Potential interactions between populations of Softshell Clams *(Mya arenaria*) and Eastern Oysters (*Crassostrea virginica)* in temperate estuaries, a literature review

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POTENTIAL INTERACTIONS BETWEEN POPULATIONS OF SOFTSHELL CLAMS (*MYA ARENARIA*) AND EASTERN OYSTERS (*CRASSOSTREA VIRGINICA*) IN TEMPERATE ESTUARIES, A LITERATURE REVIEW

by

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ABSTRACT

This literature review summarizes results from studies on Softshell Clams (*Mya arenaria*) and Eastern Oysters (*Crassostrea virginica*). The main objective of the review is to provide a comprehensive outlook of potential interactions between wild and cultivated bivalves in temperate estuaries. The review first describes the biology (e.g.: life cycle, feeding habits) and ecology (e.g.: habitat, distribution, competition, predation) of both species. Effects from pathogens are also reviewed. The review then focuses on potential interactions between natural populations of the two species. Potential interactions between cultivated Eastern Oyster and wild Softshell Clam populations are finally presented.

RÉSUMÉ

Cette revue de littérature résume les résultats d'études effectuées sur la mye commune (*Mya arenaria*) et de l'huître américaine (*Crassostrea virginica*). L'objectif principal de la revue est de fournir une perspective détaillée des interactions potentielles entre des populations cultivées et naturelles de bivalves vivant en milieu estuarien tempéré. La revue débute par une description de la biologie (e.g. cycle de vie, alimentation) et de l'écologie (e.g. habitat, distribution, compétition, prédation) des deux espèces. Les effets des organismes pathogènes sont également présentés. La revue porte par la suite sur les interactions potentielles entre des populations naturelles des deux espèces. Les interactions potentielles entre des huîtres américaines cultivées et les myes communes retrouvées en milieu naturel sont finalement présentées.

1. INTRODUCTION

Estuaries and sheltered bays represent the main habitats for many species of coastal bivalves that live in or on bottom sediments (e.g.: Little, 2000). These habitats are common in eastern Canada, where a great supply of nutrients from rivers, rocky shores, and salt marshes makes estuaries and bays productive areas for bivalves and other benthic marine organisms (Fisheries and Oceans Canada, 1996). Bivalves have a great influence on the physico-chemical characteristics of estuarine ecosystems which, in turn, provide a permanent or temporal habitat for several plant and animal species. Bivalves are also important modulators of suspended materials and nutrients and a food source for many predators, including humans.

Bivalve fisheries support an important industry throughout Atlantic Canada, including Quebec (QC), New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PEI) and Newfoundland and Labrador (NL). The main species harvested in the littoral zone are the Blue Mussel (*Mytilus edulis*), Eastern Oyster (*Crassostrea virginica*), and several clam species such as the Softshell Clam (*Mya arenaria*), Northern Quahog (*Mercenaria mercenaria*), Surf Clam (*Spisula solidissima*) and common Razor Clam (*Ensis directus*). All these bivalves may coexist in temperate estuaries along the North-West Atlantic coastline.

Eastern Oysters have sustained an important fishery in the southern Gulf of St. Lawrence (sGSL) since the early days of colonization (Morse, 1971). By the mid 1800's, there was already some evidence of excessive fishing pressures on the resource with notable declines in landings and losses of natural oyster reefs in a number of bays (Morse, 1971). In addition, oyster beds nearly disappeared in PEI around 1915 and in NB and NS in the 1950s because of an unidentified epizootic event commonly known as Malpeque disease (Lavoie, 1995). The combined effects of stock reduction due to disease and fishing pressures resulted in a decline in Eastern Oyster stocks throughout the sGSL in the order of 90-99% (Lavoie, 1995) and may have affected the distribution and abundance of other bivalve species due to alterations in habitat availability, competition for food and space, and predator-prey relationships of the original ecosystem.

Eastern Oysters were reintroduced throughout the sGSL starting in the late 1960's from stock resistant to Malpeque disease in order to re-establish natural oyster beds and to supply market demands (Lavoie, 1995). Oyster farming activities gradually expanded during the same period (Morse, 1971; Milewski and Chapman, 2002) with a marked shift towards the use of suspended growing techniques starting in the late 1980's. This trend is believed to have modified the population dynamics of oysters, with a reduction in harvesting from natural beds and a gradual increase in harvests from cultivated beds. With this shift, concerns about possible interactions between cultured oysters and wild shellfish species have been raised. In particular, concerns about the potential interactions between cultivated oysters and wild Softshell Clam populations were broached during a number of public consultations with Softshell Clam harvesters.

This comes at a time when Softshell Clam populations throughout the sGSL are experiencing significant reductions attributable to a number of factors, including fishing pressure. For instance, the introduced Green Crab (*Carcinus maenas*) has been demonstrated to contribute to the decline of Softshell Clams in certain estuaries in the sGSL (Floyd & Williams, 2004). Since 1999, a high prevalence of haemocytic neoplasia of clams (80 to >95%) has been detected in association with mortalities in a few locations in Atlantic Canada (Bower, 2005). Physical destruction and disturbance of habitats, input of anthropogenic contaminants and nutrient enrichment leading to eutrophication are among the other stressors that are suspected of affecting Softshell Clam overall population structure and dynamics (Bower, 2005, McDowell *et al.* 1999). In light of these concerns, Fisheries and Oceans Canada (DFO) commissioned this study to the Université de Moncton to assess potential interactions between these two species, under both wild and cultured scenarios.

