

expel internal organs through the anus or through a slit in the anterior end of the body wall. Reasons for evisceration are unknown and may include predator evasion or expulsion of parasites or accumulated wastes. Some species resorb internal organs during a dormant period, presumably to reduce metabolic expenditures, and then regenerate them again at the end of dormancy. Tropical species have Cuvierian tubules, which are expelled in defense and are sticky and entangle the would-be predator.

REPRODUCTION, ECOLOGY, AND BEHAVIOR

Most species of sea cucumber have separate sexes, broadcast spawning, external fertilization, and free-swimming larval stages (Fig. 2); however other reproductive and development modes also occur. Sea cucumbers are hosts for a variety of parasitic and commensal organisms that live inside or on the sea cucumber. Some species of sea cucumber are chemically defended as a deterrent to predation; however, such chemical defense does not prevent predation by sea stars, which are the sea cucumber's principal predators. An

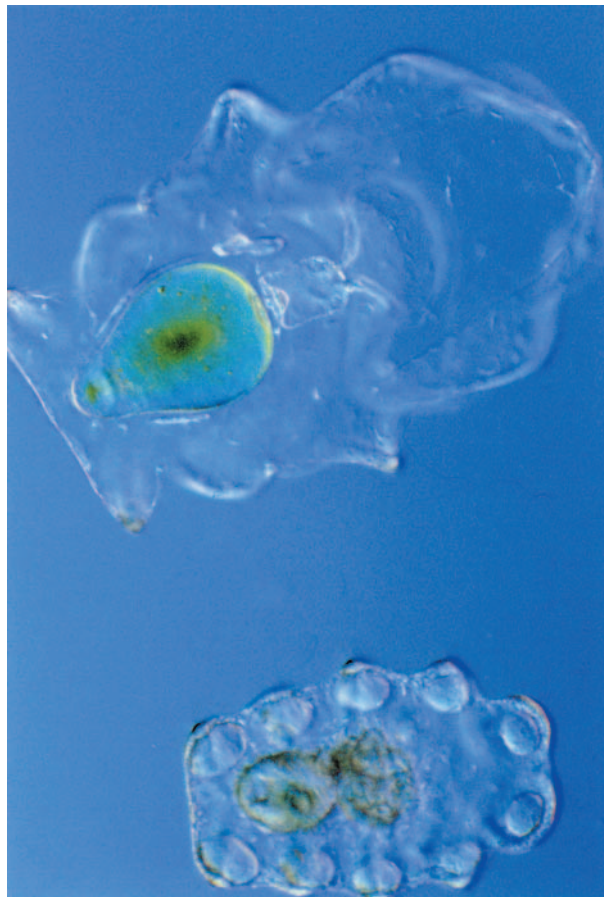


FIGURE 2 Sea cucumber auricularia (left) and doliolaria (right) larvae.
<AUG1> Photograph by the author.

individual deposit feeder can ingest and filter up to 45 kg of sediment a year, and as a result, large populations play an important role in recycling nutrients and cleaning the sea floor. The 1500 living species of sea cucumber are distributed worldwide and are found from the intertidal to the deepest parts of the oceans.

ECONOMIC AND MEDICINAL IMPORTANCE

Parastichopus californicus and *P. parvimensis* are commercially harvested on the west coast of the United States, dried, and sold for consumption as *trepang* or *beche-de-mer* in Asian markets. In the United States, sea cucumber is sold as a health supplement, primarily as a source of chondroitins and anti-inflammatory compounds for treating arthritis. Sea cucumber catch connective tissue is studied for medicinal purposes because of its similarity to human tendons and ligaments. Catch connective tissue collagen fibers can bond and break to make the tissue rigid or fluid, therefore, sea cucumbers may hold the key to repairs for injured tendons and ligaments, such as the anterior cruciate ligament (in the human knee) and the Achilles tendon.

SEE ALSO THE FOLLOWING ARTICLES

Brittle Stars / Echinoderms / Food Uses, Modern / Materials, Biological / Sea Stars / Sea Urchins

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SEAGRASSES

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Seagrasses are rooted vascular plants of terrestrial origin that have successfully returned to the sea with several adaptations that allow them to live submerged in the

ocean. These plants occupy sandy, muddy, and rocky substrates in every sea in the world and provide habitat for entire communities of associated species. Seagrasses play an important role in the geomorphology and ecology of coastal ecosystems by stabilizing sediments, recycling nutrients, and forming the base of oceanic detrital food webs. Despite their great importance, they are currently facing many natural and anthropogenic threats from coastal development, pollution, and climate change.

