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CHAPTER 3. The Biology of Shellfish in Rhode Island

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Section 300. Introduction

1. The purpose of this chapter is to outline and describe the various biological and morphological characteristics of the different commercially and recreationally important shellfish species described in the SMP. Other description for each species includes habitat preferences, overview of the ecology, and population dynamics. In addition, this chapter offers detailed descriptions and background information on issues identified by stakeholders that relate to the biology of shellfish. Recommendations for management and research are included in this chapter.
2. Effective shellfish management is contingent on a reasonable understanding of the biology of each of the species being managed. Knowledge of the life history of a species coupled with an understanding of the role that environment/ecosystem plays in the development of the shellfish population leads to an ability to predict population trends and to manage harvest rates that allow for a sustainable supply of product in the long-term. This chapter will summarize our current state of knowledge with respect to biology of the shellfish species that are the focus of this management plan, namely:
 - a. Those species currently being harvested commercially in Rhode Island waters:
 - Quahog (*Mercenaria mercenaria*)
 - Soft Shell Clam (*Mya arenaria*)
 - Blue Mussel (*Mytilus edulis*)
 - Smooth (Channeled) Whelk (*Busycotypus canaliculatus*)
 - Knobbed Whelk (*Busycon carica*)
 - b. Those species that have historically been harvested commercially in Rhode Island waters:
 - Eastern Oyster (*Crassostrea virginica*)
 - Bay Scallop (*Argopecten irradians*)
 - c. Other species that may be targeted with future fishing efforts:
 - Razor Clam (*Ensis directus*)

Section 310. Issues Identified by Stakeholders

1. Throughout the Shellfish Management Plan (SMP) planning process, the SMP team has met with stakeholders to identify issues and concerns regarding all aspects of shellfish, including but not limited to environmental issues, management, marketing, capacity building, and decision making. The following are the major themes concerning the ecology of shellfish stakeholders have identified (a full list of all issues identified by stakeholders can be found in Appendix 2.2). There is a need to:
 - a. Collect and share more information about the biology of the important commercial and recreational shellfish species in Rhode Island.
 - b. Better delineate the objectives of shellfish management in the state, including the scale managers are operating on, different management of the Bay and salt ponds, etc.
 - c. Better understand the relationship between habitat, resource density, population composition, and larval production in shellfish.
 - d. Understand shellfish size variability and economic return to the fishermen and state as a whole.
 - e. Improve our overall knowledge of the spatial distribution of shellfish in the state.
 - f. Better understand concerns such as: optimizing post-set survival of shellfish, using wild stock for aquaculture, predation, maintaining genetic diversity, and natural mortality.

- g. Investigate and better structure management of spawner sanctuaries and broodstock enhancement in the state.
- h. Investigate shellfish pests, environmental change, and understand and mitigate various human health risks.

Section 320. Mollusk Anatomy

1. All of the species identified as important in the development of the RI Shellfish Management Plan are in the phylum Mollusca. As such, they all have a body plan that is similar, as it was derived from the same ancestral form (Figure 3.1 and Figure 3.2). The primary difference between the bivalve mollusks (clams, oysters and scallops) and the gastropods (the two whelk species) is their feeding preferences. Bivalve mollusks are filter feeders and utilize their gill apparatus as a tool to filter very small food particles (phytoplankton) from the water column as they move water across their gills. The food particles are then transported to the mouth for ingestion. Whelks are carnivorous gastropods and use their shell and foot to break into a variety of clam and oyster species where they consume the soft tissue for nutrition.

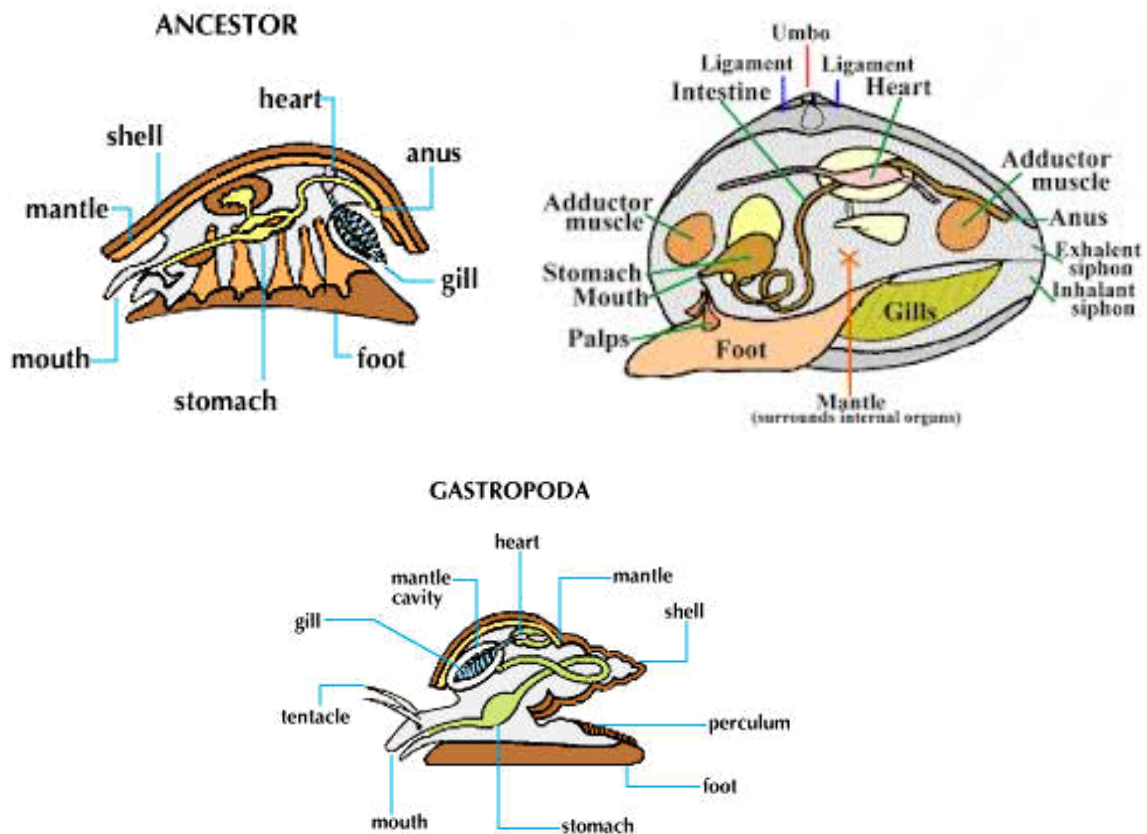


Figure 3.1. The anatomical relationship between an ancestral mollusk and modern-day bivalves and gastropods.

320.1. Generic life history stages of gastropod and bivalve mollusks

1. All animals in the Phylum Mollusca undergo a similar reproductive and development sequence that starts with the production of sperm and eggs and ends with the development of a reproductively active adult. The general development stages are identified in the schematic included as Figure 3.1.
2. Reproductive strategies in mollusks range from dioecious (separate male and female sexes throughout their life) to monoecious (having both sexes in the same organism – hermaphroditic) to individuals

that change sex as they age (often changing from male to female – protandrous). With the exception of the whelks, the majority of shellfish are broadcast spawners, in that they release their eggs and/or sperm into the water column where fertilization occurs following the chance encounter of a sperm with an egg. As such, an important factor in reproductive success of wild shellfish is the number of gametes released (usually characterized by overall egg production) and the relative nearness of one gamete to the other, often a function of the density of the adults in the environment or the pattern of water movement over the spawning population. The unique reproductive characteristics of the shellfish emphasized in this document are included in Table 3.1.

3. As noted previously for the clams, oysters and scallops, egg and sperm are released into the water column where fertilization occurs as the two gamete types encounter each other. Once fertilized, cell division begins, leading to the formation of a multicellular, free-swimming non-feeding trochophore stage, usually within 24 hours of fertilization. The trochophore will rapidly start to produce a shell and a specialized structure for locomotion and feeding (the velum) as the larva transforms into a veliger in about 36-48 hours. In a series of transformational changes, the free-swimming larvae progresses through multiple veliger stages before acquiring a foot (the pediveliger) and beginning to search for an appropriate place to settle out. It is during this free-swimming phase, which can last up to 4 weeks depending on species and environment, that larvae are transported and dispersed around the bay or coastal pond, by way of wind and water currents. The duration of the free-swimming veliger stages for each of the relevant species are included in Table 3.2.

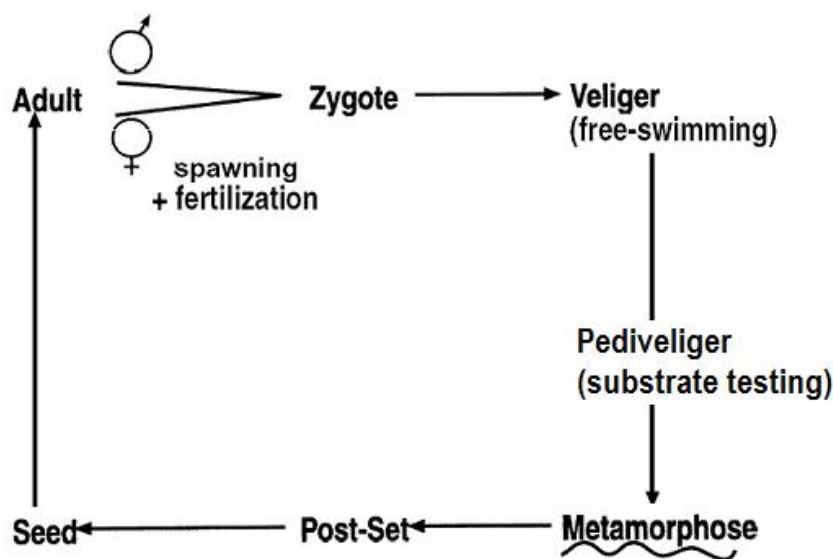







Figure 3.2. A generalized schematic of the developmental stages of a mollusk.

Table 3.1. Summary of the reproductive characteristics of commercially important shellfish in Rhode Island.

Common Name	Genus/Species	Longevity	Reproductive Strategy	Age at first spawn	Length at first spawn	Range of Egg Production	Reproductive timing in RI	References
Quahog	<i>(Mercenaria mercenaria)</i>	up to 46 years	Protandrous	2nd year	22 to 37 mm	1.6 to 24.6 x10 ⁶	early June to late July	Brice[?] 2002; Rice 2002
American Oyster	<i>(Crassostrea virginica)</i>	up to 20 years	Protandrous	♂ - 1 year ♀ - 2 years	> 35 mm	0.01 to 66 x 10 ⁶	early June to late July	Kennedy 2009; Loosanoff 1965
Soft Shell Clam	<i>(Mya arenaria)</i>	up to 28 years	Dioecious	2nd year	29 - 30 mm	1.0 to 3.0 x10 ⁶	early May	Newell & Hidu 1986; Belding 1910
Bay Scallop	<i>(Argopecten irradians)</i>	2 - 3 years	Hermaphroditic	2nd year	variable	0.5 to 1.0 x10 ⁶	June	Leavitt & Karney 2005
Blue Mussel	<i>(Mytilus edulis)</i>	18 - 24 years	Dioecious	2nd year	> 25 mm	8.0 to 10.0 x10 ⁶	April to May	Newell 1989; Newell et al. 1982
Razor Clam	<i>(Ensis directus)</i>	3 - 7 years	Dioecious	1.5 years	80 mm	≤ 12.0 x10 ⁶	April to May	Kenchington et al. 1998; Cardoso et al. 2011
Smooth (Channeled) Whelk	<i>(Busycotypus canaliculatus)</i>		Protandrous?	♂ - 6.9 years ♀ - 8.6 years	155 mm	20 - 50 eggs per capsule; 20 - 150 capsule's per string	June through September	Magalhaes 1948; Peemoeller and Stevens 2013
Knobbed Whelk	<i>(Busycyon carica)</i>	85 years	Protandrous?	3 - 5 years	146 mm	34 - 35 eggs per capsule; 100 - 120 capsule's per string	June through September	Magalhaes 1948; Angel 2012

Table 3.2. The approximate duration of the larval stages of shellfish important to Rhode Island waters. The duration of each stage is influenced primarily by environmental temperature and food availability.