To better understand the interactions between cultured and wild bivalves it is important to look at the general biology of the species to identify the levels at which they may share common characteristics. Interactions between cultured bivalves and the environment, including their association with other wild species, have been outlined in various studies (e.g.: Mazouni *et al*., 2001; Cranford *et al*., 2003; Newell, 2004; Ruesink *et al*., 2005; Miron *et al*., 2005; McKindsey *et al*., 2006; Vandermeulen *et al*., 2006 and references therein). These studies usually looked at interspecific competition for food resources, dissolved and particulate material fluxes between cultured bivalves and the water column and the effect of biodeposits on the sea bottom. To our knowledge, very few studies have looked at the specific relationship between the Eastern Oyster and the Softshell Clam. Thus, inferences on potential interactions were made by considering studies with species occupying similar niches.

The present work is a literature review of the biology and ecology of the Softshell Clam and the Eastern Oyster. It summarizes results from studies done in temperate coastal ecosystems on specific biological and ecological aspects of both species. The information gathered is intended to help stakeholders and managers understand the biology and habitat requirements of these species. The review underlines how each of these species may influence the abiotic and biotic components that characterises sGSL estuaries, and focuses on potential interactions that may be inferred by their respective biology and uses of aquatic habitats during various life stages.

2. SOFTSHELL CLAM [1]

The Softshell Clam (*Mya arenaria* Linnaeus, 1758) is a bivalve mollusc with a thin and brittle, chalky white shell that appears grey or yellow in young individuals and almost black in individuals living in areas with high organic content (Fisheries and Oceans Canada, 1993). Its shell is oval, rounded and slightly elongate in outline and gaps at both ends; they have long incurrent siphons that draw in food but which cannot be fully withdrawn into the shell (see Figure 1). It is an important commercial, recreational and traditional resource in the Maritimes. Early records and archaeological evidence (two to three thousand years) indicate that the Softshell Clam was an important component of aboriginal diet and subsequently of European settlers (Fisheries and Oceans Canada, 1997; Milewski and Chapman, 2002). Today, over 600 commercial clam fishing licences are issued every year in eastern NB alone. The estimated mean annual landing value of the commercial Softshell Clam fishery reached $700,000 in NB in 2003 (Fisheries and Oceans Canada, 2005a).

2.1. Distribution

The Softshell Clam is widely distributed in coastal waters of both North American and European coastal waters. Abraham and Dillon (1986) noted that the most significant factor affecting Softshell Clam distribution is salinity; the species tends to be euryhaline (10-25 ppt), with some of the population overlapping in lower and higher salinity zones. In general, its latitudinal distribution is influenced by water temperature. The Softshell Clam is found from Labrador to Cape Hatteras (North Carolina) along the east coast of North American. It is abundant in Chesapeake Bay and northward but scarce in the south (Tyler-Walters, 2003). On the eastern Pacific coast, it has spread to south of Monterey (California) and northward up to Alaskan waters. It is also found from the Kamchatka Peninsula (Russia) to the northern regions of the Japanese islands along the western Pacific coast (Ristich *et* al, 1977; Fisheries and Oceans Canada, 1993).

In the Maritimes, the Softshell Clam is found from the intertidal zone to a depth of 9 m throughout NB, NS and PEI (Fisheries and Oceans Canada, 1996). Softshell Clam beds

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[1] Synonyms: soft clam, squirt clam, steamer, longneck, long clam, belly clam, nannynose or sand gaper.

are found at various locations along the coastline of the Bay of Fundy, the Northumberland Strait, the Baie des Chaleurs, and Baie St. Georges (LeBlanc and Miron, 2005, 2006).

2.2. Life cycle

2.2.1. Gametes and reproduction

The Softshell Clam is a dioecious species that reaches sexual maturity at about four years, depending on the latitude (Strasser, 1999; Fisheries and Oceans Canada, 2001a). In the sGSL, sperm and egg maturation is usually complete by the month of June and spawning can occur between early June and early July (Sullivan, 1948; Fisheries and Oceans Canada, 2001a). In the Maritimes, spawning peaks are generally observed in mid-July and are linked to monthly tidal cycles and warmer water temperatures (Fisheries and Oceans Canada, 1993). Males usually spawn first. They release a pheromone in the water column at the same time that stimulates females to spawn (Newell and Hidu, 1986). Among the potential spawners, approximately 25% will release their gametes.