SEAGRASS BIOLOGY

Although the vast majority of marine intertidal plants are algae, there is one large group of true flowering plants (angiosperms) that have evolved to live in the ocean. These are seagrasses. *Seagrass* is the common name for a large group of flowering plants that have evolved from terrestrial plants and have become specialized to live in the marine environment. Seagrasses are not true grasses and are more closely related to water lilies and terrestrial plants such as lilies. Seagrasses are commonly found on tidal mudflats in estuaries, on shallow sandy areas close to the coast, in coral reef lagoons, and in shallow rocky intertidal areas; they can grow as deep as 60 meters.

Like terrestrial plants, seagrasses harvest energy from light to carry out photosynthesis and have leaves, conducting tissues, and roots (Fig. 1). Unlike terrestrial plants, however, seagrasses do not possess the strong, supportive stems and trunks required to overcome the force of gravity on land. Rather, the natural buoyancy of water supports seagrass leaves, enabling them to remain flexible



FIGURE 1 Anatomy of a seagrass plant, showing roots, rhizomes and leaves. Illustration by Jessica Altstatt.

when exposed to waves and currents. Gas vacuoles keep the leaves erect and maximize light interception when submerged. Seagrasses grow like backyard grasses with roots and rhizomes (horizontal underground stems that form extensive networks below the substrate surface). The roots and rhizomes of seagrasses are often buried in sand or mud, or directly attached to rock, and they serve to anchor the grasses and absorb nutrients. Seagrasses can propagate vegetatively through growth and branching of this rhizome. Along the rhizome at intervals are erect shoots, which bear the leaves and leaf sheaths. The leaves may vary in length from a few millimeters to several meters. Leaves, usually green, are produced on vertical branches and also absorb nutrients. The stems and leaves of seagrasses contain veins and air channels so that they can carry fluid and absorb gases. Seagrasses rely on light to convert carbon dioxide into oxygen via photosynthesis. The oxygen is then available for use by other living organisms. Seagrasses have thin, permeable cell walls to enhance external gas exchange, and gas vacuoles and aerenchyma tissue to facilitate internal gas exchange. Aerenchyma tissue forms gas conduits that run from the leaves to the roots and allows the passage of photosynthetically produced oxygen to roots and rhizomes.

Marine algae (commonly referred to as seaweeds) are plants that also colonized the sea and may be confused with seagrasses; however, they are more primitive than seagrasses. In contrast to seagrasses, seaweeds do not have a true root system (they have holdfasts) and do not have veins that carry molecules around the plant. Seaweeds have spores and do not flower or produce fruit, while seagrasses produce flowers, seeds, and fruit.

Assuming that the seagrasses gradually evolved from freshwater plants, one of their biggest hurdles to overcome was adapting to saltwater. Like celery placed in saltwater, the roots of most plants rapidly lose water if they are immersed in seawater. Salt-loving plants (halophytes), such as the seagrasses and mangroves, generally have a lower concentration of water molecules (lower water potential) in their root cells, so they can take in water. They maintain lower water potentials in their roots by having higher internal salt concentrations than seawater and by losing water at the leaf surface. Since high internal salt concentrations can be lethal to plant cells, some halophytes can excrete excess salt through their leaves and stems.

HABITAT AND DISTRIBUTION

Seagrass beds are found in the shallow coastal waters of every sea in the world. Worldwide, there are about 12 major divisions, consisting of approximately 60 species

of seagrasses. They are mainly found in bays, estuaries, and coastal waters from the mid-intertidal (shallow) region down to depths of 50 or 60 meters. Seagrass distributions are extremely sensitive to variation in light and cannot live at depths lower than where photosynthetic benefits outweigh respiratory costs. Because light transmission in water is a function of water clarity, turbidity, and sediment load, seagrass distributions are strongly affected by eutrophication and other anthropogenic effects that influence water clarity. For example, seagrass beds in Chesapeake Bay historically occurred at depths of over 10 meters but are restricted today to depths of less than 1 meter because of reductions in water clarity, and therefore in light transmission, by organic fertilizer runoff and eutrophication.

Seagrasses range from the straplike blades of eelgrass (*Zostera caulescens*) in the Sea of Japan, at more than 4 meters long, to the tiny (2–3-centimeter), rounded leaves of sea vines (e.g., *Halophila decipiens*) in the deep tropical waters of Brazil. Vast underwater meadows of seagrass skirt the coasts of Australia, Alaska, southern Europe, India, eastern Africa, the islands of the Caribbean, and other places around the globe. They provide habitat for fish and shellfish and nursery areas to the larger ocean, and they perform important physical functions of filtering coastal waters, dissipating wave energy, and anchoring sediments. Seagrasses inhabit all types of substrates, from mud to rock. The most extensive seagrass beds occur on soft substrates like sand and mud. Seagrasses occupy coastal waters from tropical to temperate regions. The number of species is greater in the tropics than in the temperate zones, and only two species, *Halophila ovalis* and *Syringodium isoetifolium*, occur in both regions.