Common Name	Genus/Species						Rearing temperature; Reference
		Trochophore	D-stage veliger	Umboned veliger	Pediveliger	Metamorphosis	
Quahog	<i>(Mercenaria mercenaria)</i>	12 - 24 h	1 - 5 d	3 - 15 d	8 - 20 d	10 - 21 d	@ 24-28°C; Hadley & Whetstone 2007
American Oyster	<i>(Crassostrea virginica)</i>	12 - 20 h	20 - 48 h	6 - 7 d	10 - 12d	14 - 21 d	@ 21-21°C; Stallworthy 1978
Soft Shell Clam	<i>(Mya arenaria)</i>	12 - 24 h	1 - 5 d	6 - 7 d	10 d	10 - 35 d	@ 19-24°C; Loosanoff & Davis 1964
Bay Scallop	<i>(Argopecten irradians)</i>	12 - 24 h	17 - 48 h	5 - 6 d	10 d	10 - 14 d	@ 23°C; Leavitt & Karney 2005
Blue Mussel	<i>(Mytilus edulis)</i>	5 - 24 h	1 - 3 d	8 - 12 d	24 - 30 d	25 - 30 d	@ 15°C; Hayhurst 2001
Razor Clam	<i>(Ensis directus)</i>	12 - 15 h	1 - 4 d	5 - 7 d	8 - 12 d	13 - 16 d	@19°C; Flanagan 2013

4. Setting (metamorphosis) in bivalves is often stimulated by the exposure of a pediveliger that is competent to metamorphose to a specific habitat type. The setting cues vary with the species and our current state of knowledge is summarized in Table 3.3. When appropriate habitat is encountered, the pediveliger will attach itself to the substrate, normally through the action of byssus threads, and will transform to the adult body form by resorbing the velum, developing gills and undergoing other morphological changes. With setting, the shellfish leave the larval phase and enter into the juvenile stage of development, defined as post-metamorphic but prior to reproductive maturity.

Table 3.3. Setting cues for the shellfish species included in Chapter 3.

Common Name	Genus/Species	Setting Preference	Reference
Quahog	<i>(Mercenaria mercenaria)</i>	mud/sand substrate is preferred with low silt/clay and organic content	Mulholland 1984
American Oyster	<i>(Crassostrea virginica)</i>	hard substrate, preferably shell material	Kennedy 1996
Soft Shell Clam	<i>(Mya arenaria)</i>	soft muds, sands, compact clays, coarse gravel, and cobble - sandy mud preferred	Newell & Hidu 1986
Bay Scallop	<i>(Argopecten irradians)</i>	seagrass beds or similar structure	Belding 1930; Fay <i>et al.</i> 1983
Blue Mussel	<i>(Mytilus edulis)</i>	stable hard substrate	Newell 1983
Razor Clam	<i>(Ensis directus)</i>	coarse sand	Flanagan 2013

5. The exception to the general reproductive cycle outlined above occurs with the whelks. Both whelk species reproduce via internal fertilization followed by the production of an elongated egg mass consisting of individual capsules linked together in a string and anchored to the substrate by a series of empty capsules. The multiple larval development stages occur within the capsule, where the larvae progress using non-fertile eggs as a nutrient source. The juvenile post-metamorphic whelks emerge from the egg capsules through an exit port in the side of the capsule. With this form of development, the dispersal of crawling juvenile whelks is much more limited than that of bivalves, which are free-swimming for up to 4 weeks during early development. On average, both whelk species deposit 20 to 50 eggs per capsule with a string consisting of 20 to 150 capsules.
6. While for some species, primarily the oyster, once they have set they are permanently attached to the substrate they have chosen, the bulk of our shellfish species have the capacity to continue to change location as they grow through the juvenile stage. Some have the capacity to actively move by swimming (bay scallop and razor clam) or “walking” with their foot (mussel and quahog) while others can initiate a passive mechanism for movement, including incorporation into the sediment bedload transport associated with tidal currents (soft shell clams or quahogs) or forming a tool for dragging in the current (byssal drifting in razor clams). Although the details of why a juvenile shellfish may initiate movement are not well understood, it is assumed that the environmental conditions associated with the initial settlement site may not be appropriate and the shellfish can initiate their variety of dispersal tools to change their location based on the chance of landing at a more suitable site. In general, as an individual clam grows larger, their ability to move becomes more restricted such that large-scale movement in adults is rarely observed.
7. Growth in individual shellfish, from larva to adult stages, is dependent on a variety of factors that mostly can be reduced to water quality parameters, such as temperature, dissolved oxygen or salinity, and food availability. Water temperature in these ectothermic animals controls the rate of metabolism and many other important biological processes, such as filtration and feeding rates. As such, shellfish growth rate varies seasonally with the fastest growth rate occurring within the range of water temperatures described as optimal for the species and the growth progressively decreasing as the temperature moves away from the optimal range. Salinity and dissolved oxygen have much the same affect on growth as conditions shift away from optimal ranges; however, these are generally not observed as seasonal variations but rather are associated with specific environmental events, such as episodes of heavy rainfall or degrading eutrophic plankton blooms.
8. Food availability for filter feeding shellfish is a function of the plankton quality and flux. Plankton quality reflects the nutrient composition of the single-celled alga as well as the physical characteristics of the filtered particle; for example, filter-feeders target specific size ranges of particles for ingestion. Plankton flux is a function of the density of the microalgal particles in the water column combined with the rate at which the particles are available to the animal for filtration,

i.e. the flow of particles across the siphonal intake of the individual shellfish. Many factors influence food flux, including the level of primary productivity in the water body, the water flow characteristics associated with the location where the shellfish settled, and the density of competing filter-feeding organisms in the vicinity of the individual clam, oyster or scallop. Situations such as reduced water flow, low plankton productivity or high densities of filtering organisms in the neighborhood, can all lead to a reduced availability of food for an individual resulting in slower growth.

9. The exception to a general discussion on mollusk feeding is the predatory gastropods, the whelks (*Busycotypicus canaliculatum* and *Bustcon carica*). Rather than filter food particles from the water column, these two snails are active predators and scavengers that have a mouth part (proboscis) adapted for inserting into a mollusk that has been opened slightly and initiating a (presumptive) toxin-mediated release of saliva that relaxes and/or kills the prey and allows the valves to be opened further, to the point where the radula can tear off sections of prey flesh for ingestion. The strategy for initially opening the prey varies depending on the overall morphology of the shellfish (Carriker 1951). If it is a bivalve that cannot completely seal shut its valves (e.g. soft shell or razor clam) then the proboscis has easy access to the soft tissue once the whelk grasps the valves of the prey with its muscular foot. If the bivalve can tightly seal its valves shut (i.e. quahog or oyster), the whelk grasps the valves with its foot and waits for the bivalve to gape slightly as it starts to pump respiratory currents following the disturbance. As the bivalve gapes, the whelk inserts the edge of its shell beak into the gap, wedging the valves open. With this foothold, the whelk works the valves open by prying until it can insert its proboscis into the valves and relax the adductor muscles of the clam or oyster further. Another strategy reported for the whelks is to hold the bivalve in its foot and hammer at the ventral margin of the shell to chip away the thinner edge of the shell and gaining access to the soft tissue by breaking open a gap in shell margin. This has consequences to the predator, in that it also break the shell of the whelk such that often it has been reported that during some time intervals, there whelk does not grow and it is proposed that the energy normally applied to growth is reallocated to shell repair resulting in zero size increase over time (Castagna and Kraeuter 1994).
10. The overall effects of changes in the growth patterns of shellfish can impact such important shellfish population/management parameters as recruitment into the fishery, i.e. attainment of a legal size threshold; age and/or size at first reproduction; fecundity; and life expectancy. While not all projected changes to the environment are negative, for example increased water temperature may lead to more rapid shellfish growth resulting in earlier recruitment into the fishery, they are changes that will need to be recognized and accounted for as shellfish management strives to improve the production of shellfish resources in Rhode Island.
11. Before delving into the aspects of shellfish biology that directly affects issues identified as important to the management of shellfish in Rhode Island, a quick summary of the unique attributes of each of the important shellfish species are presented below.

Section 330. Unique Attributes of Shellfish Species Important to Rhode Island

330.1. Quahog (*Mercenaria mercenaria*)

(Stanley & Dewitt 1983, Eversole 1987, Pratt *et al.* 1992, Whetstone *et al.* 2005)

Other common names: hard clam, hard-shelled clam, round clam, littleneck clam, top neck clam, cherrystone clam, and chowder clam.

Table 3.4. Environmental conditions reported for the quahog (*Mercenaria mercenaria*).

TEMPERATURE	Overall Range	Optimal Range
Culture Stage	(°C)	(°C)
Spawning	20.0 - 30.0	26.0
Larval rearing	15.0 - 33.0	22.5 - 26.6
Juvenile to Adult	0.0 - 35.0	20.0 - 31.0
SALINITY	Overall Range	Optimal Range
Culture Stage	(ppt)	(ppt)
Larval rearing	15.0 - 35.0	20.0 - 32.5
Juvenile to Adult	10.0 - 35.0	24.0 - 32.0
DISSOLVED OXYGEN	Critical Levels	
Culture Stage	(mg/L)	
Larval growth	>2.4	>4.2
Juvenile to Adult	>1.0 (for up to 3 weeks)	
pH	Overall Range	Optimal Range
Culture Stage		
Larval growth	6.75 - 8.75	7.50 - 8.50
TURBIDITY	Critical level	
Culture Stage	(mg/L)	
Larval growth	<750	
WATER FLOW	Optimal flow	
Culture Stage	(cm/s)	
Juvenile to Adult	30 - 50	
SUBSTRATE	Sand, mud, shell, gravel mixtures	

1. Range

The native range of the quahog is from the Gulf of St. Lawrence to Texas with a peak in abundance from Cape Cod, Massachusetts to Virginia. It has been successfully introduced into California (Crane 1975), Hawaii (Ziegler 2002), Europe (Richardson & Walker 1991) and China (Chang *et al.* 2002).

2. Morphology and Identification

This clam has a thick shell with short siphons and sometimes has a purple band on the ventral margin of the inside of the shell. It can grow up to 130 mm with morphometric ratios of length/height: 1.25, and length to width: 1.90. The elliptical shell is grayish white with concentric growth lines observable on the shell exterior.

3. Habitat

The quahog is an infaunal clam that burrows near the sediment surface and preferentially settles in sand to sandy mud. Adults can be found buried to about 2 cm in depth with smaller individuals burrowing deeper. Primarily subtidal, found up to a depth of 20 meters, the quahog is also found intertidally in bays and estuaries.

