminescent hot spots were found within a kilometer of carbonate and coral mounds, where the mean number of events was an order of magnitude higher. These areas were characterized by moving luminescent targets, likely ostracods, that released patches of luminescent material into the water around the bait, so that at times the entire baited area was illuminated for minutes (Gillibrand et al. 2007a). An inverse relationship between bioluminescence and depth was found on the seafloor in the Mediterranean Sea (Craig et al. 2009). There was also a west-to-east gradient in decreasing density of bioluminescent organisms, which matched the general surface productivity in the region (Bricaud 2002). These seafloor observations also correlated well with the vertical distributions of bioluminescence in the area (Priede et al. 2008).

Coastal Distributions

While many of the early surveys of bioluminescence potential were conducted on ocean basin scales, recent work has emphasized the transition areas from the open ocean to the shoreline. For all oceanographic disciplines, the temporal and spatial dynamics in coastal regions present a new set of challenges, and developing suitable instrumentation for quantifying the distributions of

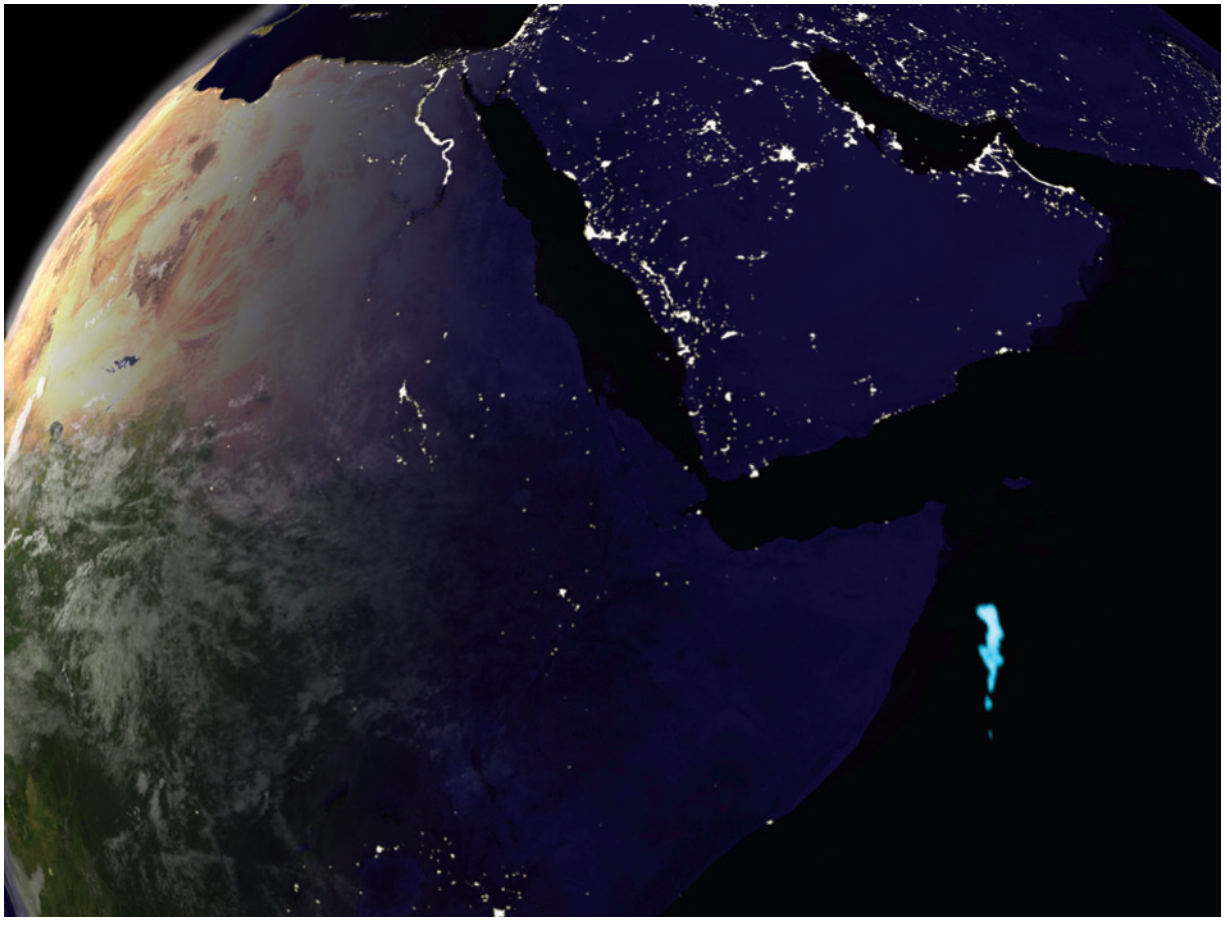

Figure 9

Milky Seas. A composite rendering showing a satellite perspective of the first bioluminescent milky sea recorded from space (Miller et al. 2005, 2006). The bright blue patch is 300 km long and covers an area roughly equal to that of the Hawaian archipelago. Although it is represented on the correct size scale, the data from the satellite low-light sensor were enhanced (see Miller et al. 2006 for details), and thus the event appears brighter than it would if viewed by eye from this perspective. The image was generated by creating a two-dimensional mercator projection including the low-light event, background layers of the Blue Marble (source: NASA), Nighttime City Lights of the World (source: NOAA), and cloud cover derived from Meteosat data (courtesy S.D. Miller). The composite projection was then mapped onto a sphere and rendered using Cheetah3D.

