Who makes light and why?

Bioluminescence is visible light made by living creatures. Such creatures are rare on land but extremely common in the oceans. A list of some of the many different kinds of bioluminescent creatures in the world, classified by the different environments in which they live, gives some sense of the relative significance of bioluminescence in the marine environment, compared to in the terrestrial and freshwater realms (Table 1).

Bioluminescent creatures occur in all oceans at all depths with the greatest numbers found in the upper 1000 m of the vast open ocean. The prevalence of bioluminescence here is a consequence of the unique visual characteristics of this environment. This is a world without hiding places where sunlight filtering down through the depths decreases approximately 10-fold for every 75 m of descent until all visible light disappears below 1000 m. In this twilight realm the light is dim and blue and highly directional so that the only creatures that are visible are those directly overhead or those that produce their own light with bioluminescence. In this context bioluminescence can aid in the survival of an organism in three critical ways:

1. Bioluminescence can help an animal find food. When looking for something in the dark a flashlight is a very handy tool and many animals have built-in bioluminescent flashlights. The aptly named flashlight fish is a good example (Video clip 1). Bioluminescence can also serve as a lure to attract prey. The viperfish, Chauliodus sloani (Figure 1) has a luminescent lure on the end of a modified fin ray that it can arch forward in front of its mouth. In the dim depths all the prey sees is a glowing morsel. But when it strikes it is quickly impaled by the enormous fangs that give the viperfish its name (Figure 2). These fangs are so long that if they were inside its mouth the fish would impale its own brain.

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Marine bioluminescence
Why do so many animals in the open ocean make light?

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Fig. 1 Fig. 2
Bioluminescence can help attract a mate.
For example, while the bioluminescent cheek lights on the deep-sea loosejaw fish may serve to locate prey in the dark, they probably also function in mate selection, since the light organs of males (Figure 3) are much larger than those of females (Figure 4). The odd-looking jaw structure, from which the loosejaw gets its name, allows for an exceptionally wide gape to accommodate very large prey. A deep-sea dweller that is generally known only from dead specimens brought up in nets, it was an extremely rare occurrence to be able to observe this specimen alive. This fish was brought up from a depth of 600 m using a net with a thermally-insulted capture device that can be closed at depth. By keeping them cold animals that would normally be killed — literally cooked alive — in warm surface waters, survive for hours or even days in the lab. Because the body composition of this fish is 92% water, it was not killed by the enormous pressure differential, which would be lethal to any fish with a swimbladder (see box below).

Swimbladders
Many bony fish have a swimbladder or gas bladder that gives them neutral buoyancy. This saves the fish from having to expend energy to prevent itself from sinking. However, such a fish only has neutral buoyancy at one particular depth. If the fish rises above the level of neutral buoyancy the result can be disastrous. As the water pressure is reduced, the swimbladder expands and the fish gains increased lift — it must therefore keep swimming downwards or it will continue to rise. A deep-sea fish that is unable to loose air from its swimbladder will arrive at the surface with the expanded swimbladder protruding from its mouth or even ruptured.
Table 1
Bioluminescent creatures found in marine, terrestrial and freshwater environments. A more comprehensive list, using scientific nomenclature, may be found in Reference [1]. Phyla are in bold type. Links to Web sites with more information are in blue.

### MARINE

- **Bacteria**
- **Dinoflagellates**
- **Radiolarians**
- **Sponges**
- **Coelenterates**
  - Scyphozoa (Jellyfish);
  - Hydrozoa: Hydroids, Hydromedusae;
  - Siphonophores;
  - Anthozoa: Sea fans, Soft corals, Sea pens,
  - Sea pansies.
- **Ctenophores** (Comb jellies)
- **Nemertean**s (Ribbon worms)
- **Molluscs**
  - Sea slugs, Boring bivalves, Cuttlefish, Squid,
  - Vampire squid, Octopods
- **Annelids**
  - Polychaeta (Bristle worms), Parchment tube worms,
  - Scale worms, Fireworms
- **Arthropods**
  - Pycnogonids (Sea spiders), Copepods, Ostracods
  - (Sea fireflies), Malacostraca, Opossum shrimp,
  - Amphipods, Euphausiids (Krill ), Decapod shrimp
- **Bryozoa** (Sea mats)
- **Chaetognaths** (Arrow worms)
- **Echinoderm**s
  - Crinoids (Sea lilies), Holothurians (Sea cucumbers),
  - Asteroids (Starfish), Ophiuroids (Brittle stars)

### TERRESTRIAL

- **Hemichordates** (Acorn worms)
- **Chordates**
  - Tunicates: Sea squirts;
  - Pyrosomes (Fire cylinders); Larvaceans
- **Vertebrates**
  - Sharks, Anchoovies, Gulper eels, Spookfish,
  - Slickheads, Shining tube shoulders, Bristlemouths,
  - Hatchetfish, Viperfish, Dragonfish, Snaggletooth
  - fish, Loosejaws, Pearleye fish, Lantemfish, Morid
cod, Merluccid hake, Rat-tails, Midshipman fish,
  - Anglerfish, Pinecone fish, Flashlight fish, Ponyfish,
  - Drums