4. Fisheries

The quahog is the fifth largest fishery landed in Rhode Island with a dockside value of approximately \$5 million in 2012. It is the largest fishery within Narragansett Bay and the coastal ponds of the state,

where it is harvested by bullrake or by SCUBA. Dredging for quahogs is not allowed in RI state waters. In addition, there is a significant recreational fishery for quahogs within the state, again by hand harvesting in intertidal and shallow subtidal areas.

5. *Population Dynamics*

The quahog is commonly found throughout Narragansett Bay and in all of the RI coastal ponds although the highest densities are located in the upper one-half of the Bay. It can exist in very dense assemblages in RI waters, where reported densities have been as high as 500 individuals/m² with an average density of 78/m² in an area historically known for strong quahog production (Greenwich Bay) (Rice *et al.* 1989). Based on the latest projection of standing stock in Narragansett Bay by RIDEM Marine Fisheries, the stratified mean density of quahogs across the Bay is consistently between 2 and 3 quahogs per meter square (RIDEM 2014). Natural mortality is similar to most bivalves, where the highest rate of natural mortality occurs during the earliest life history stages and the rate decreases as the bivalve grows.

6. *Growth Characteristics*

Quahog growth in Narragansett Bay has been carefully monitored over many years, with the current growth characteristics depicted in Figure 3.3 (Rice *et al.* 1989). The time to achieve legal size in Narragansett Bay quahogs has been getting longer over the past 50 years where the current estimate for a quahog achieving legal size is approximately 3-4.8 years (Figure 3.4, Jones *et al.* 1989, Henry & Nixon 2008).

7. *Ecology*

- a. **Feeding Habits:** The quahog feeds by filtering phytoplankton from the water column so growth is dependent on the food quality as well as the rate of delivery of the food particle to the siphons of the clam (food flux). Recent research suggests that changes in the patterns of phytoplankton presence in RI waters may be affecting the growth and reproduction of the quahog although more research is necessary to fully understand these changes (Henry and Nixon 2008).
- b. **Parasites and Disease:** No significant disease situations have been noted for wild quahogs in Rhode Island although monitoring of selected batches of wild quahogs has recognized numerous inconsequential maladies (Smolowitz, pers. comm.) One situation of a potentially significant quahog disease (Quahog Parasite Unknown – QPX) was reported at an aquaculture site in Winnapaug Pond (Westerly, RI) in the mid-2000's although the situation was quickly recognized and the infected organisms were removed from the pond, resulting in no further development of the disease in local waters.
- c. **Predation:** It is widely recognized that natural mortality, i.e. predation, is the primary population control factor in wild quahogs. A list of common predators on the quahog are included in Figure 3.5, along with the maximum size of clam that can be preyed on by each predator species (from Bricelj 2005). On average, the quahog is reported to reach a size threshold where predation becomes significantly less a controlling factor at between 25 and 35 mm length, due to the degree of thickening of the shell (REF).

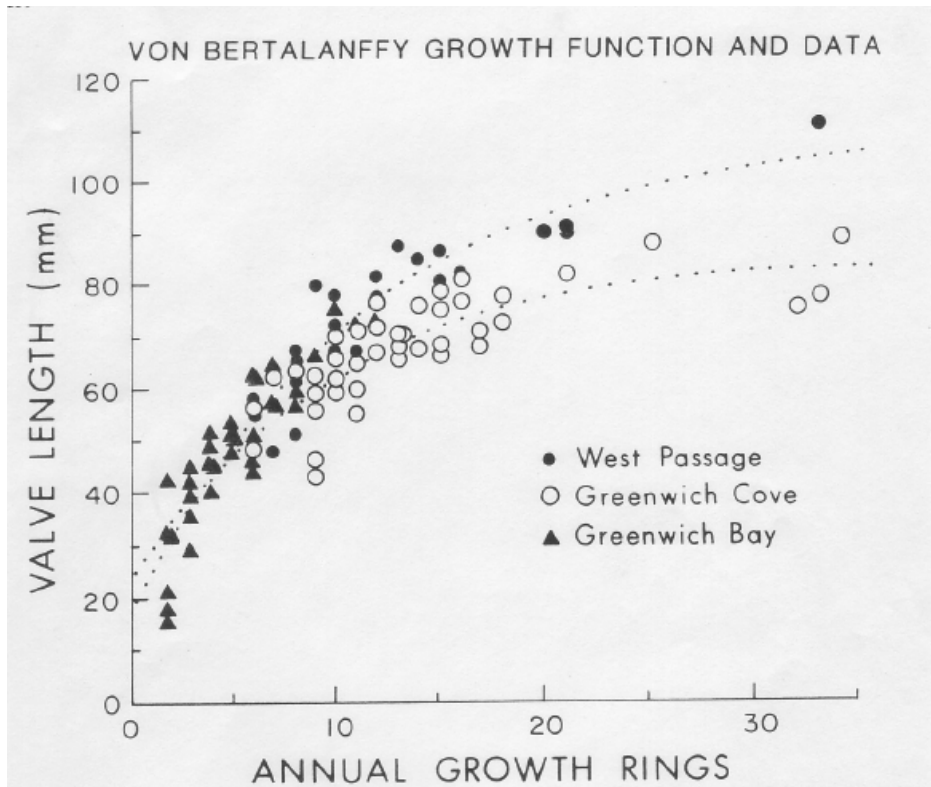


Figure 3.3. The valve length of quahogs from three Narragansett Bay sites plotted as a function of age (Rice et al. 1989).

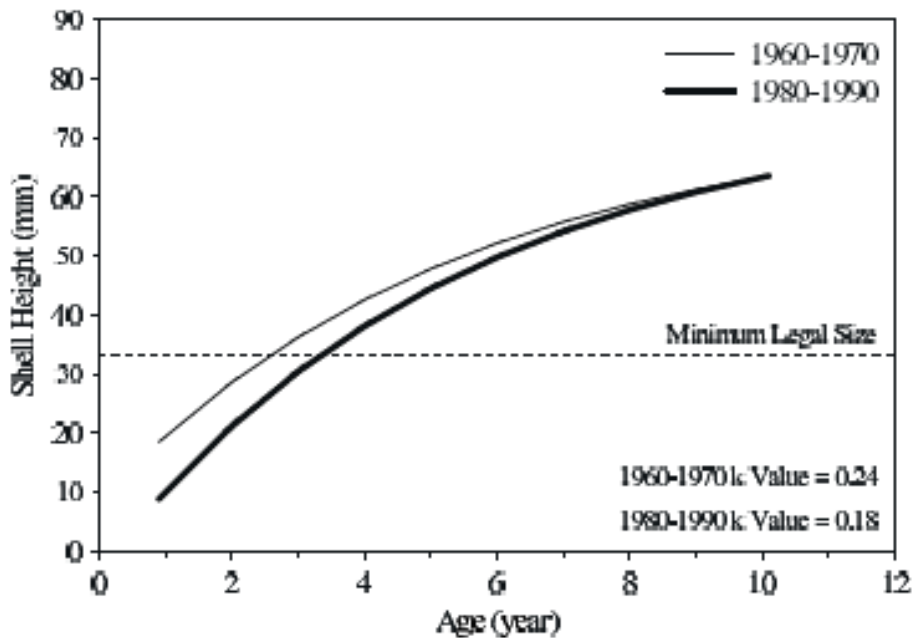


Figure 3.4. Growth curves for Narragansett Bay quahogs demonstrating the increasing time to achieving legal size (Henry & Nixon 2008).

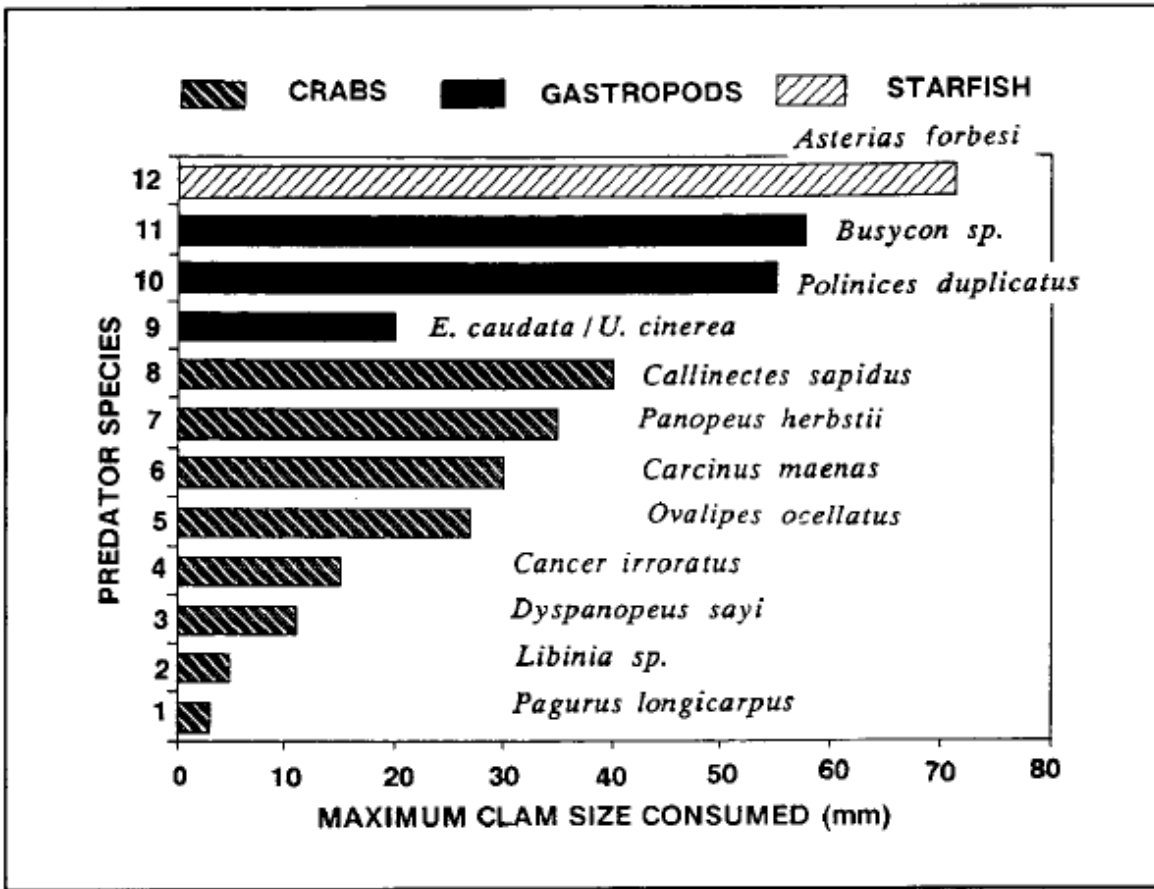


Figure 3.5. Maximum shell length (mm) of quahogs consumed by common predators of the quahog (Bricelj 2005).

330.2. Eastern Oyster (*Crassostrea virginica*)(Galtsoff 1964, Sellers & Stanley 1984, Kennedy *et al.* 1996)

Other common names: Eastern oyster, cupped oyster

Table 3.5. Environmental conditions reported for the American oyster (*Crassostrea virginica*).