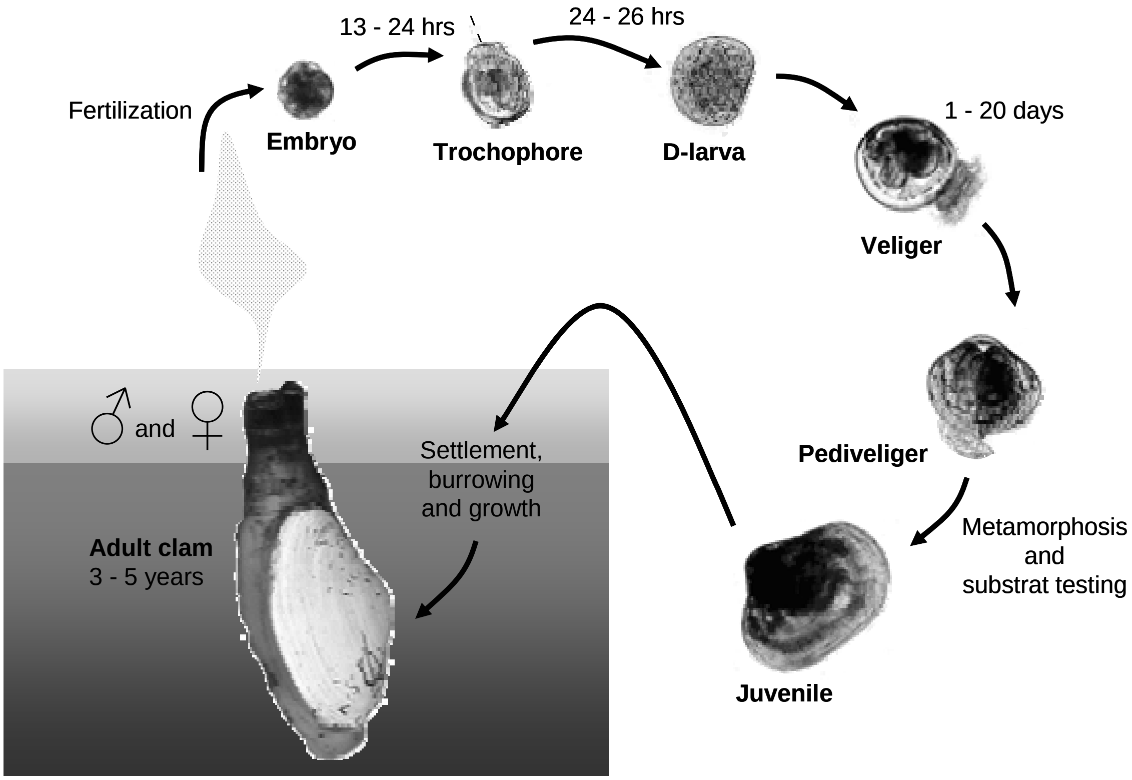

Figure 1: Life cycle of the Softshell Clam <u>Mya arenaria</u> (adapted from Abgrall, unpublished)

Fertilization is external. Eggs and sperm are released in the water through the excurrent siphon (Figure 1). A ratio of 7-10 spermatozoons per egg is needed to ensure fertilization. The fecundity of Softshell Clams is very high, offsetting high egg and larval mortalities. The number of eggs per female varies from 120,000 to 5 million,, depending on the physical environment and female size (Strasser, 1999). Less than 0.1 % of the eggs produced in a spawning season result in successful settlement (Newell and Hidu, 1986). Since mortality rate decreases and fecundity increases with clam size, the older and larger individuals of the population contribute most of the settlers (Newell and Hidu, 1986). The fertilized egg develops into a trochophore larva after 13 to 24 hours. Trocophores are able to swim at the water surface where they feed on microplanktonic organisms. The trochophore larva metamorphoses 24 hours later into a veliger larva. Veligers have a ciliated organ called velum which is used for locomotion and to gather small food particles during larval feeding (Zardus and Martel, 2002).

2.2.2. Veligers

Free-swimming larvae that are between 1 and 20 days old are called veligers (Figures 1 and 2). They usually remain in the water column for a period of about two weeks before settling on the sediment. During their planktonic stage, the larvae are subject to tidal and wind-driven currents, waves, and other events that affect water movement. Water movement in turn affects larval dispersal.

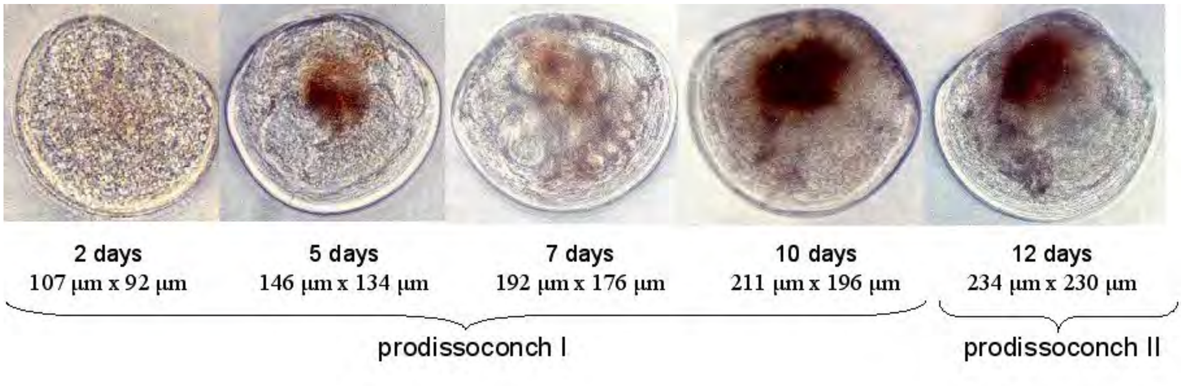

Figure 2: Softshell Clam veligers at different ages. Veligers can be divided into prodissoconch I and prodissoconch II. The latter is characterised by the formation of a beak-like projection called umbo (Doiron, 1997).