### FRESHWATER

- **Molluscs**
  - Limpet (*Latia*)

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**Fig. 5**

*The deep-sea shrimp, Acanthephyra purpurea, uses light to temporarily blind a predator, the lightfish, Gonostoma elongatum.*

3. **Bioluminescence can protect an animal from its predators.** For example, some animals, such as the deep-sea shrimp (Figure 5), use their bioluminescence to distract or blind a predator. In this case the shrimp actually vomits light into the face of its attacker and then back flips away into the darkness.

Other animals use their bioluminescence to ‘scream’ for help. Once an animal is caught in the clutches of a predator its only hope for escape may be to attract the attention of something bigger and nastier that may attack and eat whatever is eating it. Click on the image (Figure 6) to see the ‘scream’ of this jellyfish. This amazing light show is known as a ‘burglar alarm’ display.
Bioluminescence from the belly of the lanternfish, *Ceratoscopelus maderensis*.

*The deep-sea jellyfish, Atolla wyvillei.*

*The hatchetfish, Argyropelecus affinis.*

One of the multitude of lanternfish (Myctophids) that populate the twilight depths of the ocean. The jewel-like light organs on its belly and flanks are known as photophores.

Bioluminescence from the belly of the hatchetfish obliterates its silhouette. Light scattering underwater blurs the individual sources into one diffuse source that perfectly matches the colour and intensity of the sunlight filtering down from above.

*The benttooth bristlemouth, Cyclothone pallida.*

Bioluminescence from the belly of the lanternfish, *Ceratoscopelus maderensis*. 
Bioluminescence also functions as camouflage. In the twilight depths the silhouette of an animal seen against the dim blue light filtering down from above is an easy target. This is why many open ocean predators like the hatchetfish (Figure 7) have upturned eyes and an upturned mouth. But the hatchetfish is also prey to bigger fish swimming below it, so to make itself harder to see, it has a narrow silhouette and silver sides. It also emits bioluminescence from its belly that is a perfect match in colour and intensity to the sunlight filtering down from above (Figure 8). If a cloud goes over the sun, dimming the sunlight, the fish dims its bioluminescence so it continues to blend into the background. This trick, called counterillumination, is something that you need to see to believe. One testament to its effectiveness is the enormous numbers of animals that use it. Some of these include: the benttooth bristlemouth (Figure 9), which is the most common vertebrate on the planet; lantern fish (Figure 10); viperfish (Figure 1), scaly dragonfish (Figure 11); krill (Figure 12) and squid (Video clip 3).

Many animals use bioluminescence for more than one purpose. This blackdragon fish (*Melanostomias bartonbeani*) (Figure 13), for example, has a flashlight next to each eye that it can use to look for prey or signal mates, it has a chin barbel that it can use as a lure, it has light organs arrayed along its belly that it can use to hide its silhouette and it has luminous bodies embedded in the gelatinous dermis and between the fin rays that it can use for a burglar alarm display, which you can see if you click on the picture of the fish (Video clip 4).

Fig. 11
*The scaly dragonfish, Stomias brevibarbatus, produces bioluminescence from photophores arrayed along its belly and from a chin barbel that it uses as a lure.*

Fig. 12
*Like most euphausiids, Meganyctiphanes norvegica has photophores that it uses for counterillumination (lower image).*
How do they make light?

How do living creatures make light without burning up? They do it through a highly efficient chemical reaction involving an enzyme called luciferase and a substrate called luciferin. Different animals produce very different versions of these chemicals (Figure 14).

For example, firefly luciferin is assembled from the amino acids, tyrosine and cysteine, while luminescent bacteria use a reduced riboflavin phosphate (FMNH₂) and dinoflagellates use a tetrapyrol, which is related to chlorophyll. These very different chemistries are indicative of the fact that bioluminescence has evolved independently many different times during evolutionary history. In fact bioluminescence is a great example of convergent evolution, where similar characters evolve independently in response to similar selective forces. In the case of bioluminescence the selective pressure was based on the need to survive in dim light environments.

Besides many different chemicals, there are also many different ways of activating those chemicals. For example, in dinoflagellates the luciferin and luciferase are stored in organelles called scintillons and, when the cell’s membrane is stretched or distorted, hydrogen ions rush in triggering a flash. On the other hand in jellyfish the ion that triggers the flash is calcium rather than hydrogen. In fact calcium-regulated photoproteins (stable complexes of luciferin and luciferase) extracted from jellyfish have proven enormously valuable in research on the role of calcium as an intracellular messenger.