TEMPERATURE Culture Stage	Overall Range (°C)	Optimal Range (°C)
Spawning		20.0
Larval rearing	20.0 - 30.0	25.0
Juvenile to Adult	-1.7 - 36.0	20.0 - 30.0
SALINITY Culture Stage	Overall Range (ppt)	Optimal Range (ppt)
Larval rearing	3.1 - 30.6	24.5 - 29.8
Juvenile to Adult	0.0 - 42.0	14.0 - 28.0
DISSOLVED OXYGEN Culture Stage	Critical Levels (mg/L)	
Larval growth	<1 (for 11 h); optimal > 4.0	
Juvenile to Adult	<1 (for 5 days); optimal > 4.0	
pH Culture Stage	Overall Range	Optimal Range
Larval growth	6.0 - 9.0	6.75 - 8.75
TURBIDITY Culture Stage	Minimum level (mg/L)	
Larval growth	<750	
WATER FLOW Culture Stage	Optimal flow (cm/s)	
Juvenile to Adult	> 10	
SUBSTRATE	Hard surface, prefer shell material	

1. *Range*

The American oyster can be found from the Gulf of St. Lawrence in Canada down the Atlantic seaboard to Florida and into the Gulf of Mexico to the Yucatan. It is also found in the West Indies to Venezuela. *C. virginica* has also been introduced around the world, including the west coast of the U.S., Hawaii, Japan, Australia, and Great Britain (Ahmed 1975).

2. *Morphology and Identification*

The shell shape is highly irregular and asymmetrical, with the top (left) valve being flatter than the cup-shaped lower (right) valve. Environmental conditions influence the shell shape and thickness although in general the hard shell is ornamented with radial ridges and fluted edges and grows from a narrow umbo (hinged) end in a fan to the wider ventral edge.

3. *Habitat*

American oysters are an estuarine species that are most commonly associated with hard substrate, where they attach by permanently cementing their shell to a solid surface and existing as an epifaunal organism. Although the oyster prefers to attach itself to shell hash (cultch), it will settle on a variety of hard materials if submerged in the estuary. Intertidal oysters in RI are subjected to higher mortality due to winter low temperatures and ice. Due to the oyster's high tolerance for brackish water systems, they are mostly located in the mid to upper reaches of the estuary as a result of reduced disease and predation pressure, although they can exist in full strength seawater if protected from natural mortality.

4. Fisheries

In Rhode Island, the oyster was a significant fishery at the turn of the 20th century although the bulk of the fishery was derived from oyster beds seeded and maintained by private companies (Rice 2006). Following the demise of the oyster industry over the 1930 to 1950 interval, there have been insignificant landings of oysters in Rhode Island until the modern-era of oyster aquaculture was introduced in the 1990's. Today, the oysters landed in RI are almost entirely farmed and they had an ex-vessel value of over \$4.3 million in 2013 (Beutel 2014).

5. Population Dynamics

Oyster populations in RI waters have a history of being very sporadic in abundance. While the capacity of RI waters to support oyster growth is excellent, the recruitment of young oysters into local populations is extremely variable with large oyster sets occurring very infrequently (on a scale of tens of years). Oysters are capable of releasing enormous amounts of larvae so larval supply is not considered a problem in population recruitment. The reason for the variability in oyster sets is not known but is most likely associated with high natural mortality. No routine assessment of oyster stocks are conducted in state waters.

6. Growth Characteristics

American oysters grow very well in Rhode Island waters, as is exemplified in Figure 3.6 – a plot of the growth rate of three strains of hatchery produced oysters deployed on a farm in Narragansett Bay (from Gomez-Chiarri *et al.* 2010). On a farm, a market-sized oyster (~3 inches valve height) can be produced in 2 years. No data are available on oyster growth in the wild in RI.

7. Ecology

Where present, the oyster is considered to be an important ecological species, in that it provides a host of ecological services to estuarine communities (Newell 2004). These include water filtration with enhanced denitrification of particulate organic material through coupling pelagic-benthic processes, stabilization of submerged and intertidal sediments, and enhancement of bottom habitat complexity. Because of the economic value of oysters and the ecological services provided, there have been numerous attempts to restore oyster beds in Rhode Island waters.

- a. Feeding Habits: Adult oysters feed on relatively small organic particles, predominantly phytoplankton in the 3 – 20 mm size range and are well known for the volume of water they can filter under optimal conditions (up to 5 l/h) (Figure 3.7, zu Ermgassen *et al.* 2012). Given their filtering capacity, oysters are often identified as providing a filtering service that is unsurpassed under natural conditions in the estuary.
- b. Parasites and Disease: There are numerous diseases that have had a profound impact on oyster populations throughout their range. In both wild populations and cultured oysters, three important diseases resulting from protistan parasites are Multinucleated Sphere Unknown (MSX) caused by *Haplosporidium nelsoni*, Seaside Organism (SSO) caused by *Haplosporidium costale* and Perkinsus Disease (dermo) caused by *Perkinsus marinus*. This combination of parasite-based diseases has decimated wild oyster populations through the U.S. range of the oyster and continue to be a problem wherever oysters exist. In addition, a fourth bacterial disease, Juvenile Oyster Disease (JOD) caused by *Roseobacter crassostrea*, has been impacting farmed nursery-stage oyster seed in Rhode Island and throughout the northeast in recent years. In all cases, there are general strategies that can be implemented to reduce the risk of disease in oyster populations but no effective cures have been developed.
- c. Predation: As an epifaunal species, the oyster is susceptible to a wide variety of predators, from starfish to crabs and carnivorous gastropods. The primary means to control these predators is to exclude them from access to the individual oysters, which is relatively easy in a farm situation. However, wild and/or restored oyster beds are often susceptible to large-scale predation. Means to reduce predation pressure, particularly if managing restored oyster beds, is to seek areas with

routine inundation by low salinity waters (provides a barrier to marine predators) and/or placing larger (2 inch) oysters in the beds.

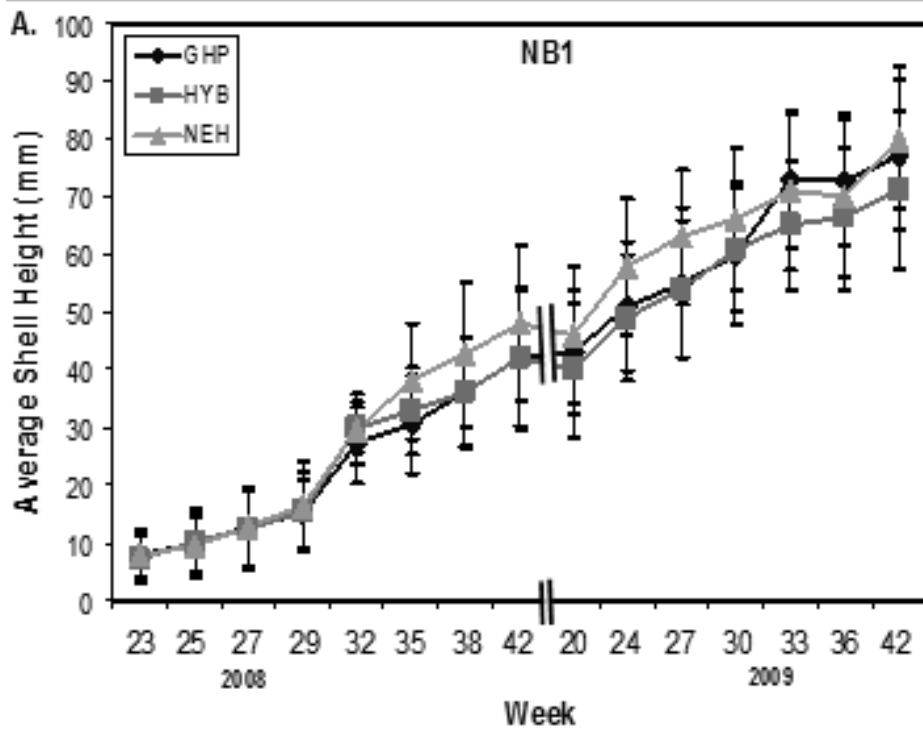


Figure 3.6. A plot of the growth performance (valve height increase) of three strains of hatchery produced oysters held on a farm in Narragansett Bay (from Gomez-Chiarri 2010).

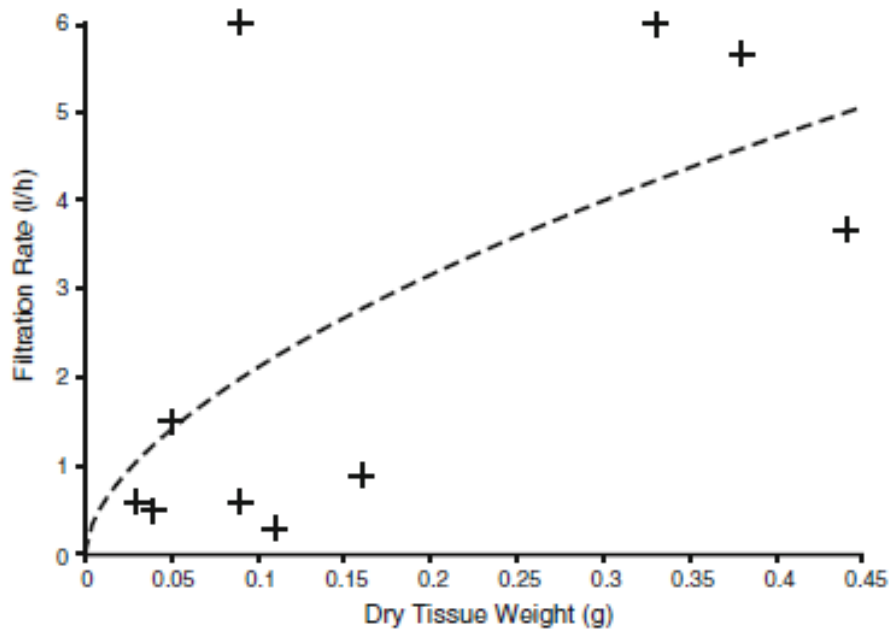


Figure 3.7. Oyster filtration model developed by zu Ermgassen et al. (2012): $(FR = 8.02W^{.058}e^{(-0.015T-27)^2})$; where FR is filtration rate (l/h), W is the soft tissue dry weight (g) and T is temperature ($^{\circ}C$) fitted to field collected data ($R^2 = 0.71$).

330.3. Soft Shell Clam (*Mya arenaria*)

(Newell & Hidu 1986, Baker & Mann 1991, Weston *et al.* 2010)

Other common names: steamer clam, nannynose clam, pisser clam, long-neck clam, sand gaper, Ipswich or Essex clam

Table 3.6. Environmental conditions reported for the soft shell clam (*Mya arenaria*).

TEMPERATURE Culture Stage	Overall Range (°C)	Optimal Range (°C)
Spawning	> 12	15 - 16
Larval rearing	12.0 - 34.4	22 - 24
Juvenile to Adult	-2 - 28	17 - 23
SALINITY Culture Stage	Overall Range (ppt)	Optimal Range (ppt)
Larval rearing		16 - 32
Juvenile to Adult	Apr-33	10 - 33
DISSOLVED OXYGEN Culture Stage	Critical Levels (mg/L)	
Larval growth		
Juvenile to Adult	> 2.8	
pH Culture Stage	Overall Range	Optimal Range
Larval growth		
TURBIDITY Culture Stage	Minimum level (mg/L)	
Juvenile to Adult	<300	
WATER FLOW Culture Stage	Optimal flow (cm/s)	
Juvenile to Adult		
SUBSTRATE	Soft muds, sands, compact clays, coarse gravel, and cobble - sandy mud preferred	

1. Range

Commonly found from Labrador, Canada to Florida along the Atlantic coast with the highest densities from Maine to Virginia. As the population extends southward it transitions from intertidal to subtidal and can be found up to depths of 200m. It has also been introduced into Europe, from Norway to the Black Sea and on the west coast from California to Alaska.

