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Northeastern Regional Aquaculture Center

University of Maryland, 2113 Animal Science Building
College Park, Maryland 20742-2317
Telephone: 301-405-6085, FAX: 301-314-9412
E-mail: ssadams@umd.edu Web: http://www.nrac.umd.edu

Biology of the Bay Scallop

Dale Leavitt, Roger Williams University, RI
Rick Karney and *Amandine Surier,* Martha's Vineyard Shellfish Group, Inc.

Introduction

The bay scallop is a unique representative within the family of commercially important bivalve mollusks. It is one of eight species of scallops commercially harvested and one of only three scallop species cultured beyond a research stage in the United States.

Taxonomically, the genus contains three subspecies and have been found from Nova Scotia (Canada) to Colombia (Central America); however, the range is generally considered to extend from Cape Cod (Massachusetts) south along the entire Atlantic coast and into the Gulf of Mexico through Texas. In recent history, there have been no scallops in South Carolina, Georgia or eastern Florida. The bay scallop has also been introduced to China.

Anatomy

Shell: As a member of the Phylum Mollusca and the Class Bivalvia, the bay scallop possesses two shells, defined by a round outline with ribs (or plicae) radiating out from a winged or "eared" umbo. As the scallop grows, it lays down distinct growth lines as concentric circles around the perimeter of the shell. Slower growth during the winter months concentrates the lines in a specific winter "check" mark, or annulus. Although this check mark is sometimes used as a harvest management tool, any disruption in feeding, such as rough handling, might result in the formation of aberrant non-annual shell checks.

Although both valves are equal in length and width, the right or bottom valve is slightly more convex than the left or top valve. Shell coloration is highly variable (Figure 1). As in finfish, the left or upper shell colors provide camouflage while the bottom (right) shell usually is much lighter (white or yellow) and lacks ancillary markings. The coloration of the top valve is most often

Figure 1. Shell coloration is highly variable.

dark grey, black or brown. White-striped, orange, yellow and pink/red shell phenotypes also occur naturally. These rare color morphs have been increased in hatchery strains to improve the appearance of scallops marketed in the shell.

Mantle: The mantle consists of three folds, each serving a separate function. The first fold lies immediately interior to the shell and is responsible for the synthesis of the shell along the thickened outside margin. Attached next is the sensory fold with its unique tactile organs (tentacles) and eyes (ocelli) (Figure 2). The mantle and guard tentacles are assumed to have tactile and chemosensory functions. The eyes are light and motion-sensing organs interspersed between the tentacles. They are bright blue to brown and their structure is comparable to that of higher animals. They serve as another means to monitor the surrounding environment and detect predators.

Figure 2. Unique tentacles and eyes characterize the scallop.

The third fold is the velar fold, a muscular flap that plays an important role in swimming. Acting as a flapper valve, it extends to seal the valve margins. When the valves are forcefully closed, the water is ejected along the areas adjacent to the hinge, propelling the bay scallop forward.

Musculature: The anterior adductor muscle, common in most bivalves, is absent in the adult bay scallop. The posterior adductor muscle is overdeveloped and the primary means for the scallop to close its shell (Figure 3).

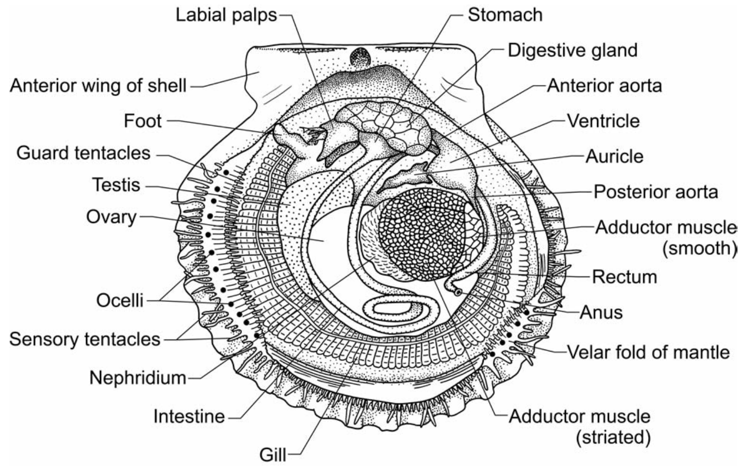

Figure 3. Diagram of the internal structure of a bay scallop with the right valve removed (redrawn by Virge Kask from Pierce 1950).