North America is home to several different species of seagrasses. *Zostera marina* (commonly known as eelgrass) is the dominant seagrass of temperate latitudes along both the Atlantic and Pacific coasts. It grows in muddy substrates along wave-protected shallow-water bays and estuaries. Along the Atlantic coast, eelgrass is replaced by two other species of seagrasses in the warmer waters from the Carolinas to the Caribbean. *Thalassia testudininalis* (commonly known as turtlegrass) and *Halodule wrightii* (commonly known as shoalgrass) are the dominant seagrasses in this region. These species are ecologically important as nursery habitat for fishes and an important food source for endangered species such as manatees and sea turtles. Along the Pacific coast, wave-swept rocky intertidal habitats are uniquely occupied by several species of *Phyllospadix* (commonly known as surfgrass). Surfgrass roots and rhizomes can attach directly to rock, and surfgrass beds



FIGURE 2 Intertidal surfgrass bed, *Phyllospadix torreyi*. Photograph by the author.

can occupy vast amounts of space in the low intertidal and shallow subtidal regions of rocky shorelines (Fig. 2).

REPRODUCTION

Seagrasses can reproduce through sexual or asexual methods. Seagrasses, which spend most, if not all, of their time submerged, have developed methods of underwater flowering and pollination for sexual reproduction. In sexual reproduction, the plants produce flowers, and water carries pollen from the male flower to the ovary of the female flower. Most, but not all, seagrass species produce flowers of a single sex on each individual, so there are separate male and female plants. The resulting fruit are often carried some distance from the parent plant before the seeds are released. In some seagrasses, such as surfgrass, the seeds (Fig. 3) have small hooks and barbs (like an anchor) and are specially designed to become entrapped in bushy algal species where they can germinate, produce roots, attach to the rock, and grow. Flowering is seasonal in most seagrasses; a few species complete their life cycle within one year and are known as



FIGURE 3 Seed of *Phyllospadix torreyi*. Photograph by Todd Huspeni.

annuals. These annuals produce seeds that can remain dormant in large “seed banks” for several months. Seed banks ensure that the species can survive until conditions return to stimulate the seeds to germinate.

Seagrasses can also grow by asexual (or vegetative) reproduction. New “plants” arise without flowering or setting seed. As mentioned previously, all seagrasses have horizontal underground stems called rhizomes. Seagrasses grow vegetatively by extending and branching their rhizomes in the same way that grass in a lawn grows. This allows significant areas of seagrass meadow to form from only a few shoots. In this way, seagrasses can recover after being damaged by grazers such as dugongs or disturbed by storms. The growth of seagrass after disturbance is critical to their survival. If all plants of a meadow are lost, a seagrass meadow needs seeds available or vegetative shoots translocated from a nearby meadow before it can recover. The ability of seagrass meadows to recover depends on the species of seagrass.

SEAGRASS ECOLOGY

Seagrass communities are highly productive and dynamic ecosystems. They provide habitats and nursery grounds for many marine animals and act to stabilize substrates and recycle nutrients. Seagrass communities may vary from a few plants or clumps of a single species to extensive single-species or multispecies meadows covering large areas of the bottom. The rhizomes and roots of the grasses bind sediments on the bottom, where nutrients are recycled by microorganisms back into the marine ecosystem. The leaves of the grasses slow water flow, allowing suspended material to settle on the bottom. This increases the amount of light reaching the seagrass bed and creates a calm habitat for many species.

Seagrasses perform a variety of functions within ecosystems and have both economic and ecological value. The high level of productivity, structural complexity, and biodiversity in seagrass beds has led some researchers to describe seagrass communities as the marine equivalent of tropical rainforests. Although nutrient cycling and primary production in seagrasses tends to be seasonal, annual production in seagrass communities rivals or exceeds that of terrestrially cultivated areas. Within seagrass communities, a single acre of seagrass can produce over 10 tons of leaves per year. This vast biomass provides food, habitat, and nursery areas for a myriad of adult and juvenile vertebrates and invertebrates. Further, a single acre of seagrass may support as many as 40,000 fish and 50 million small invertebrates. Because seagrasses support such high biodiversity, and because of their sensitivity to

changes in water quality, they have become recognized as important indicator species that reflect the overall health of coastal ecosystems.