bioluminescence potential is no exception. High productivity and the complexity documented for physical and biological parameters, including bioluminescence (Blackwell et al. 2008), required development of new, smaller portable sensors that were amendable to a wide range of platforms. Herren et al. (2005) document the development of such a sensor and its integration into moorings, remotely operated vehicles, autonomous underwater vehicles (Shulman et al. 2003, 2005; Moline et al. 2005b), undulating tow bodies, cabled profilers (Moline et al. 2007, Oliver et al. 2007), and coastal ship-profiling units (Herren et al. 2004). Analogous laboratory-developed systems are in use (Lapota et al. 1994, Cussatlegras 2001) and some are commercially available (Kim et al. 2006, Orrico et al. 2008). While fluorometers give a proxy for autotrophic fluorescence, these sensors allow for the evaluation of higher planktonic trophic levels. As a result, they provide new insight

into the distribution of bioluminescence in the coastal zone (Moline et al. 2001, 2005a, 2005b) and some of the time- and space-dependencies of the distributions (Blackwell et al. 2008).

Bioluminescence has also been used to address coastal processes. Bioluminescent dinoflagellates are not uniformly distributed through the water column but may be preferentially accumulated into marine snow particles (Alldredge et al. 1998). This can result in light production per volume that is 60–180 (Puget Sound, Washington; Herren et al. 2004), or 200–45,000 (California coast; Haddock 1997) times higher in particles than in an equivalent volume of surrounding seawater, and 1–78% of the total light in the upper water column can be attributed to aggregate associates (Herren et al. 2004, Haddock 1997). Since bioluminescence has been shown to deter grazing on individual dinoflagellates through the startle and burglar-alarm functions discussed above, luminescence-enriched marine snow may avoid consumption, leading to changes in carbon-settling rates.

Using the differences between the bioluminescence flash kinetics of planktonic dinoflagellates and zooplankton, it is possible to measure relative abundances of the two groups within a volume using a single sensor on an autonomous vehicle (Moline et al. 2009, 2009b). By distinguishing between the two trophic groups, their interactions were revealed on a regional scale in the context of a periodic upwelling cycle. This effort was part of a larger study combining a number of observational tools to provide near-synoptic regional views of bioluminescence (**Figure 10**). The spatial dependencies of bioluminescence in coastal waters have relevance for a number of applied themes. Examples of three specific research areas where bioluminescence is being used are harmful algal blooms (HABs), thin-layer ecology, and ocean modeling.