In the United States, only the adductor muscle is consumed and has commercial value. In other markets, the scallop in consumed "roe on" (muscle and gonad) or whole (muscle, gonad and viscera).

Gills: Respiration and feeding in the bay scallop are the function of four plate-like gills located as pairs on each side of the visceral mass (Figure 3 and 6). Water flows through the scallop mantle cavity and across the gill plates, driven by the synchronous beating of ciliated regions on both the ventral mantle surface and the gill filaments. Because the bay scallop mantle has no specialized fused siphon regions, the inhalant current flows in across the circumference of the shell margin while the exhalant current flows out of a narrow post-dorsal region of the shell.

Filtration and Digestion: In addition to oxygen, the cilia-driven water delivers food particles to the gill surface. The particles are filtered and sorted through the combined action of finely spaced cilia and mucus, and moved into the mouth. The food is digested through the gastrointestinal tract, a continuous passage consisting of the esophagus, stomach, intestine, rectum and anus (Figure 3). Other particles are rejected as pseudofeces and flushed into the excurrent flow.

Foot: The foot, although useless to adult scallops, is used by juveniles to reach and settle in their preferred habitat after metamorphosis. It is used for crawling and manipulating or attaching threads secreted by the byssal gland located at its base.

Reproductive System: The bay scallop is a simultaneous functional hermaphrodite which means that adults can release sperm and eggs in the same spawning event. The distinct crescent-shaped gonad lies antero-ventral to the adductor muscle and over the visceral mass. As the gonad matures, it becomes plump and its outer black membrane disappears to reveal two distinct brightly colored areas. The white to cream-colored area starting at the base of the gonad and running along its exterior edge is the male testis.

The female ovary is generally a larger portion of the total gonad and can be red, pink or orange when ripe (Figure 4). Upon spawning, the gonad empties gametes into the excurrent side of the mantle cavity. After spawning, the gonad shrinks and the colors become dull. Given the ability to pry open the valves of a live scallop and view the gonad, it is relatively easy to assess the reproductive condition and degree of ripeness of the scallop nondestructively.

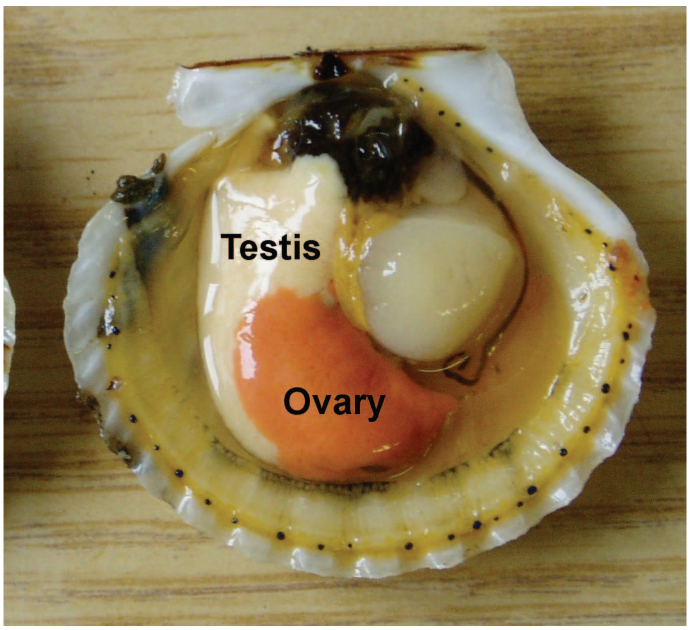

Figure 4. Anatomy of a ripe bay scallop.

On average, the bay scallop is reproductively mature by the beginning of the second growth season (1 year old) at a size of 50-60mm. Given that the total life expectancy of the bay scallop is 12 months to 2 years, an individual scallop normally has one opportunity to reproduce during its life span. Under some circumstances, bay scallops may live long enough to spawn a second time, although such scallops are a small component of the year class.

Being a simultaneously functional hermaphrodite, the bay can self fertilize generally resulting in low to no survival. To minimize self-fertilization, the bay scallop discharges sperm and eggs at different times within a single spawning event, usually starting with sperm then switching to eggs although it can sometimes switch back and forth between sexual products.