2. Morphology and Identification

The soft shell clam's general shape is elliptical (length to width ratio of 2.6 to 3.2) where the maximum length can approach 11 cm along the longest axis. The relatively thin and brittle valves are grey to white from the exposed prismatic shell layer although vestiges of a periostracum often can be observed along the ventral growth margin but is worn away by the abrasive nature of the sediment. The mantle is fused along the ventral margin with a small gap to allow for extension of the foot. The soft shell clam cannot totally close the valves so the mantle is always exposed.

3. Habitat

The soft shell clam is an infaunal bivalve that can be found buried at depths in the sediment of up to 30 cm due to their ability to elongate and extend their siphons to the sediment surface. They are found in a wide variety of sediment types from gravel to fine mud and are intertidal at the northern portion of their range but become more limited to subtidal areas in the southern end of the range, due to the

increasing temperature of exposed intertidal sediments as one moves south. They have been collected at depths approaching 15 m in coastal bays and estuaries.

M. arenaria is considered a euryhaline species, capable of withstanding salinity levels from 4 to 33 ppt. With this capability, soft shell clams are often found throughout estuarine environments.

4. Fisheries

This clam supports both a recreational and commercial fishery in Rhode Island. Recreational harvesting is generally accomplished by shore diggers in the intertidal and shallow subtidal areas. Commercial harvesting generally is undertaken by SCUBA and can be also accomplished by bullrake if the densities are high enough, as was the case in the Conimicut area of Narragansett Bay in 2008 (?). Because recruitment of soft shell clams in Rhode Island is highly variable, the overall commercial value of the soft shell clam fishery fluctuates widely.

5. Population Dynamics

Soft shell clams can settle into an area in phenomenally high densities, e.g. recorded post-settlement spat densities of $>100,000/m^2$ have been reported (Pfitzenmeyer 1962), although these high densities decline rapidly over the first growing season, due to a combination of predation and emigration from high-density areas. Optimal density for soft shell clam growth has been reported to be between 161 and 269 clams/ m^2 (Belding 1910). The distribution of soft shell clam spat is influenced by local water currents as the small juvenile clams can move in a flow field via bedload transport, leading to high densities of spat in areas where the current flow is interrupted by structures on the sediment surface leading to aggregations of clams in the vicinity of these structures.

6. Growth Characteristics

Due to their susceptibility to predation, particularly when small, soft shell clam juveniles grow exceedingly fast during their first year post-settlement (Goshima 1982) as the depth of their burial is dependent on the size of the clam (Figure 3.8) and the deeper they bury the higher their capability of predator avoidance (Zaklan & Ydenburg 1992). Therefore, soft shell clam growth rate slows dramatically once it has achieved a size threshold of approximately 30-40 mm thus allowing the clam to reside deeper than 10 cm in the sediment.

Sediment type is an important factor in clam growth, along with the more recognized influences of temperature and food availability. Overall, the coarser the sediment type, the slower the clam growth rate and the heavier the shell thickness (Newell & Hidu 1982).

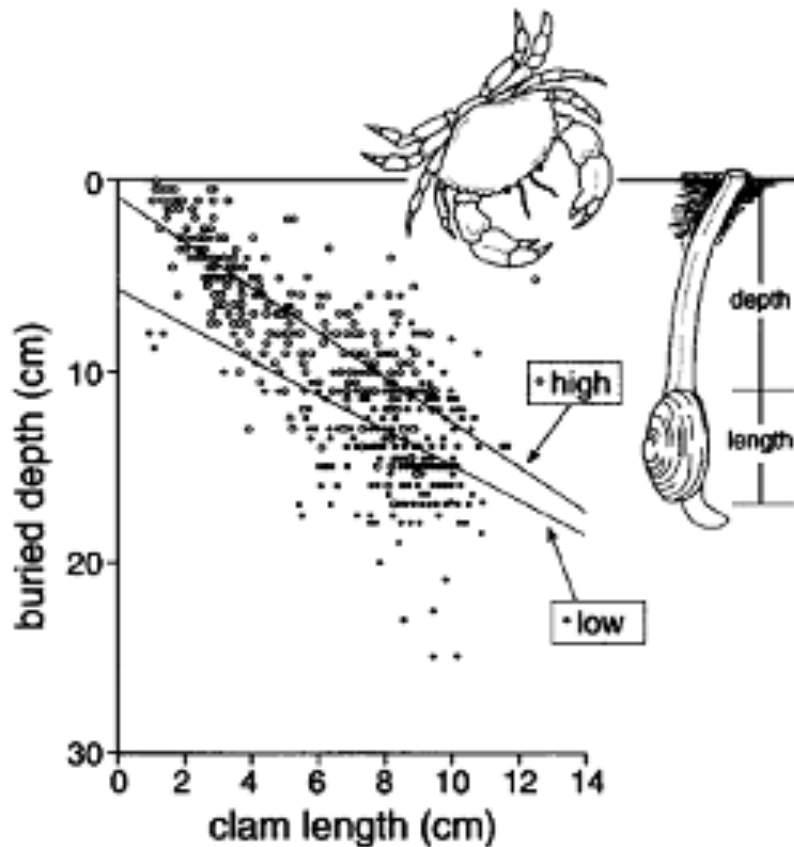


Figure 3.8. The overall relation between soft shell clam length and burial depth (from Zaklan and Ydenberg 1997).

7. Ecology

- a. **Feeding Habits:** In addition to filter feeding, where the soft shell clam targets phytoplankton in the 5 – 50 mm range, the soft shell clam is a deposit feeder, where it can ingest bacteria and benthic diatoms associated with the sediment. Hence the frequent occurrence of “grit” in the stomach, which leads to a need to purge the clam of sediment prior to preparation for eating.
- b. **Parasites and Disease:** Overall, there are relatively few significant pathological agents that affect the soft shell clam. Gonadal and hemocytic neoplasias have been reported for *M. arenaria* and have been noted in sporadic large-scale mortality events. The soft shell clam has also been reported as being affected by a protistan parasite (*Pekinsus chesapeaki*) although little information is currently available concerning this disease.
- c. **Predation:** Having only depth of burial as a defensive tool, the soft shell clam is highly susceptible to predation and it is thought that predation is the single most important factor in controlling soft shell clam populations. The list of potential predators is long, including birds, fishes, crabs, predatory worms, and carnivorous gastropods. In addition to burial depth, sediment type has also been reported as deterring predation where clams living in coarser sediments (gravel or sand with cobble) are less susceptible to predation although they also do not grow as rapidly as clams in mud or sand.

330.4. Bay Scallop (*Argopecten irradians*)(Fay *et al.* 1983, MacKenzie 2005b, Leavitt & Karney 2006, Leavitt *et al.* 2010)

Other common names: Atlantic bay scallop

Table 3.7. Environmental conditions reported for the bay scallop (*Argopecten irradians*).

TEMPERATURE Culture Stage	Overall Range (°C)	Optimal Range (°C)
Spawning		>16.4
Larval rearing	19 - 28	25
Juvenile to Adult	0 - 32	22
SALINITY Culture Stage	Overall Range (ppt)	Optimal Range (ppt)
Larval rearing	19 - 35	25 - 32
Juvenile to Adult	19 - 35	31.2
DISSOLVED OXYGEN Culture Stage	Critical Levels (mg/L)	
Larval growth	>1.38	
Juvenile to Adult	>1.5	
pH Culture Stage	Overall Range	Optimal Range
Larval growth		
TURBIDITY Culture Stage	Critical level (mg/L)	
Juvenile to Adult	500	
WATER FLOW Culture Stage	Optimal flow (cm/s)	
Juvenile to Adult	<1.0	
SUBSTRATE	seagrass beds or similar structure	

1. *Range*

Although the bay scallop can be found from Nova Scotia, Canada to Columbia, Central America, the range is generally considered to extend from Cape Cod, MA to the mid-coast of eastern Mexico. Across that range, three subspecies of bay scallop have been identified, with the northern strain common to Rhode Island (*Argopecten irradians irradians*) ranging from Cape Cod to New Jersey (MacKenzie 2005a).

2. *Morphology and Identification*

The overall shape of the bay scallop shell is round with a pair of asymmetrical wings extending beyond the hinge line at the umbo. The shell color varies from grayish brown to a subdued rose color to a bright orange and sometimes there are white stripes radiating from the umbo to the shell margin. The lower (right) shell is frequently lighter in color to the upper (left) shell. The shell is composed of an array of folds or ribs radiating from the umbo to the shell margin to impart strength to the relatively thin and light shell.

3. *Habitat*

Bay scallops are routinely located in eelgrass beds, as the three-dimensional structure of the eelgrass allows for protection of newly settled scallop spat from predation by providing an elevated location where they can byss themselves to the upright fronds. With the demise of the extensive eelgrass beds due to eelgrass blight and other environmental factors, the bay scallop has adapted by using other structures, such as macroalgae, to provide protection from predation.

4. Fisheries

The fishery for bay scallops in Rhode Island waters reflects changes in bay scallop abundance throughout its range in the U.S. Bay scallops were so plentiful in Greenwich Bay in the late 1800's that a portion of the waterfront along Greenwich Cove was referred to as "Scaloptown" (Pesch *et al.* 2012.) However, with the demise of eelgrass beds due to wasting disease, a key habitat for the bay scallop, coupled with overfishing and various environmental insults, the bay scallop populations crashed throughout Rhode Island by the late 1970's. Today, it is a rare occurrence to be able to harvest enough bay scallops to provide a meal, let alone a commercial catch.

5. Population Dynamics

Due to their relatively short life span (2.5 years at the most), the structure of a bay scallop population generally is defined as two year classes, young of the year and 1-year old individuals. Densities of bay scallops can approach 50-75 individuals/m² although these densities are not the norm, which is 5 – 25 individuals/m² in a productive bed.

6. Growth Characteristics

Given its short life span, the bay scallop is a fast growing bivalve that can reach reproductive maturity within the first year of their existence. Growth rates of 3.8 to 4.5 mm per month have been reported in Massachusetts during the summer months (Belding 1910).

7. Ecology

The bay scallop is a key species currently being studied by the US-EPA to better understand the role of environment and environmental stressors in structuring the populations of important aquatic resources. The models generated from these studies (e.g. Table 3.8) will provide information on the link between the environment and the population trends of this commercial resource (US-EPA).

- a. Feeding Habits: Growth is largely dictated by water temperature and food availability, which is a function of food particle density and delivery rate (current speed). Normal feeding position is to sit with its right valve on the bottom, often oriented in the current to allow for the current to augment the pumping action of the cilia on the gills. Flow rate across the animal is thought to influence the growth but the data are conflicting as to what levels of flow may be detrimental to growth.
- b. Parasites and Disease: Mortality due to disease and/or parasites is not routinely observed in wild scallop populations, although a few specific disease situations have been described for cultured bay scallops. One problem commonly observed in wild bay scallops is the occurrence of the commensal pea crab. While they are not direct parasites, they can inflict damage to the scallop soft tissue and disrupt their feeding processes.
- c. Predation: Given its epifaunal life style and its relatively weak shell, the bay scallop is highly susceptible to predation, as is demonstrated by the survivorship estimates suggested by the US-EPA (2014) in Table 3.8. A wide variety of predators attack bay scallops with the most effective being crabs that possess the mobility required to counter the swimming escape response that bay scallops exhibit. Scallops also retain the capacity to byss onto structures throughout their juvenile stages allowing them to attach on structures (e.g. eelgrass) that are elevated off the sediment surface thereby avoiding the normal range of many benthic predators.