Bioluminescence and Harmful Algal Bloom Detection

The documented increase in harmful algal blooms in recent years has stimulated efforts to detect and monitor bloom events (Babin et al. 2008, Ramsdell et al. 2005). Currently, HAB detection relies on laborious cell counts and costly cruises in response to water discoloration and fish kills. Although effective for bloom detection, these methods lack the potential to collect data across the necessary time- and space-scales to accurate assess or forecast bloom dynamics (Schofield et al. 1999, Kirkpatrick et al. 2000). Remotely sensed ocean color is subject to cloud conditions and satellite coverage, and can only be applied to the near surface at high cell densities (Tester et al. 1998). To overcome these limitations, there is a need to discriminate between phytoplankton taxa in situ, detect cells at a range of concentrations throughout the water column, and be able to track movement over short periods to account for lateral advection and diurnal vertical migration. Kim et al. (2006) demonstrated a real-time monitoring system along the Korean Peninsula for the occurrence of dinoflagellates using bioluminescence. One important outcome of the study was that even though the dinoflagellate species of principal concern was not bioluminescent, nutrient conditions tended to support the growth of a number of dinoflagellates species, including bioluminescent species, and therefore, the measurement could be used as an indicator. Similar findings have been reported in Monterey Bay where extreme red tides have been reported (Shulman et al. 2005, Ryan et al. 2008) and there has been a shift of the dominant phytoplankton group from diatoms to dinoflagellates since 2004 (Jester et al. 2009). Although a systematic phylogenetic analysis of links between bioluminescence and toxicity in dinoflagellates has not yet been reported, it is interesting to note that according to the National Provasoli-Guillard Center for Culture of Marine Phytoplankton, of the 34 bioluminescent strains, half are also toxic. There are numerous reports of both toxic and bioluminescent species occurring across the globe (Tyrrhenian Sea: Zingone et al. 2006; Sea of Japan: Baek et al. 2008; Aegean Sea: Aligizaki et al. 2009; Baltic Sea: Kremp et al. 2009; Black Sea: Morton et al. 2009; United States: Jester et al. 2009). Thus, luminescence may be an important tool to monitor the development and movement of HAB species in coastal waters.