Veligers are adapted to live long periods in the water column and, as their mobility increases, their behaviour tends to increase in complexity to respond to various environmental stimuli related to orienting, feeding and dispersing (Zardus and Martel, 2002). Most bivalve veligers possess several sensory organs that allow them to respond to light (phototaxis), gravity (geotaxis) and pressure (Zardus and Martel, 2002). They swim upward in a helical path (Jonsson *et al.*, 1991). Gravity and light normally act as orientation cues allowing veligers to migrate vertically (Chia *et al*, 1984; Zardus and Martel, 2002). Larval distribution is also often related to the presence of high food concentrations near the surface (Raby *et al.*, 1994; Dobretsov and Miron, 2001). It is not known if Softshell Clam veligers display daily vertical migration. Such behaviour would allow them to stay near the bottom during the day, to escape predators, and swim near the surface at night to feed on other plankton.

The distribution and migration of larvae in the water column are linked to a combination of behavioural responses (Kingsford *et al.*, 2002) and hydrodynamic features (Tremblay and Sinclair, 1990). Behavioural responses in most bivalve larvae are often linked to turbulence as well as to pressure, temperature and salinity gradients. Raby *et al.* (1994) observed in the Baie des Chaleurs (Quebec) that Blue Mussel veligers tend to aggregate below the halocline. In contrast, Tremblay and Sinclair (1990) observed that sea scallop veligers were unable to aggregate below the halocline in shallow areas off the coast of Grand Manan Island (NB). Such responses have not been studied for Softshell Clam larvae.

2.2.3. Pediveligers

Softshell Clam veligers metamorphose into pediveligers. During metamorphosis, the larva loses its velum and develops a muscular foot (Figure 3). The loss of the velum contributes to a major reduction in larval swimming and feeding abilities. The effectiveness of the cilia as a means of locomotion thus decreases with larval size (Chia *et al.*, 1984). Pediveliger size varies between 0.25 and 1 mm (Aucoin *et al.*, 2004).

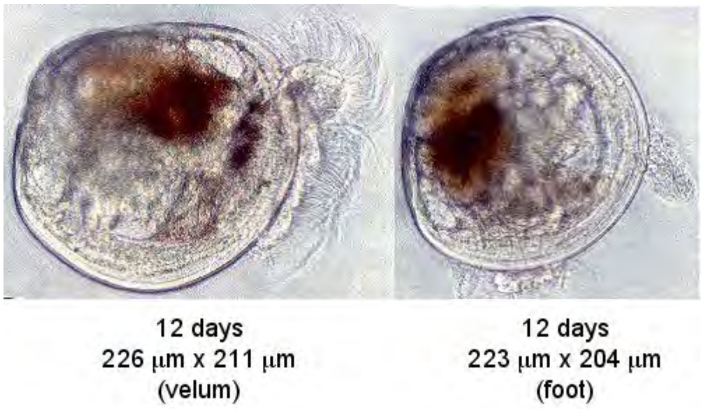

Figure 3: Softshell Clam pediveligers showing the loss of the velum and the development of the foot (Doiron, 1997).

This larval stage lasts for between 12 and 16 days and is characterized by its exploration of the substrate and subsequent settlement. Pediveligers can postpone settlement for up to 30 days and continue their growth until they find a suitable substrate (Tyler-Walters, 2003). In contrast to veligers, the size of pediveligers at the time of settlement depends on the availability of suitable substrates rather than on food availability (Aucoin *et al.*, 2004).

Bivalve pediveligers display negative phototaxis and positive geotaxis near the time of settlement (Bayne, 1965; Zardus and Martel, 2002). This behaviour is influenced by water current. Jonsson *et al.* (1991), for instance, showed that common cockle (*Cerastoderma edule*) larvae descend to the bottom by gravity when water flow is slow. These larvae were confined to the layer immediately above the substrate (i.e. viscous sub layer) at flow > 10 cm/s, and drifted above the sediment in the flow direction.

2.2.4. Juveniles

Softshell Clam pediveligers metamorphose into juveniles at a size of approximately 1 mm. Newly metamorphosed juveniles settle to the bottom where they crawl and explore the substrate with their extensible foot (Figure 4). Early juveniles remain fairly mobile.