Table 3.8. Estimates of survivorship and fecundity for the bay scallop generated by the US-EPA for inclusion in the population dynamics model (US-EPA 2014).

Stage	Survivorship	Fecundity
larvae	0.001%	0
juveniles on SAV	20%	0
benthic juveniles	20-50%	0
adults (year 1)	10-20%	$12.6 \times 10^6 - 18.6 \times 10^6$
adults (year 2)	0%	$6.9 \times 10^6 - 10.2 \times 10^6$

330.5. Blue Mussel (*Mytilus edulis*)

(Newell 1989, DFO 2003, Morse & Rice 2010)

Other common names: sea mussel, common mussel

Table 3.9. Environmental conditions reported for the blue mussel (*Mytilus edulis*).

TEMPERATURE	Overall Range	Optimal Range
Culture Stage	(°C)	(°C)
Spawning	> 10	14.0
Larval rearing	5 - 20	16 - 22
Juvenile to Adult	0 - 29	5 - 20
SALINITY	Overall Range	Optimal Range
Culture Stage	(ppt)	(ppt)
Larval rearing	5 - 34	25 - 33
Juvenile to Adult	0 - 34	30 - 33
DISSOLVED OXYGEN	Critical Levels	
Culture Stage	(mg/L)	
Larval growth		
Juvenile to Adult	>0.1	
pH	Overall Range	Optimal Range
Culture Stage		
Larval growth		7.8 - 8.3
TURBIDITY	Critical level	
Culture Stage	(mg/L)	
Larval growth	> 250	
WATER FLOW	Optimal flow	
Culture Stage	(cm/s)	
Juvenile to Adult	> 10	
SUBSTRATE	Stable, hard surface	

1. Range

Commonly found throughout the northern hemisphere in polar and temperate waters. In North America, it ranges from Labrador, Canada to Cape Hatteras, North Carolina. A related subspecies, *Mytilus edulis platensis*, which may be a separate species (*Mytilus chiensis*), can be found in the southern hemisphere.

2. Morphology and Identification

The blue mussel is an elongated triangular-shaped bivalve where the umbonal beak forms one of the angles in the triangle and the ventral margin forms the other two. It can achieve heights of 7 – 10 cm.

The shell is covered by a shiny black-blue outer layer (periostracum) with fine concentric growth lines.

3. *Habitat*

As an epifaunal bivalve, the mussel lives attached to any form of intertidal or submerged hard substrate using a well-developed byssus thread system. They often congregate into large assemblages with mussel attaching to mussel. Some mussel beds have been reported to be more than a meter in depth. Mussels have the capacity to make and break byssus threads and can move readily if they need to reposition themselves to improve their growth environment. Mussels are both euryhaline and eurythermal, allowing them to survive in a wide variety of estuarine and bayside locations along the Atlantic coastline.

4. *Fisheries*

The blue mussel supports a very small commercial fishery in Rhode Island where it is harvested for bait and for food by bullrake or mechanical dredge. The recreational harvest of mussels for human consumption in RI is probably a much larger demand on the resource over commercial harvest but no data are available on this effort. Recently, efforts have initiated to commercially farm the blue mussel in Narragansett Bay, using continuous rope culture hanging from surface longlines.

5. *Population Dynamics*

Mussel density and size class distribution is affected by a variety of environmental variables (Figure 3.9). Having a high level of fecundity, blue mussel spat can set in very high densities on appropriate substrate. Initial spat settlement in the range of 20 to 200 per cm² has been observed although initial mortality rates can be very high and decreasing as the mussel grows in size. Standing density on a mussel bed has been reported to be 20,000 to 100,000 per m² (Dar *et al.* 2013) In culture on hanging ropes, mussel density stabilizes to 500 to 600 individuals per meter of rope as they approach a 50-60 mm harvest size.

6. *Growth Characteristics*

Figure 3.9 represents factors that influence the structure (density and size class) of a blue mussel population. However, the size class distribution is dependent on the growth rate of the individual mussels such that many of the same factors are the most influential in controlling the growth of the blue mussel. In considering this, under optimal conditions a mussel can grow to 3 inches in length in 2 years while if any of these factors are suboptimal then the time interval to achieve that size can be extended to up to 20 years.

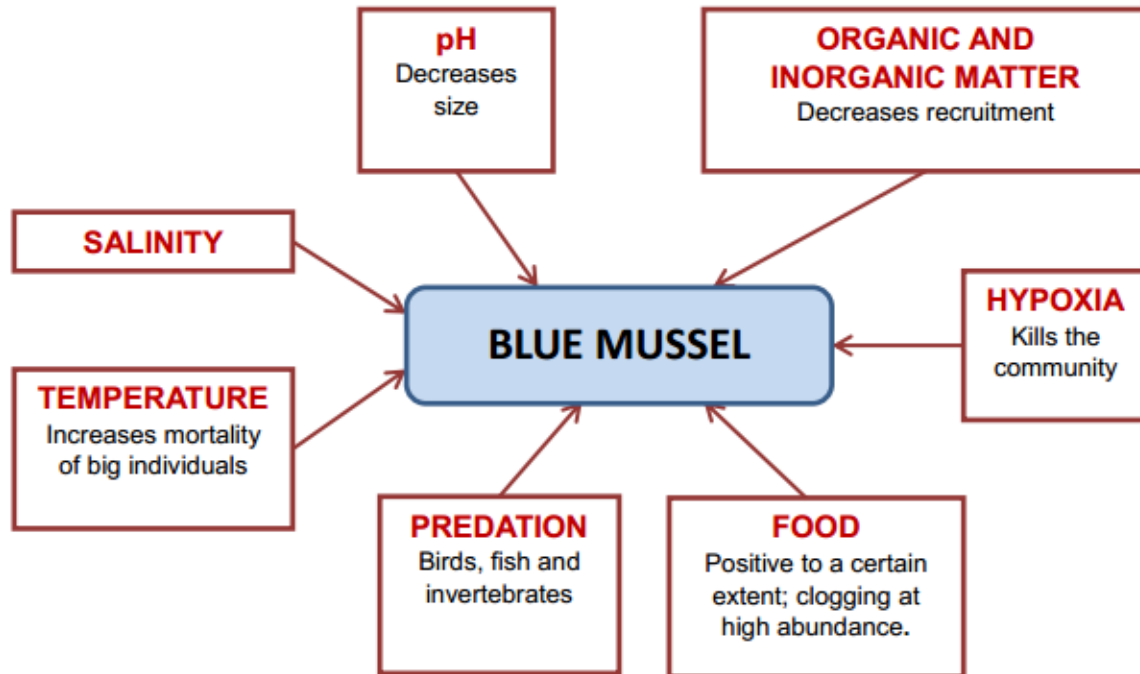


Figure 3.9. Factors influencing blue mussel population structure (from Dar et al. 2013).

7. Ecology

- a. Feeding Habits: As is true of many of the bivalve mollusks, the blue mussel is a suspension feeder. The feed by filtering phytoplankton particles from the water column through the sieving action of the gill filaments and associated mucous. Recent work suggests that the mussel feeds at a continuous rate when chlorophyll levels are between ~0.5 and ~6 mg Chl-a per liter (Riisgard 2011).
- b. Parasites and Disease: While there are a number of pathologies that affect the blue mussel (Table 3.X), relatively few studies have been reported addressing mussel diseases in the Rhode Island area. Current work at the Aquatic Animal Diagnostic Laboratory at Roger Williams University (funded by Rhode Island Sea Grant) is investigating the health status of blue mussels in the Narragansett Bay area.
- c. One parasite that may be an important factor in structuring Narragansett Bay mussel populations is the digenetic trematode, *Proctoeces maculatus* (Sunila et al. 2004). It is routinely observed in local mussels and trematodes similar to this species have been implicated in castrating blue mussels as they invade the gonadal tissue (Newell 1989).
- d. Predation: Predation on the blue mussel is high and originates from a number of predators, including lobsters and crabs, whelks and drilling snails, sea stars, fish and birds. Generally, predation pressure decreases as the individual mussel grows in size and shell strength. As a mussel approaches 4-5 cm in length, it is only susceptible to the largest and most aggressive predators.

330.6. Razor Clam (*Ensis directus*/*Ensis americanus*)

(Kenchington 1998, Leavitt 2010)

Other common names: Atlantic or American jackknife clam, razorfish

TEMPERATURE Culture Stage	Overall Range (°C)	Optimal Range (°C)
Juvenile to Adult	3 - 30	6 - 23
SALINITY Culture Stage	Overall Range (ppt)	Optimal Range (ppt)
Juvenile to Adult	13 - 35	28 - 32
DISSOLVED OXYGEN Culture Stage	Critical levels (mg/L)	
Juvenile to Adult	>3.0	
pH Culture Stage	Overall Range	Optimal Range
Larval growth		
TURBIDITY Culture Stage	Critical level (mg/L)	
Juvenile to Adult	200	
WATER FLOW Culture Stage	Optimal flow (cm/s)	
Juvenile to Adult		
SUBSTRATE	fine sand with little silt	

Figure 3.10. Environmental conditions reported for the razor clam (*Ensis directus*). (Note: Relatively little information is available on preferred or adequate habitat for the razor clam.)

1. *Range*

Commonly found along the North American shore of the Atlantic Ocean from Labrador to South Carolina. In 1978/79, it was introduced into the Elbe estuary in Germany where it has rapidly spread and now ranges from Spain to Norway and the west coast of Sweden and across the English Channel to the UK.

2. *Morphology and Identification*

The razor clam is easily recognized in Rhode Island waters as the shell shape is long and narrow (the length being 5-8 times the width of the shell) with a slight arc to the length. The only other species that approaches this configuration is the stout razor clam (*Tagelus plebius*) but it does not achieve the adult length of up to 10 inches that is observed in the razor clam *Ensis*. The shell is relatively thin and fragile and is covered with a plastic-like tan to brown cuticle (periostracum) that is somewhat hydrophobic and sheds wet sediment readily. A distinguishing characteristic of the razor clam is the large muscular foot that is often observed extending out from the anterior part of the shell in this highly active and mobile bivalve.

3. *Habitat*

Razor clams prefer silt-free sand environments, generally indicating an area with good water flow; however, they have been observed in mud and gravel. They are normally located in the low intertidal to subtidal areas and, most likely, occur out into deep waters, as divers in Narragansett Bay have retrieved them at a depth of 20 feet or more and there is one report of a razor clam retrieved at 101 foot depth in an Army Corp of Engineers Monitoring Report (Charles & Tufts 1997) while Christian *et al.* (2010) report them occurring in waters up to 35 m deep. A similar species in Ireland (*Ensis siliqua*) is routinely harvested at depths exceeding 14 m (46 feet) (Clark & Tully 2011).