Reproduction

The natural spawning cycle of the bay scallop varies with the environmental conditions associated with the geographic distribution of the species. In the northeast, the majority of scallops ripen in May and spawn in June, with most of the population totally expending their gametes by the end of July. In the southeast, the spawning season is later, ranging from July-August to September-November. The difference is attributed to differing temperature thresholds for the initiation of gonad development and spawning. Multiple spawning peaks are not uncommon in a given year.

Larval Stage

Under optimal conditions, the bay scallop develops from fertile egg to post-set spat in 10 to 14 days (Figure 5). Overall, the fertile egg (50-60 μm in diameter) begins cleavage 40 to 50 minutes after fertilization.

The ciliated blastula forms within 5 hours and invaginates to a gastrula within 9-10 hours. A trochophore, with its distinctive apical tuft of cilia, is swimming in the water column within 12 to 24 hours.

The D-stage, or straight-hinge veliger (75-100 μm), develops within 17 to 48 hours with an average time of 22 hours at 23^{o} C. The veliger acquires its name from the presence of the velum, its swimming and feeding organ. It is the first feeding stage as well as the first with paired valves. Shell formation in D-stage larvae progresses from the early prodissoconch I when the valves are first laid down to the prodissoconch II stage where concentric growth rings in the shell can be observed as the larvae begin to grow.

In the hatchery, mortality is generally high until the prodissoconch II stage, then drops through the remainder of the larval rearing period.

As the shell grows, the umbo becomes more pronounced and overgrows the straight-hinge morphology. It is during the umbonated stage that the balance organ is first noted. Approximately 10 days post-fertilization, an eyespot forms within the balance organ signaling the onset of metamorphosis. The foot appears along with the byssal organ which will allow the competent larvae to select and attach to the appropriate substrate. At this point, the pediveliger (175-200 μm) is alternately crawling and swimming as it begins to investigate substrate for settlement. This stage can last from hours to days depending on the rearing conditions and the availability of adequate substrate. After settlement, the gills form (Figure 6) and a pair of statocysts develop. The velum is resorbed although the scallop can still swim through actions of the foot and, later, via valve clapping.

Behavior

Mobility: The most distinguishing character of juvenile and adult scallops is their ability to move more rapidly and over longer distances than other bivalves. The scallop's movements are achieved with rapid flushing of the water from its mantle cavity. These behaviors are termed coughing, jumping and swimming. The direction and distribution of the expelled water is controlled to some degree by the configuration of the mantle. Bay scallop swimming behavior results from a variety of stimuli, primarily population density and predator exposure. When juveniles are grown in raceways or floating cages, swimming activity increases with stocking density and is used as a visual clue that the scallops are overcrowded. Scallops will also swim towards preferred habitat such as seagrass beds when released within visual distance of the structure.