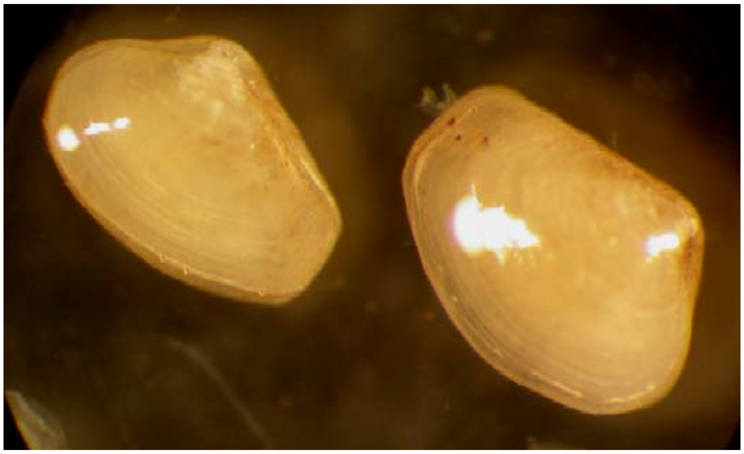

Figure 4: Softshell Clam juveniles showing a thicker and darker shell (Abgrall, unpublished).

Exploration and settlement depend on the type of substrate and surrounding flow regimes. Juvenile clams may get resuspended or eroded from the sediment's top layer and relocate themselves (Roegner *et al.*, 1995; Norkko *et al.*, 2001; Hunt, 2004a,b, 2005). This allows individuals to resettle in a more suitable substrate by drifting with the flow. The relocation may be active or passive. Juveniles may also temporarily anchor themselves to small sediment particles with their byssal threads (Newell and Hidu, 1986; Fisheries and

Oceans Canada, 1993). These particles may be moved by tidal and wind-driven currents, thus increasing their risk of resuspension (Sigurdsson *et al.*, 1976; Hunt and Mullineaux, 2002). Juveniles may then release their byssal attachment and burrow quickly into the sediment to avoid bedload transport. Softshell Clam juveniles become less mobile as they grow and start to lose their ability to relocate. Limited by the length of their siphon, juveniles usually burrow in the top 2 cm of the sediment (Hidu and Newell, 1989). They establish a permanent burrow when they reach a size of about 6 mm. The Softshell Clam burrows deeper by using its extensible and mobile foot as its size increases (Tyler-Walters, 2003; Fisheries and Oceans Canada, 1993).

2.2.5. Adults

In the Maritimes, Softshell Clams become mature at a shell length of about 35 to 40 mm. They can be harvested when they reach 50 mm. In warmer areas, the Softshell Clam reaches sexual maturity earlier and is considered an adult at a size of ≥ 25 mm (Figure 5) (Tyler-Walters, 2003). Growth rate varies seasonally and depends on food availability and various environmental factors (Newell and Hidu, 1986).

Figure 5: Softshell Clam adult with the foot and siphon exposed (Abgrall, unpublished).

Adult growth rate is also related to current, sediment type, and intertidal height. The shell of adults can reach a maximum length of about 10 cm. Some individuals have been reported to exceed 15 cm (Fisheries and Oceans Canada, 1993). Growth rate varies during the year with slow growth in late spring and late fall and a period of relatively rapid growth in the summer (Beal *et al*., 2001). Softshell Clams usually live 10 to 12 years. However individuals over 25 years old have been recorded in the Bay of Fundy (Strasser, 1999; Tyler-Walters, 2003).

2.3. Habitat

2.3.1. Substrate

Softshell Clams are ubiquitous, year-round endobenthic residents of the sGSL. They generally inhabit intertidal and the shallow subtidal zones, although a few individuals may be found at greater depths, some having been reported in areas between 150 and 200 m (Strasser, 1999). Juveniles and adults usually inhabit mud or sand flats and are unevenly distributed in patches (Abraham and Dillon, 1986; Newell and Hidu, 1986; Banner and Hayes, 1996). Clams may also be found in hypoxic or anoxic environments. There, they use the calcium carbonate from their shell to buffer the acidic products of anaerobic respiration (Newell and Hidu, 1986). Since excessive silt tends to reduce growth rates, Softshell Clams are usually found in sediment with a silt composition < 50 % (Newell & Hidu, 1986). They have greater difficulty burrowing in sediments where the mean particle size is > 0.5 mm. Individuals inhabiting coarser sediment invest more energy in shell width and thickness than length (Newell and Hidu, 1982). The Softshell Clam grows faster on the lower shore where food is more abundant. In the Maritimes, suitable substrates for Softshell Clams are found in estuaries, embayments, tidal mudflats and sandy beaches (Fisheries and Oceans Canada, 1996; LeBlanc and Miron, 2005).

Marine estuaries and tidal flats present important challenges for Softshell Clams. These habitats are feeding grounds for predators such as lobsters, crabs, gastropods and over-wintering waders and shorebirds. Marine estuaries are also physically challenging since these habitats change constantly and tend to accumulate sediments from rivers, streams, brackish marshes, salt marshes, and sand dunes (Little, 2000). Despite the effects of the dominant regional tidal regime, their population dynamics are mostly regulated by local small-scale hydrodynamics (Leblanc and Miron, 2006). In addition to variation in sediment sizes, Softshell Clams are also exposed to variation in sediment composition (organic and inorganic material). When sediments contain large amounts of organic matter, breakdown by bacteria can lead to considerable O_2 depletion and the accumulation of H_2S in the sediments (Hamilton, 1985; Wang and Chapman, 1999). The vertical position of the clam's siphon in the sediment determines the clam's rate of O_2 consumption and the length of time it can sustain O_2 depletion (Collip, 1921). Adult clams may tolerate higher H_2S concentrations than small individuals that are unable to detoxify H_2S effectively and are therefore more vulnerable to H_2S (Jahn *et al.*, 1997; Laudien *et al.*, 2002).

