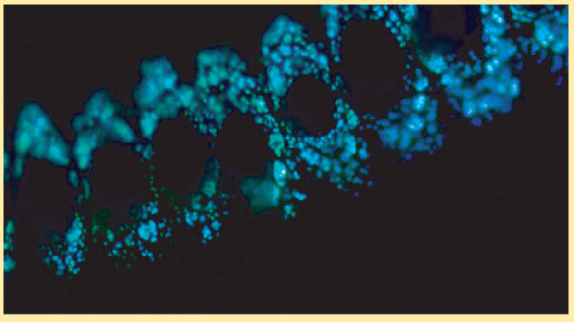
HOT TOPICS IN MARINE BIOLOGY 7.1

Bioluminescence, Night Vision, and Death in the Deep

Deep-sea organisms live mainly in the dark, lit very slightly from above and intermittently at depth by the many bioluminescent. Because of these poor light conditions, we expect that the detection of predators and prey will not be dependent upon vision. But, if so, why is bioluminescence so common? Why do fish have eyes? Why do midwater fish have such large mouths, as we see in anglerfishes and dragon fishes?

The wonder of deep midwater creatures was first appreciated mainly from those collected in nets that were brought to the surface. Grace Pickford, a great pioneer of deep-water biology, described in great detail the wondrous *Vampyroteuthis*, an animal that shares the features of both squids and octopus. She interpreted this correctly as evidence of the ancient ancestral position of this creature. It was not until many decades later that this animal was routinely seen from submersibles (**Box Figure 7.1**). *Vampyroteuthis* is luminescent on much of the body, including the tentacles. Deep-sea fish were also brought up, whose giant mouths and prominent teeth, depending on the species, gave us evidence of voracious predators.

But most of the deep's wonders, the gelatinous zooplankton, were rendered into mush by the time they came up in the nets of oceanographic vessels. These are the jellies, including true jellyfish, siphonophores, comb jellies, larvaceans, and salps. It took the direct observations from submersibles to appreciate their abundance and diversity, and especially their behavior.



BOX FIG. 7.1 The deep-sea *Vampyroteuthis*: (bottom) animal as seen from a submersible; (top) close-up of arm tips, showing bioluminescence. (Photos by Steve Haddock)

We still do not understand entirely the basis for this abundance and diversity. At bathyal depths, there are no actively growing phytoplankton populations; just a few dead and live cells drift downward. Usually, the dead particles are aggregated, and the aggregates, called **marine snow**, often have embedded microorganisms and smaller zooplankton. This may be the base of the deep-water food web, and these particles may be consumed by smaller zooplankton such as copepods. Larger gelatinous invertebrates and fishes may consume these smaller zooplankton and provide food for other larger fishes such as anglerfishes. Studies in the past 20 years have resulted in the seemingly endless discovery of new species. But the other amazing outcome is the very abundance of these deep-water forms. When you think of the volume of the deep-sea environment, you are looking at probably the largest marine community type on the planet, and yet we know so little about it. Gelatinous zooplankton are amazingly diverse in their morphology, ecology, and adaptations. Observations from submersibles, usually equipped with high-definition video, have captured their behavior and to some extent their distribution in the water column. Work by Bruce Robison (2004) of the Monterey Bay Aquarium Research Institute and colleagues has been especially important in bringing us a sense of the diversity and abundance of deep-water organisms and the dynamics of population change.

Early work showed that bathypelagic animals were rather sluggish and had reduced metabolic rates when compared to similar animals living in the upper parts of the water column (Childress, 1995). Cold temperature explains part of this, but also there probably is less food available and also less need to escape fast-swimming visual predators. Many deep-water plankton and nekton are poorly muscularized and seemingly adapted for low food supply. An excellent example is the bathypelagic doliolid salp *Pseudusa bostigrinus*, which is found in the eastern Pacific in depths of about 1,100–1,900 m. As mentioned in the text, salps are usually continually beating a tail that moves food particles through a "house." But deep-sea particle density is much lower, and this group has lost in evolution its mucus-filtering apparatus, found in shallow-water relatives. The deep-sea salp *P. bostigrinus* has evolved a form that more resembles a jellyfish that faces its mouth opening upward (**Box Figure 7.2**). By doing this, it can propel itself upward to capture zooplankton prey.

You could easily visualize the deep abyss as a slow-moving murder mystery where one false move leads to a shot in the dark, and death. One of the coolest defenses involves a number of nonbioluminescent worms, fishes, and comb jellies that roll into balls to resemble jellyfish, which are less attractive prey hiding in plain sight. Avoiding predators in midwater is a major challenge because you are so exposed. But the wide presence of bioluminescence illustrates a number of surprising strategies of deceit that help various species to escape or avoid predators. So many deep-sea zooplankton and swimming nekton are bioluminescent that the phenomenon immediately becomes a central point of the discussion in deep-sea biology.