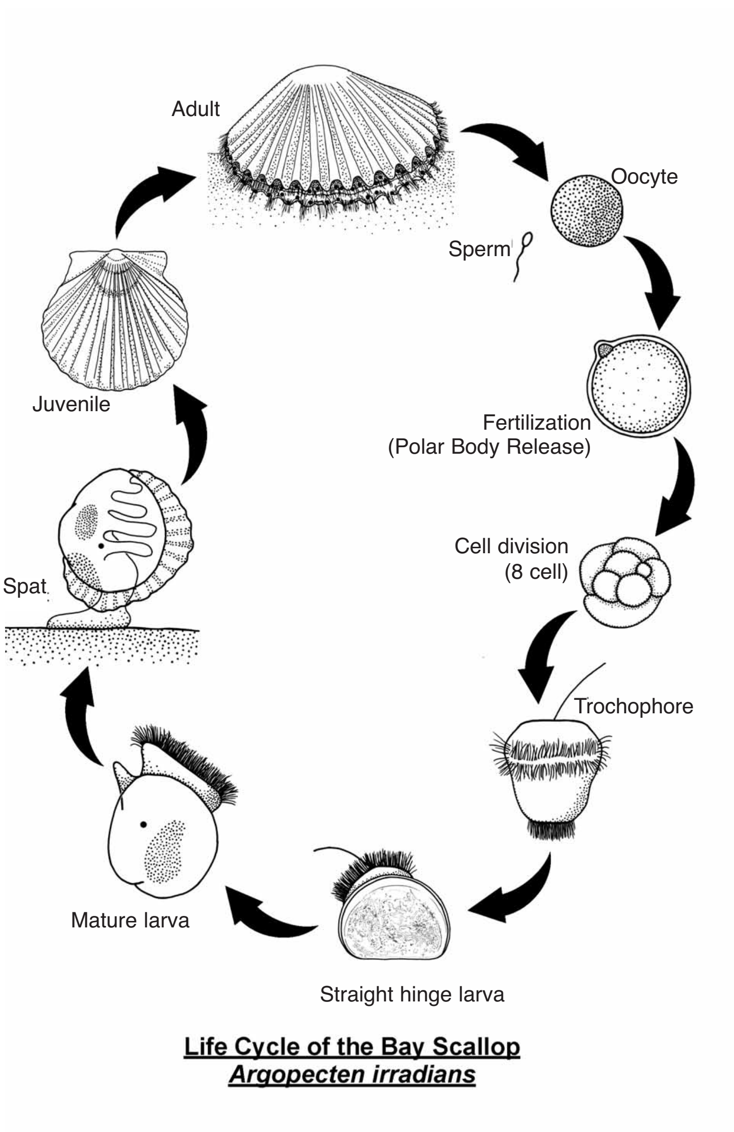

Figure 5. Developmental stages in the life cycle of the bay scallop. Illustration by Virge Kask, UConn.

Figure 6. After settlement, the gills form.

Environmental Conditions

Water Quality: The bay scallop occurs in an estuarine environment and thus tolerates fairly large ranges of water quality conditions, as outlined in Table 1.

Feeding: The normal feeding position of an adult scallop is to rest on the bottom on the right shell with a shell gape of approximately 20 degrees. Feeding depends on a directed flow of water across its gills, driven by the gill and mantle cilia and channeled in specific trajectories from a non-localized inhalant region to a more localized exhalant region. Given the lack of a fused inhalant or exhalant siphon, the efficiency of feeding is susceptible to exterior water flow characteristics. Scallops held experimentally with their inhalant region upstream show increased growth over those animals held with their inhalant region downstream.

In their natural habitat, the primary food resources for the bay scallop include phytoplankton, benthic diatoms, bacteria and organic aggregates formed by macrophytic detritus. In general, adult bay scallops filter particles in the range of 5 to 12 µm by trapping them in mucus in the interfilamentary spaces of the gills although very large particles (950 µm) have also been observed in their stomachs.

Table 1: Water quality conditions for the bay scallop.

Parameter	Value
Temperature	
Egg Maturation	>20 ^{O}C
Trochophore	22 – 28 ^{O}C
Larvae	19 – 28 ^{O}C
Metamorphosis	16 - 32 ^{O}C
Juvenile growth (optimal)	22 ^{O}C
Adult	-6 - 35 ^{O}C
Salinity	
Trochophore	>22.5 psu
Larvae	25 to 32 psu
Juvenile	19 to 34 psu
Adult	12 to 35 psu
Dissolved Oxygen	
Larvae	>3.64 mg/L
Adult	>1.5 mg/L
pH	
Adult (tolerance)	7.0 to 8.6
Adult (optimal)	7.7 to 8.2
Ammonia (96 h LC_{50})	
48-h veligers (23•C & 32psu	6.33 mg NH_3/L
D-shaped veliger (110mm)	7.84 mg NH_3/L
Umbonated veliger	5.25 mg NH_3/L
Adult	<0.15 mg NH_3/L
Turbidity	
Adult	<500ppm
Food Concentration	
Optimal	0.94 to 9.66 mg dry weight/L

Ultimately, the absolute concentration (density) and size of food particles available to the scallop are the most important determinants of growth. The bay scallop can adapt to reduced particle concentrations by increasing filtration rate and particle retention efficiency to maintain feeding at a relatively constant rate.

Although food limitation can result in reduced growth in high-density standing stocks during the warmer months, it is generally not a limiting factor in wild scallop populations.

Habitat: The bay scallop has very specific habitat preferences. At metamorphosis and settlement, it attaches itself by byssal threads to three-dimensional structures such as the upright stems of vascular plants, macroalgae, hydroids, or even, concrete blocks (Figure 7).

Figure 7. Bay scallops attach themselves to burlap threads.

Eelgrass beds (Figure 8) are ideal habitat for bay scallops as they provide substrate and slower flow fields within which the larvae can attach, positively enhancing recruitment. This could explain why the bay scallop population declined in association with the large-scale loss of the eelgrass *Zostera marina* in the 1930s. Although eelgrass beds are the habitat of choice throughout the northern end of the range of the bay scallop, many seagrass species as well as selected species of macroalgae may also serve as adequate habitat. On the other hand, large amounts of macroalgae may be detrimental to bay scallop populations due to the risk of anoxia occurring under the algal mat and bay scallops have been observed moving away from them.