4. Fisheries

The harvest of razor clams has traditionally been a small intermittent fishery supplying a very limited market. During the past 10 years, the market for razor clams has dramatically increased such that harvesters can receive \$2.00 to \$6.00 per pound for the product. Traditionally, the harvest has been by hand using a conventional four-tined clam rake or by hydraulic excavation in the intertidal areas during low tide. More recently, local harvesters have used a “salting” technique to extract the clam from the sediment where granular salt is dropped or a saturated salt solution is sprayed in the burrow of the clam resulting in the mobile animal evacuating the burrow (Krzyzewski & Carey 2005).

5. Population Dynamics

The bulk of the information that is currently available on razor clams has resulted from intensive studies performed on the species along the Wadden and North Seas in Europe, where the clam was introduced around 1978. It was feared the clam would out-compete native shellfish species as it established itself in the region. While it has generally been accepted that the introduction will have little adverse effect on native bivalve populations, researchers are now considering commercial uses of the species as the global market demand increases (Freudentahl & Nielson 2005).

E. directus has been reported to initially recruit at exceedingly high levels, for example 2,000 individuals/m² in an established population in Chesapeake Bay (Maurer *et al.* 1974) and up to 30,000 individuals/m² along the French coast, a location where they were recently introduced (Luczak *et al.* 1993). However, razor clams are highly mobile and will routinely redistribute themselves via swimming, crawling and byssal-drifting until they select an appropriate habitat (Armonies 1992). Between redistribution and overwinter mortality, those initial densities can drop to less than 4% of the original density (Beukema 1995), with intertidal survival on the order of 0% at mean tide level (MTL: 80 cm above low tide level (LTL), <10% between MTL and LTL, and >30% at sites exposed during spring tides only (Beukema 1995). Armonies (1999) reported large-scale mass mortalities of razor clams of varying sizes (from 1 year-old to 4 year-old populations) off the island of Sylt in Denmark that may have been disease related although no pathology was reported in the study.

Mortality rates are very high for post-set razor clams and remains relatively high into the second and third years of growth. Dannheim and Rumohr (2012) estimated the mortality rate of the population during years 1 and 2 post-set to be in the range of 74-85% per year (7% per month) with the highest level of mortality occurring in the March to May time interval.

6. Growth Characteristics

Razor clams grow rapidly (up to 12-13 mm per month) where the fastest growth is observed after their first year post-set (Figure 3.11; Dannheim and Rumohr 2012). They can approach their adult length (up to a maximum of 254 mm) within 4-5 years post-set (Figure 3.12).

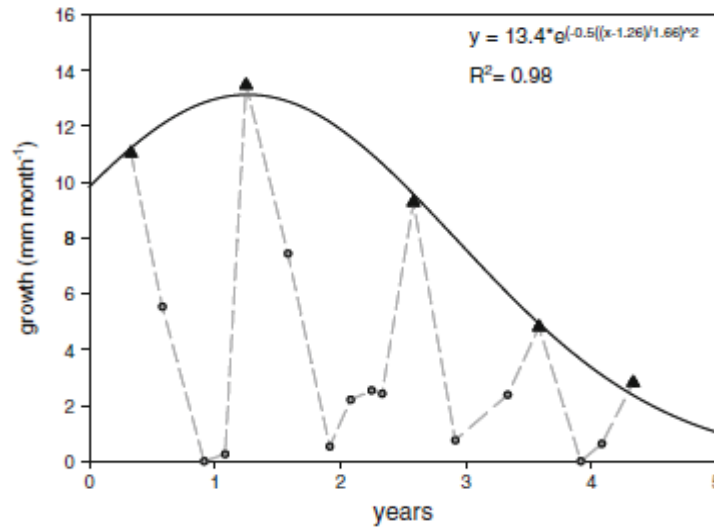


Figure 3.11. Growth rate of razor clams along the inner German Bight as a function of age where the grey circles indicate seasonal changes in growth while the black triangles indicate the maximum growth rate in the summer (from Dannheim and Rumohr 2012).

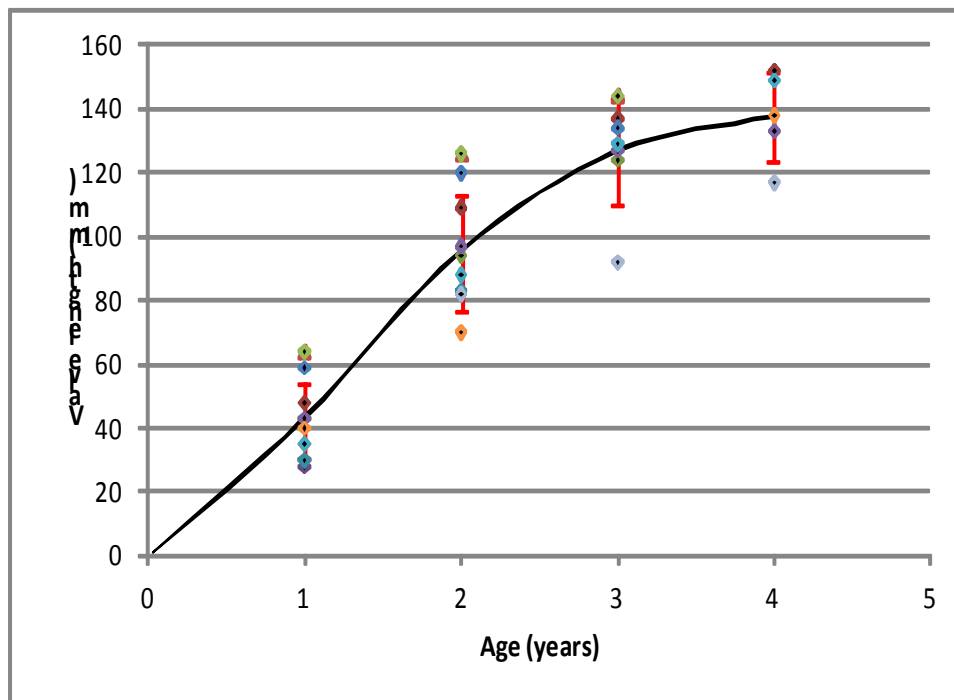


Figure 3.12. The average (\pm standard deviation in red) growth of razor clams reported from a compilation of European studies (modified from Dannheim and Rumohr 2012).

7. Ecology

- a. Feeding Habits: The razor clam is a filter feeder, pumping phytoplankton-laden seawater through their gills and removing the food particles, similar to most other bivalves. Their normal posture when feeding is to reside at the sediment surface, often protruding slightly above the surface (Figure 3.13), to allow the short siphons access to open water.
- b. Parasites and Disease: Mass mortalities have been routinely observed in the European razor clam populations (Dannheim and Rumohr 2012) however researchers have not provided a reasonable explanation as to their occurrence. No surveys have been conducted on disease status of natural

populations of razor clams in the northeastern U.S. region so little is known as to their current susceptibility to disease and parasites. It has been reported that non-native *Ensis directus* in the North Sea region have a high prevalence of parasites routinely found in native bivalves in the vicinity (Krakau *et al.* 2006)

- c. Predation: With their relatively light-weight and fragile shell, razor clams are attacked by a large array of predators. Primarily, they are preyed on by crabs, *Cerebratulus* nemerteans, carnivorous gastropods and birds. The one advantage the razor clam has in avoiding predation is their capacity for rapid movement both in substrate and above the substrate. Winter and Hosoi (2011) reports that the razor clam can dig quickly (~1 cm/second) and deeply (up to 70 cm depth) when disturbed and have been observed avoiding moon snail predation by digging through sediment following the arch of their shell resulting in them backing up out of the substrate meters from the point of initiation of their digging (Schnieder 1982). In addition, they can leap on the sediment surface and swim in a manner similar to the bay scallop (Drew 1907). All of these behaviors are used routinely to avoid predation on the flats.



Figure 3.13. A razor clam, flanked by two infaunal anemones, feeding at the surface by extending its valves into the water column to a small degree (source: <http://www.diverrosa.com/Nederland/Zeelandbrug/ZLB-050713%20Amerikaanse%20zwaardschede,%20Ensis%20americanus.html>).

330.7. Channeled Whelk (*Busycotypus canaliculatus*)

(Magalhaes 1948, Angel 2012)

Other common names: Smooth whelk

Environmental conditions for the knobbed whelk (*Busycotypus canaliculatus*): there is not enough information to construct a table of environmental conditions associated with the biology of the channeled whelk.

1. Range

This whelk species ranges from Cape Cod to central Florida (in the St. Augustine to Cape Canaveral region).

2. Morphology and Identification

One of two large predatory whelks in Rhode Island waters, the channeled whelk easily can be differentiated from its relative, the knobbed whelk (*Busycon carica*), by morphology of the shell. The channeled whelk is generally smaller (maximum length of 17.78 cm and average length of 15.25 cm

and width at its widest part of 6.62 cm in Massachusetts (Gould 1841). As is true of both whelk species, the males are normally smaller than females of the same age. Smooth whelks have a thinner shell and the siphonal area of the shell is narrower and more distinctly differentiated from the main portion of the shell than that observed in the knobbed whelk. There is a markedly hirsute periostracum layer over the exterior of the shell and the animal is a light tan or beige color.

3. *Habitat*

The channel whelks free ranges over a wide variety of habitat types as it searches out prey. It is regularly observed in sand and sand-mud habitats and is often completely buried in the sediment. Alternatively, it can be found on mussel or oyster beds, gliding over the surface seeking out its next meal. This mobile species has been reported to be capable of moving at a maximum rate of 24.9 cm per second (85-90 mm animal at 21-23°C; Shaw 196x). In moving, the channel whelk is more active during periods of low light and appears to move mostly at night during the summer months. It also seems to be more active later in the cold season as it is less sensitive to low temperatures than the knobbed whelk.

4. *Fisheries*

While this species and the knobbed whelk were originally fished to remove them from the population to protect other mollusk resources from predation, the fishery developed about 100 years ago as a food resource. More recently, the value of whelks has been increasing (from \$1.67 per pound in 1967 (Davis and Sisson XXXX) to \$2.07 per pound in 2012 (Angel 2012) as lobster fishing in the region has been falling off, resulting in an increasing fishery on the whelks developing over the past 5 years. Smooth whelks trap more readily than knobbed whelks, e.g. in a pot fishery survey in Narragansett Bay by Angel (2012), 98% of the trapped whelks were channeled whelks. This may reflect differences in feeding behaviors where smooth whelk are more scavengers being attracted to the bait in the trap, compared to knobbed whelks, which may be more predatory and less apt to approach a baited trap.

The whelk fishery in Rhode Island is primarily a baited pot fishery although whelks are routinely captured in dredge and trawl efforts as by-catch and sometimes as a directed fishery in more southern states. The fishery runs from May to December, with the bulk of the effort occurring during the fall season. Regulations governing the whelk fishery are currently under review as more biological information is gathered on the productivity of the populations in the region.