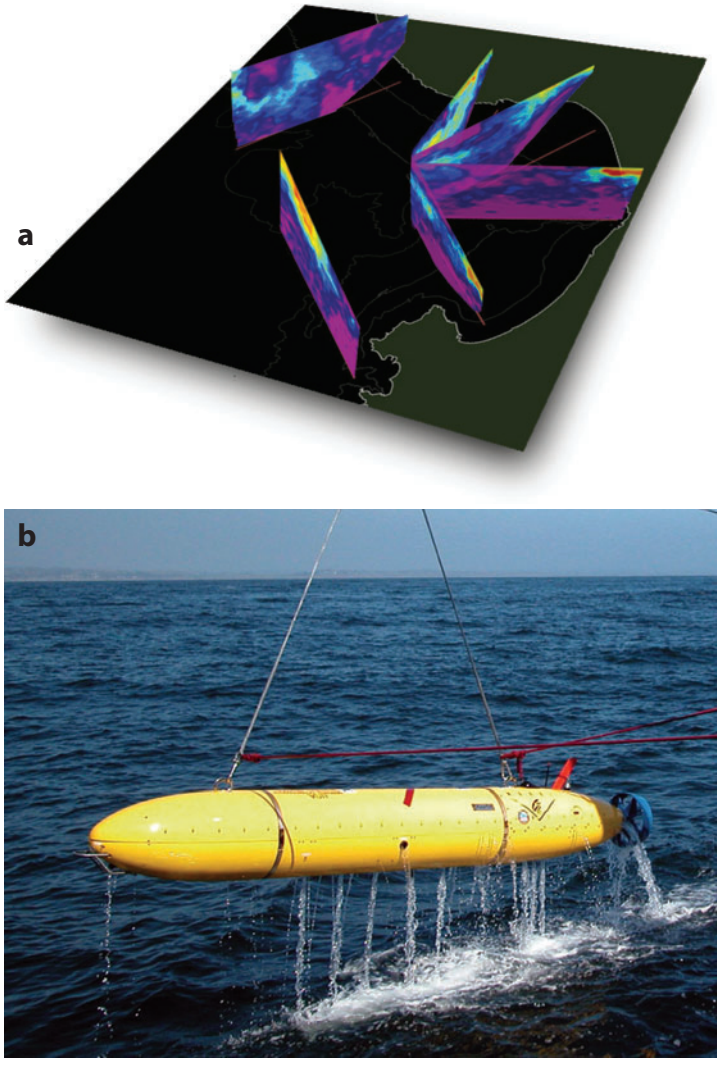

Figure 10

(*a*) Bioluminescence sections measured via an autonomous underwater vehicle. Slices of the depth distribution of bioluminescence from Monterey Bay, California, in August 2003. Data were collected over a six-day period by a bathyphotometer (*b*), taking samples while underway on board an autonomous underwater vehicle. The vertical scale, greatly exaggerated in the figure to show luminescence features, spans 3 to 40 m. Data show a near-synoptic view of the bioluminescence distribution in the epipelagic zone, with high concentrations of luminescence in a near-nearshore band and in a deeper offshore plume. They were used to initialize and validate a regional-scale advection–diffusion ocean model (Shulman et al. 2005).

Thin Layers

The existence of a subsurface chlorophyll maximum has been known for many decades (Steele & Yentsch 1960, Anderson 1969), and this feature can have a profound effect on the distribution of organisms and biomass in the water column. The mechanisms of formation include the physical and optical structure of the water column and the behavior of the organisms residing in

and near the feature (Deutschman et al. 1993, MacIntyre et al. 1995, Osborn 1998). At times, dense accumulations of phyto- and zooplankton can be concentrated in a vertical space that is tens of centimeters to a few meters in scale, but they can be contiguous over many kilometers (Holliday 2003, McManus et al. 2003, Cheriton et al. 2007). These layers are often missed in traditional sampling approaches yet may disproportionately influence trophic interactions (Alldredge et al. 2002), biogeochemical cycling (Rines et al. 2002), or toxin production (Rines et al. 2002, McManus et al. 2008). Because a portion of the planktonic community is often bioluminescent, this property can be used as an additional tool to define these layers. For example, luminescence measurements have revealed layers of copepods less than 0.5 m thick in the Gulf of Maine (Widder et al. 1999), suggesting that these layers coincide with the documented layering of marine snow along density discontinuities (MacIntyre et al. 1995), and they may provide an energetic benefit for the zooplankton. A three-dimensional analysis in the same location indicated that the copepods were likely organized in response to an environmental cue, such as a food source (Widder & Johnsen 2000). The formation of thin layers of bioluminescent organisms presents a challenge for other animals navigating through the environment while trying to avoid the stimulation of bioluminescence. Recent work has shown that the thickness and horizontal extent of bioluminescent layers increases at night and that there are behavioral responses between layers based on their dimensionality (Benoit-Bird et al. 2009; Moline et al. 2009, 2009a). As these layers are intrinsically linked to physical (Ryan et al. 2009), chemical (Hanson & Donaghay 1998), and biological gradients (Widder & Johnsen 2000), they are likely to provide a mechanism for maintaining high planktonic diversity in coastal waters (Dekshenieks et al. 2001).

Bioluminescence Measurements and Ocean Modeling

Modeling provides a tool to fill in the temporal and spatial gaps in the observations and provide a larger-scale view of ecosystem interactions with physical and biological factors. Bioluminescence is a measure of a portion of the total biomass, with contributions from both the autotrophic and heterotrophic communities, and can therefore be used as a tool to assess ecosystem response and interaction.