Figure 8. Juvenile scallops in eelgrass bed, Oak Bluffs, MA.

Overall, eelgrass beds greatly enhance juvenile bay scallop growth compared to barren bottom. Seagrass beds also provide a refuge against predation. Sight-feeding birds are less able to prey on bay scallops within the cover of a seagrass bed while many benthic predators are avoided because scallops attached to grasses are elevated off the bottom. Although scallops retain the ability to attach via byssal threads throughout their life, their ability to attach in the seagrass canopy is inversely proportional to their size. More than 95% of post-settlement bay scallops are attached until they are about 11 mm in shell depth. By the time they grow to 31 mm, 100% are on the bottom as they become too heavy for the byssus attachment to hold.

Genetics: The bay scallop has a diploid complement of 32 chromosomes (a haploid complement of 16) that differs from other Pectinid species investigated.

Because scallops can self-fertilize, and develop rapidly from fertilized egg to reproductive adult (less than 2 years), they are a good candidate for the development of improved selected genetic lines.

Mapping and manipulation of bay scallop genetic makeup has been applied to a variety of projects including:

- elucidation of geographical distribution of sub-species;
- identification of bay scallop larvae in the planktonic community;
- evaluation of success of restoration/restocking efforts;
- improvement of performance of selected lines for aquaculture; and
- induction of triploidy and attempts at production of a tetraploid broodstock.

Risk

Predation: Predation is the primary mechanism by which bay scallop populations are structured in the wild. Bay scallops are particularly susceptible to predation because of their epifaunal existence, the brittleness of their shell and their inability to completely close their valves. Their defense mechanisms include positioning away from the predators, swimming and rapid growth. Three phases of bay scallop life, in relation to its ability to withstand predation pressure, have been described:

1. an up-crawling behavior stage in plicated juveniles up to 20 mm, (spatial refuge)
2. an increasing ability to escape predation through swimming as they lose the ability to elevate (between 11 and 30 mm shell depth),
3. a size threshold against predation as they exceed the 35-40 mm shell depth (size refuge).

Predation pressure varies with predator type, scallop growth stage, geographical location, water depth, time of year, and habitat type. The primary predators of the bay scallop are sea stars and crustaceans, including most of the estuarine decapod crabs, although the predation pressure from crustaceans usually drops to zero in the winter months.

The polychaete worm *Polydora* sp. is a significant predator on larval and early post-set scallops. The free-swimming larval stages of *Polydora sp*. feed on larval bay scallops and can have devastating consequences in a hatchery. As the scallop grows, the metamorphosing worm larvae can burrow into the shell matrix and form a tube and cavity (commonly referred to as a mud blister), resulting in breaks, hinge and articulation failure, exposing the bay scallop to invasion by a variety of organisms.

Diseases & Parasites: Few scallop diseases were recognized prior to the advent of bay scallop aquaculture. The dense, monoculture conditions inherent in artificial propagation provided conditions for both the proliferation and the identification of a variety of pathological agents.

Hatchery cultures are susceptible to three bacterial diseases: bacterial swarming, bacillary necrosis and vibriosis. These diseases occur when naturally occurring, pathogenic, gram negative bacteria, primarily *Pseudomonas* sp. and *Vibrio* sp. are allowed to proliferate (Figure 9). Massive bacterial invasion of the soft tissues of the larvae can wipe out an entire culture in as little as 18 hours. The initial stage of the disease is followed by a secondary invasion by ciliated protozoa that feed on the bacteria.

Figure 9. A *Pseudomonas* sp infection appears as a distinct pink coloration.

The marine fungus, *Sirolpidium zoophthorum* also can infect cultured bay scallop larvae. The mycelia are easily noticeable and heavy infections can kill larvae in 2 to 4 days. In 1954, V. Loosanoff categorized the fungus as a serious obstacle to larval culture but more recent reports state that despite being frequently found, it is rarely a problem.

Chlamydia and *Rickettsia*-like intracellular parasites have been identified within the digestive diverticula, kidneys and gills of adult bay scallops and the digestive system of larval bay scallops. They are usually associated with tissue degeneration. Although the pathogens have been implicated in larval and juvenile die-offs, the precise linkage between infection and pathogenicity remains unclear.