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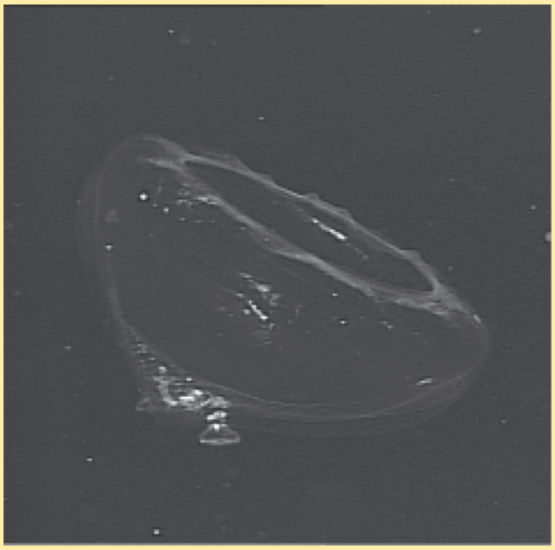
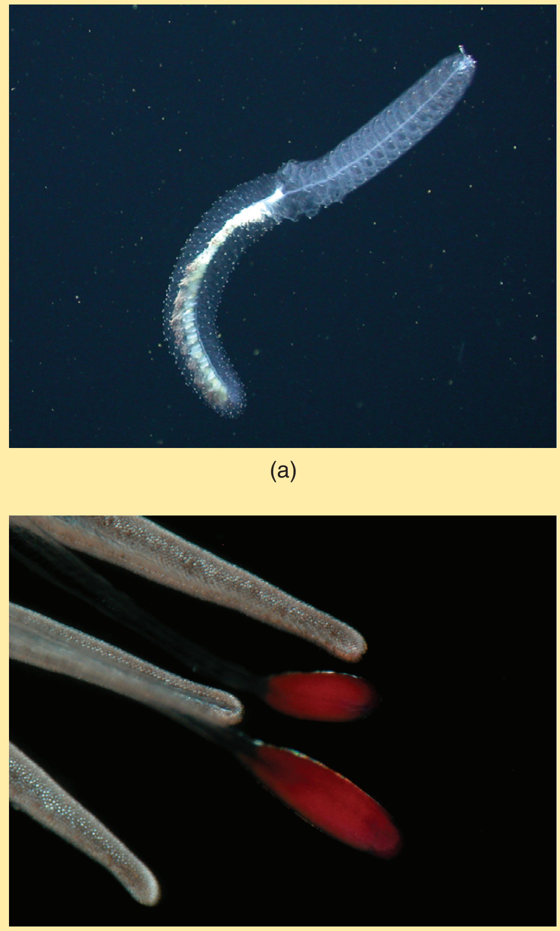


BOX FIG. 7.2 View from a submersible of the salp *Pseudusa bostigrinus*, which is modified for more infrequent meals of zooplankton in the deep sea. (From Robison et al., 2005)

Let's look again at *Vampyroteuthis*, which lives to depths of 1,200 m, where light is nearly absent. It is a sometime carnivore, but it tends to live in deep waters of low oxygen content and it has very weak muscles. It has two long filaments, related to the arms of squids, which allow it to capture particulate organic matter, the marine snow we mentioned earlier (Hoving and Robison, 2012). It can swim, but not with the sudden speed of a squid, which uses a form of jet propulsion (see Chapter 8). Although *Vampyroteuthis* can swim by flapping its fins, it is very much a sitting duck for predatory fish and diving mammals, especially those with good vision in low light. When approached, however, it uses a battery of flashes to momentarily deceive an approaching predator. It has luminescent organs at the tips of its eight arms and in more extreme situations will release a fluid loaded with luminescent particles. When touched, the animal flares its arms, which glow and dim in synchrony. With more intense stimuli, the arm tips are raised above and then release the fluid, which envelops the animal and serves as a disguising shroud (Robison et al., 2003).

An even more bizarre case is the benthopelagic sea cucumber *Enypniastes eximia*. Sea cucumbers normally live on the bottom, and this species does spend time feeding on soft sediment. But it spends a great deal of its time in the water column as a zooplankter. When a potential predator contacts this species, it sloughs off on its attacker some of its body surface, which is sticky and bioluminescent. The material slimes the predator with a glowing "paint," which now forces the predator to take evasive action from its own predators!

Nearly all bioluminescence is in the blue and blue-green part of the light spectrum. Light at these wavelengths travels a greater distance through the water column, and nearly all marine creatures detect light well in the blue end but are very poor at detecting red light, which is not prevalent in deep water. But there are some fascinating exceptions. Deep-sea fish in the family Malacosteidae, or loosejaws, have formidable teeth but also have distinct bioluminescent organs on the head beneath the eye that emit both green and red light. The red light is essentially invisible to other fish, unless perhaps they are only a few millimeters away. Loosejaws have a source



(a)

(b)

BOX FIG. 7.3 (a) The bathypelagic siphonophore *Erenna* sp.; (b) red lures at the tentacle tips. (Courtesy of Steve Haddock)

of red and infrared light that projects toward unsuspecting prey. But to have "night vision" you have to be able to detect the reflected light that returns to you. Calculations suggest that the retina of the loosejaw *Aristostomias tittmanni* can detect such light about 1 m away. One species of *Aristostomias* uses a retinal pigment that is very sensitive in the red end of the spectrum. Even more amazing is the detection system of the predatory deep-sea dragon fish *Malacosteus niger*. It uses a derivative of chlorophyll, which acts like an antenna, receiving the red light and then transferring the energy to more ordinary blue-green sensitive photopigments in the retina (Douglas et al., 1998). Imagine being a prey fish. You can be 1 m from your death, have eyes, and yet never see the final moment coming.

A remarkable instance of mimicry for the purpose of deploying a lure has been discovered. Steven Haddock investigated a deep-sea siphonophore that feeds only on fish and has a series of stalks on tentacles of feeding polyps that can glow red at the tips and contract rapidly (**Box Figure 7.3**). Haddock has concluded that this flickering makes the red tips resemble the hopping and sinking behavior that is typical of planktonic copepods (Haddock et al., 2005).

These and other fascinating natural history stories will soon be merged into more general ideas but we are only at the beginning of this exciting research program. ■