The scaleless dragonfish, Melanostomias bartonbeani, has an impressive arsenal of light organs, which are called into action when the fish is struggling in the clutches of a predator. Click on the image to see this fish swimming as seen under white light and then bioluminescing as seen with the lights out.

One thing all these different chemicals have in common is that they must react with oxygen to produce light. This oxidation reaction creates a molecule in an excited state. When the molecule returns to a lower energy level it gives up energy in the form of a photon of visible light.
One such photoprotein is aequorin, which was extracted from the jellyfish *Aequorea victoria*. Also extracted from this same jellyfish is the now more famous green fluorescent protein or GFP (Figure 15). GFP is an accessory protein that accepts energy from a bioluminescent reaction and re-emits it as light of a longer wavelength. This protein has proven very valuable to genetic engineers who use it as an assay for protein expression and function. By attaching the gene for GFP to other genes, they can tell when and where those genes are expressed by tracking when and where green fluorescence appears in the cell.

In bioluminescent bacteria light production is continuous, which is in contrast to most other luminous systems where light emission is discontinuous and regulated by neural or endocrine control. There are a few animals that have developed symbiotic relationships with bioluminescent bacteria. The flashlight fish seen in Video clip 1, for example, has a large light organ under each eye where bioluminescent bacteria grow in a nutrient-rich environment provided by the fish. The apparent flashing of these lights, seen in the video, is produced by a flap of skin that the fish slides over the light organ to block the bacterial light emission. Other animals that make use of bacterial symbionts include anglerfish that use luminescent lures packed with bioluminescent bacteria (Figure 16) and squid like the Hawaiian bobtail squid, *Euprymna scolopes* that use bacterial bioluminescence for counterillumination. Genes cloned from bioluminescent bacteria have proven useful to genetic engineers as reporter genes that can be attached to other genes and bioluminescent bacteria are also used in bioassays to test for pollutants and toxins.

**Fig. 15**
Green fluorescent protein (GFP) from the jellyfish *Aequorea victoria*. Data for this computer model was obtained from the Protein Data Bank, ID code 1EMB. See Reference [2].

**Fig. 16**
The anglerfish *Oneirodes* sp. has an elaborately shaped lure, called an esca, that is packed with bioluminescent bacteria.
Bioluminescent fact and fiction

There is a lot of misinformation about bioluminescence. Unfortunately many of these errors have been repeated so often they are beginning to be accepted as truth.

Bioluminescence is not the same as phosphorescence

Even though Steinbeck, Hemmingway and even Darwin referred to the “phosphorescence of the sea” this is a literary rather than a scientific description. Phosphorescence is the delayed emission of light from a source that has been excited by light. Examples include glow-in-the-dark paints and toys.

Bioluminescence is not the same as fluorescence

As with phosphorescence light emission is stimulated by light not by a chemical reaction. With fluorescence the excitation wavelength is always shorter, that is, higher energy, than the emission wavelength and emission ceases as soon as the excitation source is turned off. Some of this confusion may have arisen because some, but not all, luciferins are fluorescent and a few pass their excitation energy along to fluorescent proteins like GFP (Figure 15).

Bioluminescence is not the same as iridescence

The beautiful rainbow colours seen in the ctene rows of comb jellies (Figure 17) are often mistaken for bioluminescence. This misconception is exacerbated by the fact that bioluminescence in ctenophores frequently originates from along the ctene rows (Figure 18). However, as a general rule, if the illumination level is high enough to see iridescence, then it is probably too bright to see the bioluminescence.

All bioluminescence is not bacterial

This very common fallacy probably stems from the fact that most aquarium exhibits of bioluminescence include flashlight fish. The actual number of animals that use bacterial bioluminescence is small compared to the total numbers that synthesize their own light producing chemicals.

Not all comb jellies are bioluminescent

In nature there seems to be at least one exception to every rule. In this case the exception is Pleurobrachia.

Reports that the ‘Megamouth’ shark *Megachasma pelagios* is bioluminescent are probably erroneous. Descriptions of the upper jaw and palate as “remarkably iridescent” apparently were responsible for speculations of a luminous mouth for luring prey. However, there is no real evidence for bioluminescence in this shark and the fact that it is a filter-feeder makes the proposed use of bioluminescence to attract prey unlikely. There are, however, other sharks that are bioluminescent (see Table 1).

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*Fig. 17*  
Iridescence in ctenophores like this Euplokamis species is often mistaken for bioluminescence.

*Fig. 18*  
Bioluminescence in the ctenophore Euplokamis originates from the region of the comb rows.
References


Further reading


Video recording


Web sites

HBOI — More about bioluminescence

Marine bioluminescence page
[http://lifesci.ucsb.edu/~biolum/](http://lifesci.ucsb.edu/~biolum/)

Naval oceanographic office (NAVOCEANO)

Scripps bioluminescence page
[http://siobiolum.ucsd.edu/Biolum_intro.html](http://siobiolum.ucsd.edu/Biolum_intro.html)

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