As discussed earlier, sediment type also affects the resuspension of small Softshell Clams, especially when flow speed is relatively strong (29-35 cm/sec.). Softshell Clam reburies itself by pulling its body into the sediment with the help of a strong muscle located near its pedal opening. The burrowing depth of the Softshell Clam is related to its size (e.g.: Medcof, 1950; Pfitzenmeyer and Droebeck, 1967). According to St-Onge *et al*. (2007), juvenile Softshell Clams are capable of initiating burrowing in gravel and coarser sediments. They are, however, less successful in completing their burrow than in fine sediments (e.g.: sand and mud). Individuals are more susceptible to be dislodged by flows in sandy sediments than in coarser sediments; muddy sediments tend to retain juveniles more easily (St-Onge and Miron, 2007).

Softshell Clams show low tolerance to substratum loss (Tyler-Walters, 2003). When dug up or eroded from the sediments, smaller Softshell Clams (up to 40 mm) can burrow rapidly; they are then usually found near the sediment surface. Large adult individuals will have more difficulty in re-burrowing if found at the sediment surface. Orientation also plays a role in reburial rate (Ambrose *et al*., 1998). Ambrose *et al.* (1998) observed that both large and small Softshell Clams placed in vertical positions reburied more rapidly and to greater depths than they were initially positioned in than Softshell Clams placed in horizontal positions, which reburied to shallower depths than they were original positions.

2.3.2. Physico-chemical conditions

Like other benthic organisms, Softshell Clams living in estuaries must live in an environment where the salinity is spatially and temporally variable (Little, 2000). Salinity is the most significant abiotic factor affecting the distribution of Softshell Clams (Abraham and Dillon, 1986). Adults are tolerant to a wide range of salinities (10-35 ppt) (Abraham and Dillon, 1986). The Softshell Clam responds to salinity changes by closing its valves (Tyler-Walters, 2003) or by gradually reducing the rate at which it pumps water. Matthiessen (1960a) found that pumping rate varied slightly in waters between 15.5-31 ppt, became sharply reduced at salinities below 8 ppt and appeared to cease altogether at salinities of less than 4 ppt. According to Kennedy and Milhursky (1972), adult Softshell Clams require a salinity of at least 5 ppt to survive. Larvae are more sensitive to low salinities than adults. The optimal salinity for veliger and pediveliger development lies between 16 and 32 ppt, while the optimal salinity for growth and survival of juveniles and adults is between 15 and 20 ppt (Banner and Hayes, 1996).

Beal *et al.* (2001) found that rates of growth for Softshell Clams differed among locations along the tidal gradient: clams in beaches near St. Andrews, NB grew 35% faster in the lower intertidal area than in the upper one and similar results were observed near Rimouski, QC. Clams in the upper intertidal area are subjected to greater air exposure and may experience more spawning stresses and more variations and/or extremes in temperature, salinity, and oxygen concentration. Diminished food exposure may also create physiological conditions where a Softshell Clam's metabolism and ability to store and digest phytoplankton is impaired (Beal *et al.* 2001).

Variation in water temperature is also an important factor for the Softshell Clam. In the sGSL, estuaries tend to be shallow and semi-enclosed, with temperatures slightly higher than in open areas. According to Kennedy and Milhursky (1972), the adult Softshell Clam cannot survive when exposed to temperatures greater than 28ºC or less than -2ºC. However, individuals living in higher intertidal zones are more tolerant of temperature fluctuations than ones living in lower intertidal zones. The optimal water temperature for veligers and pediveligers survival is between 18ºC and 22ºC (Banner and Hayes, 1996). Water temperature also influences the length of larval life. Metamorphosis and settlement behaviouris delayed at lower temperatures (Newell and Hidu, 1986). The optimal temperature for juvenile survival and development is between 12ºC and 19ºC. The ideal water temperature for gonad maturation and spawning is between 15ºC and 21ºC (Newell and Hidu, 1986; Banner and Hayes, 1996).

Water temperature also influences the feeding and oxygen consumption rates of Softshell Clams, as does body size, metabolic rate, and oxygen concentration. However, at higher water temperatures filtration rate may decrease and some bivalve species may starve to death. While feeding, pumping rates increase with increasing temperature (Harrigan, 1956). At low temperatures (1 - 2°C), individuals continue to pump, but the rate of food assimilation is low. Changes in water temperature also regulate burrowing rates. In Chesapeake Bay, burrowing rates were greatest at 18°C, moderate from 9 to 17 and 19 to 21°C and very low at temperatures < 9°C or > 21°C (Pfitzenmeyer and Drobeck 1967). Beal *et al.* (2001) observed that burial depth is greater in fall and winter compared to spring and summer and that this was associated with decreased risk of clam mortality, since the sediment generally protects clams from extremes in temperatures. Peak mortalities in Maine were observed in late summer when water temperatures were warmest and predator activity was, coincidentally, highest (Beal *et al.*, 2001).