5. *Population Dynamics*

Reproduction in the whelks is very different than other mollusks. Rather than broadcast spawning with free-swimming larvae, the whelks undertake internal fertilization with the larval stages contained in an egg-case manufactured by the female. Length at reproductive maturity, where 90% of the population are reproductively active, is ~ 150 mm for females and 130 mm for males. There is currently an on-going debate as to whether the whelks are protandric hermaphrodites or dioecious, as some researchers report the changing of the morphology of the sex organs as the individual grows (Krauter and Castagna XXXX, Peemohler *et al.* 2013). The egg case for the smooth whelk is distinguished by the shape of the capsules, which are a series of pouches that can contain up to 80-100 individual larvae. The channel whelk capsules are arranged like pages of a book along a central backbone and each capsule is formed of two broad sheets of material joined at the edge as a sharp merging of the two sides (Figure 3.14). Eggs are laid during the summer and fall and it takes about 8 days for a female to deposit a full string of eggs, producing about 12-14 capsules a day with egg production occurring uninterrupted until completion. The egg capsules develop over the winter and hatch, with juvenile whelks being released, in March through May.



Figure 3.14. The egg capsule of the channel whelk (source: <http://matthewwills.com/2011/05/17/whelk-egg-cases/>).

Measuring the density and standing stock of a mobile animal is difficult to do accurately so density estimates are difficult to obtain. In a heavily fished area in Narragansett Bay, the density of channel whelks was estimated at ~10 individuals per 1,000m² (Sisson 1972). A follow up study using a trap-based survey method suggested a density of 11.5 to 17.4 individuals per m². Davis and Sisson (19XX) estimated that a single trap can draw in smooth whelks from a range of 3,300 m² in area surrounding the pot and based this on knowledge of the distance that a whelk can travel over a 12-hour period. Overall, *B. canaliculatus* is 5-6 times more common in local waters than the knobbed whelk (Summer *et al.* 1911).

6. Growth Characteristics

Whelks, in general, are very slow growing animals where it can take up to 8 – 10 years to reach reproductive maturity. In tagging studies, growth was noted to be very irregular and, in many cases, no growth at all (or even negative growth) was recorded over intervals of hundreds of days during the regular growing season (spring through fall) (Castagna and Kraeuter XXXX). It was speculated that the repair of shell damage resulting from feeding activities may account for a diversion of energy from overall growth to shell repair thus stopping overall growth from occurring (Castagna and Kraeuter XXXX).

Aging of whelks can be achieved by counting annual growth rings on the hard operculum associated with the base of the foot. This is easier for channeled whelks due to the thinner nature of the operculum, allowing visual inspection of the growth rings with a light box or microscope. Plotting length at age for Narragansett Bay smooth whelks, Angel (2012) demonstrated the slow growth rate of our local stocks and also allowed us to differentiate the growth rates of the larger females from the smaller males (e.g. Figure 3.15).

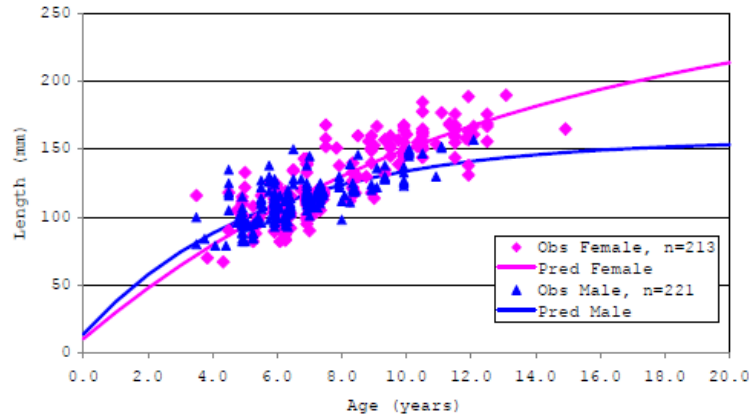


Figure 3.15. Narragansett Bay channeled whelk length at age with sexes separated (Angel 2012).

7. Ecology

- a. Feeding Habits: As noted above the smooth whelk is an active predator and scavenger. The preferred food for the smooth whelk are bivalve mollusks, which they can attack and consume readily using their shell and proboscis. The smooth whelk is not as aggressive in attacking prey as the knobbed whelk, in that it does not seem to use the hammering technique to attack tightly closed bivalves during feeding. Smooth whelks are highly capable of detecting food in their environment as they have a well-developed smell/taste facility that allows them to detect the presence of the bivalve in the vicinity and they can home in on its location readily.
- b. Parasites and Disease: Nothing is currently known on the pathology of whelks.
- c. Predation: The primary predators on whelks are crabs and birds. Large crabs can chip away at the shell margins to gain access to the soft tissue inside while gulls have been observed to lift and drop whelks on hard surfaces to crack the shell open. The primary tool that the whelks use for predator avoidance is the capacity to dig in and bury themselves in soft sediment.

330.8. Knobbed Whelk (*Busycon carica*)

(Magalhaes 1948, Castagna & Kraeuter 1994, Angel 2012)

Other common names: None

Environmental conditions for the knobbed whelk (*Busycon carica*): there is not enough information to construct a table of environmental conditions associated with the biology of the knobbed whelk.

1. Range

This whelk species ranges from Cape Cod to central Florida (in the St. Augustine to Cape Canaveral region).

2. Morphology and Identification

Knobbed whelks can be differentiated from the related smooth whelk by inspection of the shell morphology. The knobbed whelk shell is characterized by having a shoulder whorl that is accentuated by spines projecting off the whorl. The spines are highly variable in number and length but are always present on the knobbed whelk, even as small juveniles where the spines are more like knobs projecting from the whorl.

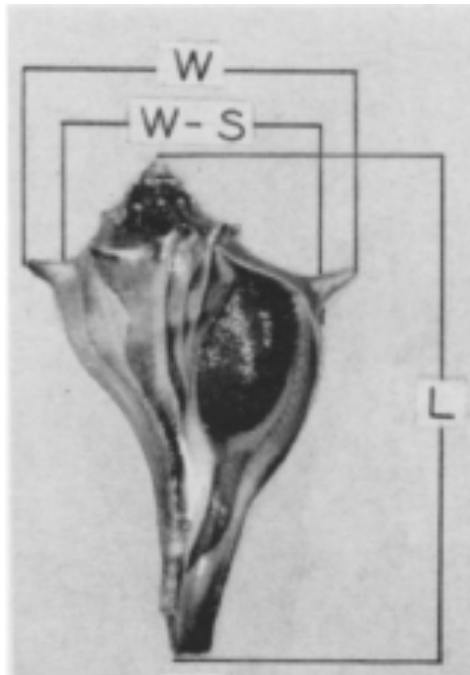


Figure 3.16. Normal measurement taken to describe the size of whelks. *L* is length, *W* is width with spines and *W-S* is width without spines (Magalhaes 1941).

Knobbed whelks are generally larger than smooth whelks with the largest size of knobbed whelks reported as 22 cm in length and 11 cm in width (Pratt 1935) (see Figure 3.16 to differentiate size measurement protocols). As with smooth whelks, the males of the knobbed whelk are generally smaller than females. The shell is grey in color and there is no obvious periostracum present.

3. *Habitat*

Whelks are generally found in shallow waters, up to depths of 46 m (150 feet), and are considered estuarine species as they are more commonly found in the shallow coastal waters. They are active at all times of the day and night, depending on the season and water temperatures and seem to have a higher tolerance to high water temperatures than the channeled whelk. As does the channeled whelk, the knobbed whelk ranges over a variety of habitat types as it ranges for prey. They are reported to be able to move about 15 to 40 m per day, with an average distance of 18 m per day. It is most commonly found in sand or sandy mud where it commonly buries itself in the sediment while seeking infaunal bivalves or avoiding predators.

4. *Fisheries*

Because the knobbed whelk is reported to not trap well, this species is primarily fished with trawling or dredging outside of Rhode Island waters. Along with the channeled whelk, knobbed whelks are being fished more heavily in Rhode Island in recent years, as the landed value increases and the lobster trap fishery declines.

5. *Population Dynamics*

Knobbed whelks also participate in internal fertilization between males and females and extrude their eggs in capsules for protection. Copulation was observed in New Jersey in May-June, egg cases were laid in mid-August to November and the capsule released juvenile whelks in mid-March through early May. The knobbed whelk egg capsule is different from the channeled whelk in that the knobbed whelk capsule has a band of material joining the two flat sides of the capsule resulting in a squared flat outer edge (Figure 3.17).



Figure 3.17. The egg capsule of the knobbed whelk (source: <http://matthewwills.com/2011/05/17/whelk-egg-cases/>).

6. Growth Characteristics

As was observed for the channeled whelk, growth in the knobbed whelk is periodic and irregular. Fastest growth is observed in the smallest individuals, e.g. lab reared whelks grew from 4 – 36.5 mm in the first year but it took them 10 years to grow to 144 mm and 14 years to get to 168.6 years (Figure 3.18). The bulk of their annual growth occurs during the interval of May to October, when water temperature is the warmest and food is plentiful. However, it is not uncommon to observe knobbed whelk that demonstrate negative growth over a measured time interval due to damage to the siphonal beak resulting from predatory activities. Based on observation by Angel (2012) the size at which 90% of the female population in sexually mature is ~150 mm and for the males it is 90-100 mm. Castagna and Kraeuter (XXXX) didn't observe viable egg cases generated by their captive population in the laboratory until 14 years of age.

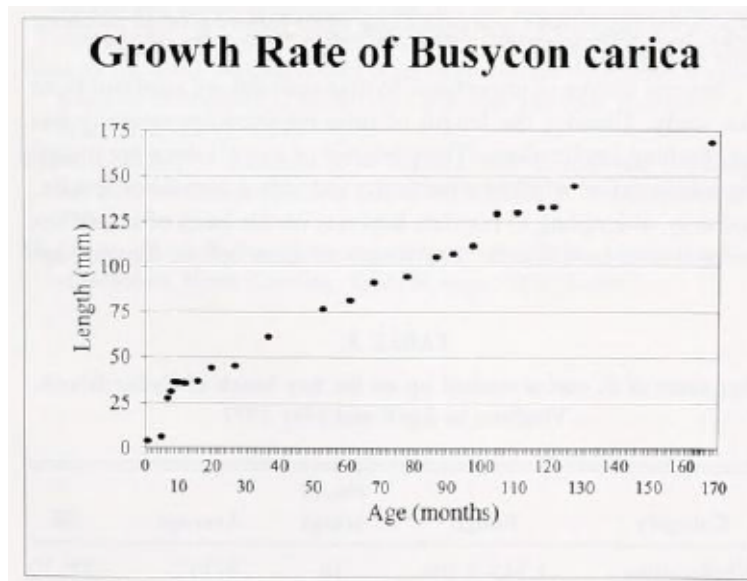


Figure 3.18. Growth of *B. carica* in the laboratory (Castagna and Kraeuter 1994).

7. *Ecology*

- a. Feeding Habits – Knobbed whelks prefer bivalve mollusks as their food and aggressively attack them. It is reported that the knobbed whelk uses the common tactic for opening bivalves by inserting their siphonal beak into a gaping pair of valves. However, they are also reported to undertake a hammering action, attempting to break away portions of the prey’s shell by forceful blows with their beak area. It is reported that they can open a medium sized quahog in about 12 minutes with this technique. Castagna and Kraeuter (1994) report that the quahog is the preferred prey for the knobbed whelk and they can consume about 1 clam per week (Carriker 1951).
- b. Parasites and Disease – Nothing is currently known on the pathology of whelks.
- c. Predation – The primary predators on whelks are crabs and birds. Large crabs can chip away at the shell margins to gain access to the soft tissue inside while gulls have been observed to lift and drop whelks on hard surfaces to crack the shell open. The primary tool that the whelks use for predator avoidance is the capacity to dig in and bury themselves in soft sediment.

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