Multiple species of protistan coccidian parasites are frequently found in wild and cultivated adult bay scallops, but not in larvae or juveniles. Primarily observed in the kidney, they can also infect the digestive diverticula, gonads and gills. Although generally believed to only be of concern for cultured scallops held at elevated temperatures, coccidian infestations in the wild can exceed 95% of a population with over 80% mortality.

The apicomplexan protist *Perkinsus karlssoni* has been reported in bay scallops from Florida, Connecticut, Rhode Island, Massachusetts and Maritime Canada. This protist is species-specific and does not infect other bivalve species. Scallops must be certified free of the *P. karlssoni* parasite prior to transport. Once introduced into an area or facility, it cannot be eradicated.

Small pea crabs *Tumidotheres* (formerly *Pinnotheres*) *maculatus* often reside in the mantle cavity of juvenile and adult bay scallops (Figure 10). The small decapod crustaceans negatively impact nutrition, disrupting the feeding processes of their hosts and competing with the scallops for food. Infested scallops appear emaciated with reduced growth and gono-somatic indices.

Non-pathogenic injury: Unlike other bivalves, whose soft tissues are protected by tightly closed shells, scallops are more likely to suffer internal damage from foreign objects or organisms. When cultured at high densities, scallops are prone to "knifing", inserting one of their valves into the gape of their neighbor, physically damaging each other's soft tissue. This commonly results in mortality of both individuals.

Harmful Algal Blooms: Harmful algal blooms (HABs) occur when environmental conditions foster the proliferation of various microscopic and macroscopic algae. The harmful impacts include human poisoning, physical impairments of life processes, and various degrees of environmental degradation.

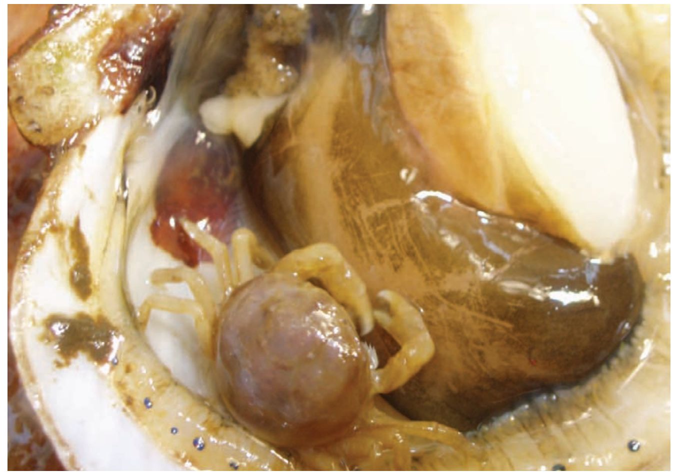

Figure 10. Pea crab infestations disrupt the feeding process.

The primary concern regarding HABs is the risk of poisoning associated with human consumption of contaminated shellfish. This risk is carefully monitored in the U.S. and harvesting is banned during HAB events. The toxic compounds are primarily produced by a variety of microscopic dinoflagellate species. During dense blooms of these algal species, filter feeding bivalves concentrate the toxic algal cells in their digestive tract and in turn can sicken or kill any organism that eats them. Scallops are not generally included in HAB monitoring programs in the U.S as only the adductor muscle is consumed. However, "roe on" and small whole scallops, a new cultured product, should not be eaten during toxic blooms.

Many of the dinoflagellates that make shellfish toxic to consumers have no negative impacts on the bivalves themselves. However, a few species have recently been implicated in bay scallop mortalities such as *Cochlodinium polykrikoides* in the Northeast (Figure 11).

Some species of algae such as *Aureococcus anophagefferens,* commonly referred to as "Brown Tide," are harmless to humans, but are still classified as HABs because of their negative impacts on shellfish populations. In the bays of eastern Long Island, a recurring bloom of *Aureococcus anophagefferens* appearing first in 1985 nearly extirpated the native population of bay scallops by 1988 through the combined impacts of starvation of adults and recruitment failure. Brown Tides have been observed from the Gulf of Maine to Virginia.

In addition to direct impacts, algal blooms can also cause scallop mortality when blooms "crash" after reaching an exceedingly high biomass leading to low oxygen stress.

More ample knowledge of the biology of the bay scallop will hopefully help potential growers further develop the culture of this valuable resource.

Figure 11. ***Cochlodinium*** **bloom on Nantucket in 2010. (Photograph by Tara Riley)**

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