2.3.3. Turbidity

Adult Softshell Clams are less affected by turbidity than juveniles. Depending on the nature of the suspended particles, filter-feeding bivalves may play a major role in reducing turbidity in aquatic ecosystems (Working Group on Marine Shellfish Culture, 2003). In general, filter-feeding bivalves are able to sort out less edible particles that they may inhale in their siphons. However, when the concentration of suspended particles becomes too high, filtration rates may decrease and some bivalve species can suffocate if they take in too many inedible particles (Stern and Stickle, 1978). Decreases in light attenuation caused by increased turbidity may lower phytoplankton and algal productivity and, therefore, diminish the food available to Softshell Clams (Tyler-Walters, 2003).

2.3.4. Currents

River flow and tidal currents play an important role in mixing the lower and upper water layers of estuaries and in modulating their productivity (Little, 2000). The rise and fall of tides creates turbulence which results in upwellings, downwellings and nutrient mixing, thus helping to distribute food to the endobenthos. Ebb and flood tides are very important for bivalve larval dispersal in estuaries and nearshore areas (Young, 1995). While vertical migration is mostly done by active swimming, lateral dispersal is enhanced by currents and tides (e.g. Gosling, 2003). Turbulence caused by wind, waves, currents and tides, both at the bottom and surface of the water, influences larval food encounter rates for Softshell Clam veligers (Young, 1995). Although turbulence may increase food encounter rates, it may also increase the risk of encountering a predator. Though the specific response of Softshell Clam larvae to turbulence is not known, they are believed to be able to detect turbulence by detecting shear velocity. Tactile simulus tends to make them withdraw their velum and thus reduces their mobility (Young, 1995).

Settlement of pediveligers and transport of juveniles are also influenced by turbulence. High turbulence may break or decrease the thickness of the viscous sublayer - the very thin region next to the bottom where turbulent mixing is impeded. Several studies by Hunt (2004 a,b) demonstrated that both hydrodynamics and active behaviours play an important role in determining the erosion and final distribution of juvenile Softshell Clams.. Hunt and Mullineaux (2002) observed that clams < 2 mm are regularly redistributed by tidal currents. As Softshell Clams grow, resuspension becomes less important due to their burrowing behaviour (Hunt and Mullineaux, 2002). Matthiessen (1960b) observed that the zonal distribution of small Softshell Clams was strongly influenced by hydrodynamic forces; as a result, small clams (2 – 15 mm) were subject to considerable changes in distribution in intertidal areas. Sediment characteristics vary with water current velocity. Coarse sediments are indicative of stronger currents while high silt-clay sediments tend to reflect slower currents. Since the Softshell Clam is found in various types of sediments, it is suggested that they can adapt to various flow regimes. Areas with strong currents often support high densities of Softshell Clams (Newell & Hidu, 1986; LeBlanc and Miron, 2005).

Water currents and wave exposure affect sediment surfaces. These factors usually increase the turbulence near the bottom and create particle movement and erosion. For instance, high wave exposure will erode fine sediments whereas low wave exposure will increase their deposition. Particle movement and erosion may lead to habitat alterations and/or Softshell Clam erosion (Dow & Wallace, 1961). Despite the patchy nature of their distribution and recruitment, Softshell Clam settlement success is considered to be high (Tyler-Walters, 2003). Figure 6 summarizes the effect of hydrodynamics on sediment types and various benthic processes, as well as on the production and behaviours of benthic communities.