Seagrass ecosystems provide habitats for a wide variety of marine organisms, both plant and animal; these include meiofauna and flora, benthic flora and fauna, epiphytic organisms, plankton and fish, not to mention microbial and parasitic organisms. The relatively high rate of primary production of seagrasses drives detritus-based food chains, which help to support many of these organisms. Birds, dugongs, and turtles also directly consume seagrasses. An adult green turtle eats about two kilograms of seagrass a day, whereas an adult dugong eats about 28 kilograms a day. As habitat, seagrasses offer food, shelter, and essential nursery areas to commercial and recreational fishery species and to the countless invertebrates that are produced within, or migrate to, seagrasses. The complexity of seagrass habitat is increased when several species of seagrasses grow together, their leaves concealing juvenile fish, smaller finfish, and benthic invertebrates such as crustaceans, bivalves, echinoderms, and other groups. Juvenile stages of many fish species spend their early days in the relative safety and protection of seagrasses. Seagrass meadows also help dampen the effects of strong currents, providing protection to fish and invertebrates, while also preventing the scouring of bottom areas. Additionally, seagrasses provide both habitat and protection to the infaunal organisms living within the substratum as seagrass rhizomes intermingle to form dense networks of underground runners that deter predators from digging infaunal prey from the substratum.

To appreciate the ecological importance of seagrasses, consider the sudden disappearance of eelgrass beds along the Atlantic coast during the 1930s. An epidemic infestation of the parasitic slime fungus (*Labyrinthula*), called wasting disease, literally destroyed the rich eelgrass meadows; the results were catastrophic. Populations of cod, shellfish, scallops, and crabs were greatly diminished, and the oyster industry was ruined. There was also a serious decline in overwintering populations of Atlantic brant geese. Areas formerly covered by dense growths of eelgrass were completely devastated, and beaches, which had been protected from heavy wave action, were now exposed to storms. Without the stabilizing effects of eelgrass rhizomes, silt spread over gravel bottoms used by smelt and other fish for spawning. This resulted in a decline in waterfowl populations that fed on the fish. Without the filtering action of eelgrass beds, sewage effluent from rivers caused further water pollution, thus inhibiting the recovery of eelgrass.

THREATS TO SEAGRASS ECOSYSTEMS

As humans have encroached on the marine environment, there have been some dramatic effects on coastal ecosystems. Because of the important structural and functional role of seagrass communities, significant disturbances to seagrass beds are likely to have significant impacts on the associated ecosystem. Many recent examples exist of extensive damage done to marine and estuarine habitats through the inadvertent destruction of seagrass communities. The loss of a number of important seagrass habitats has resulted in extensive studies of some seagrass communities and an increasing awareness of the role these plants play in our coastal marine environment. Recently a number of attempts to transplant (Fig. 4) and artificially restore seagrasses have been developed, and this work continues at many research centers around the world.



FIGURE 4 Divers transplanting eelgrass in a restoration project. Photograph by Carl Gwinn.

Seagrasses are subject to many threats, both anthropogenic and natural. The effects of many of these stresses have on seagrasses is dependent on both the nature and severity of the particular environmental challenge. Generally, if only leaves and above-ground vegetation are harmed, seagrasses are generally able to recover from damage within a few weeks; however, when damage is done to roots and rhizomes, the ability of the plant to produce new growth is severely impacted, and plants may never be able to recover.

Runoff of nutrients and sediments from human activities on land has major impacts in the coastal regions where seagrasses thrive; these indirect human impacts, while difficult to measure, are probably the greatest threat to seagrasses worldwide. Both nutrient and sediment loading affect water clarity; seagrasses' relatively high light requirements make them vulnerable to decreases in light penetration of coastal waters. Direct harm to seagrass

beds occurs from boating, land reclamation, and other construction in the coastal zone, dredge-and-fill activities, and destructive fisheries practices. Human-induced global climate change may well impact seagrass distribution as sea level rises and severe storms occur more frequently.

Threats to seagrasses can originate long distances from the coast. Coastal agriculture in upper catchments may add to sediment and herbicide loads in runoff from the land, which has the potential to destroy large areas of seagrass. Global climate change may also threaten seagrass communities. Climate change is predicted to raise sea levels, concentrations of carbon dioxide in seawater, and seawater temperatures. Rising sea levels could increase the distribution of seagrass because more land will be covered by seawater. However, rising sea levels are likely to destabilize the marine environment and cause seagrass losses. Higher concentrations of carbon dioxide in seawater could increase the area of seagrass, because more carbon will be available for growth and seagrasses could increase their photosynthetic rates. Rising sea temperatures could cause burning or death of seagrasses in some places where they are close to their thermal limit.

SEE ALSO THE FOLLOWING ARTICLES

Algae / Ecosystem Changes, Natural vs. Anthropogenic / Habitat Restoration / Light, Effects of / Nutrients / Sea-Level Change, Effects on Coastlines

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SEA LEVEL CHANGE, EFFECTS ON COASTLINES

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Sea level, the recorded height of the sea surface, can vary across a broad range of spatial and temporal scales as a result of planetary motions, glacial cycles, and tectonics.