With a large data set collected in Monterey Bay, Shulman et al. (2003) used bioluminescence as a tracer and predicted its distribution 24, 48, and 72 hours in the future. By combining observations of winds and currents and a circulation model, the authors were able to predict the three-dimensional location and intensity of the bioluminescence maximum over a 72-hour period and over distances of 25–35 km. This short-term result was later refined with a larger data set from the same location (see **Figure 10**), with the goal of optimizing sampling strategies for bioluminescence (Shulman et al. 2005). In addition to predicting short-term changes in coastal bioluminescence, they also demonstrated that optimization of bioluminescence sampling strategy to generate input to the forecast is critical for successful short-term predictions with the tracer model.

In addition to the advection-diffusion model approach, which does not consider long-term biological dynamics, there has been an effort to integrate ecosystem models into dynamic ocean models. The dynamic ecological approach is based on the development of a series of mechanistic equations linking the hydrodynamic forcing functions, nutrient concentrations, and resulting ecological structure. These types of joint ocean-ecosystem models exist in various states of complexity for phytoplankton and zooplankton populations (Bissett et al. 1999, Moore et al. 2001, Polovina et al. 2008). As the majority of bioluminescence in the euphotic zone is generated by these groups (Herring 1987, Swift et al. 1995, Piontkovski et al. 1997, Lapota 1998, Widder & Johnsen 2000), bioluminescence is likely to help in the initialization and validation of ecosystem models. Changes in phytoplankton and zooplankton distribution and abundance may be more easily related to

bioluminescence than to any other hydrodynamic diagnostic parameter. The ability to discriminate between dinoflagellates and zooplankton using optical techniques (Moline et al. 2009, 2009a) or the combination of optical and acoustical approaches (Benoit-Bird et al. 2009) shows promise of assigning quantitative to state variables in these dynamic models. Applied to large field data sets, this approach has the potential to provide models with distributions of these bioluminescent communities for initialization and validation. This leads to derivation of the mechanisms governing patch distribution, coherence, and their biological interactions on regional scales. The measure of bioluminescence highlights organismal diversity and may afford the oceanographic community a complementary tool to observe and understand planktonic communities in the ocean.

SUMMARY POINTS

1. Bioluminescence is widespread across most forms of metazoan marine life.
2. The distribution within taxonomic groups is patchy, sometimes even between sister taxa.
3. Light is typically generated by the organism itself and only rarely due to bacterial symbionts.
4. Light emitters (luciferins) are conserved, while enzymes (luciferases) are diverse and species-specific.
5. One luciferin, coelenterazine, is the light emitter for nine different phyla.
6. Based on the chemical mechanisms known, luminescence has evolved independently more than 40 times.
7. It serves a variety of functions, both offensive and defensive, even within a single organism.
8. Because a large fraction of animals is bioluminescent, quantifying luminescence can provide a proxy for heterotrophic biomass.
9. The distribution of bioluminescent organisms can be measured by automated instruments and is a useful parameter for understanding ocean ecology.

FUTURE ISSUES

1. While the genes for many luciferases are known, the mechanisms of luciferin biosynthesis are almost entirely unknown. This will be a promising area for future research.
2. Better access to live animals in good condition will give opportunities to understand natural functions of luminescence. The question of why so many animals are bioluminescent still does not have a satisfactory answer.
3. Although there have been breakthroughs in understanding the molecular basis for the major luminescence systems, the chemistry of luminescence for many organisms remains completely unknown. Promising taxa include echinoderms, polychaetes, and tunicates.
4. Improvements in remote and automated methods of detecting oceanographic-scale bioluminescence (satellites and bathyphotometers) will allow better understanding of marine ecosystem dynamics, harmful algal blooms, and how and why plankton populations fluctuate over time.

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