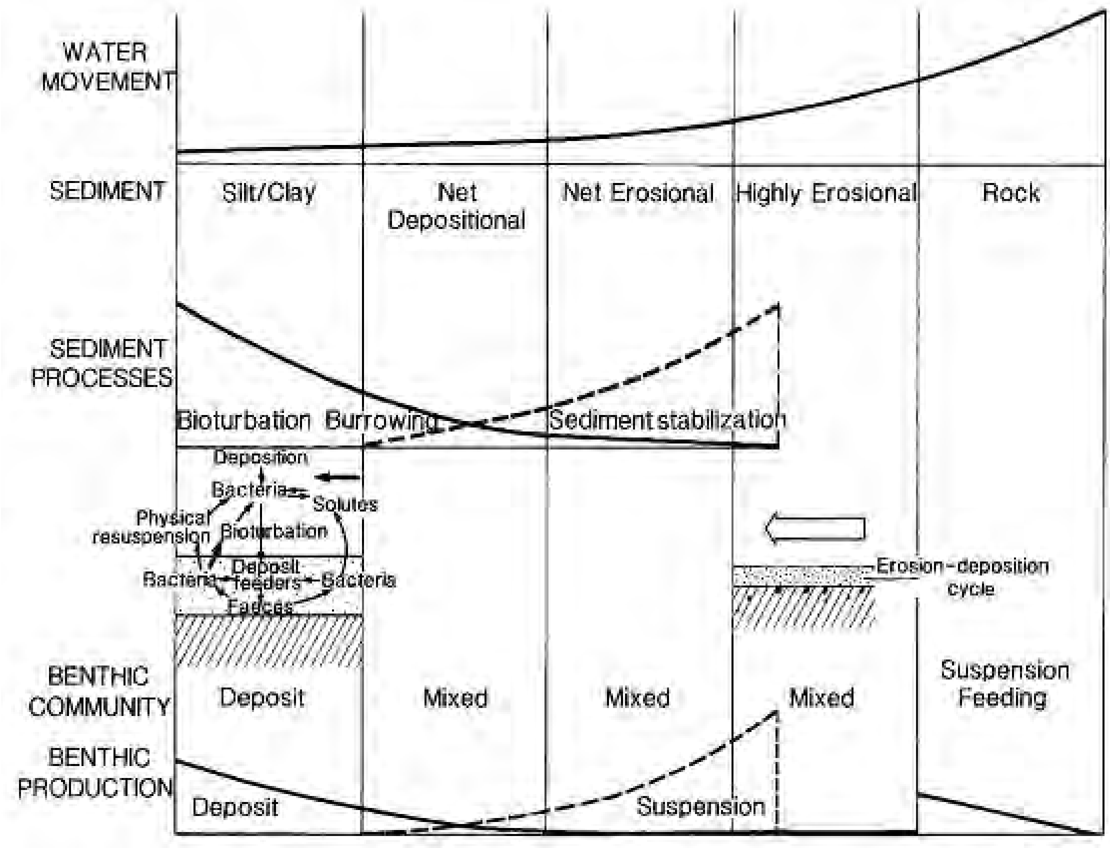

Figure 6: Benthic communities along a gradient of increasing water movement (Wildish and Kristmanson, 1997).

2.3.5. Ice

In the Maritimes, estuaries and sheltered bays are often covered with ice between December and April. A steady ice cover is beneficial to Softshell Clams since it provide a constant temperature. Under the ice, Softshell Clams survive by utilizing glycogen energy reserves (Newell and Hidu, 1982). However, when the ice melts, the Softshell Clams are exposed to sudden increases in freshwater content and variable salinity. Moving ice, rafting the sediment surface, may displace or kill juveniles that are not deeply burried. This phenomenon has been observed in Maine mudflats (Newell and Hidu, 1982). Ice turning over the sediment can bury the Softshell Clams deeper than they normally live or expose them on the sediment surface. This exposure increases their chances of freezing or desiccating and greatly increases their susceptibility to avian predators during low tides and to fish and crustacean predators during high tides (Ambrose *et al.*, 1998).

2.4. Feeding

As for all bivalves, the growth of the Softshell Clam depends on food quantity and quality, and water temperature. Water temperature affects the metabolism and feeding rate of clams as well as food concentrations (Newell and Hidu, 1986). The size of food particles ingested by Softshell Clams is highly variable. It varies as the individual grows and as it shifts from pelagic to benthic life.

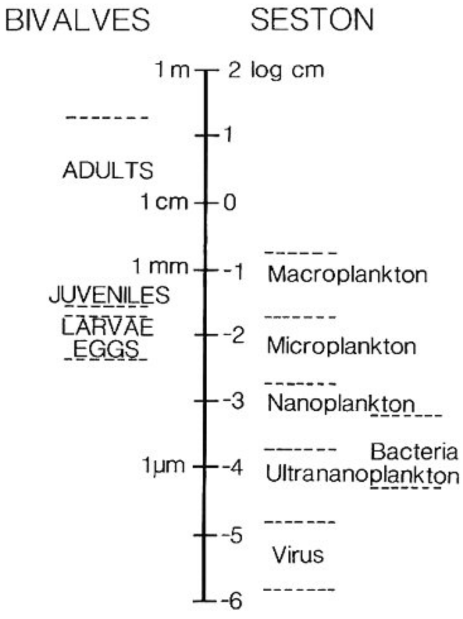

Figure 7: Comparative sizes of suspension-feeding bivalves (log scale) and their potential food (adapted from Wildish and Kristmanson, 1997).

Figure 7 summarizes the potential seston (dead and live organisms as well as organic and inorganic particles) size available for bivalves, at various stages of their life. Seston particles similar in size vary greatly in chemical, mineral and nutritional contents, as well as in shape, density and settling speed.

2.4.1. Larvae

Softshell Clam trochophores ingest suspended particles in the water column, while veligers feed on micro-phytoplanktonic organisms (Abraham and Dillon, 1986; Newell and Hidu, 1986; Sempier, 2003). The exact diet of the Softshell Clam larvae is still not well known. Stickney (1964) observed that larvae raised in laboratory fed every other day with unicellular algae (*Cyclotella*, *Phaeodactylum*, *Dicrateria*, and *Monochrysis*) showed normal growth. In nature, the thickness of cell walls and the degree of toxicity of secondary metabolites determine the usability of certain planktonic organisms as larval food (Davis and Guillard, 1958). A mixture of several species of phytoplankton is important to meet the larva's food requirements in nature and to ensure a rapid growth (Loosanoff and Davis, 1963). They also need to feed sufficiently to accumulate lipid energy stores needed for metamorphosis.

A study carried out by Raby *et al.* (1997) in the Baie des Chaleurs (Quebec) suggests that bivalve veligers are capable of actively selecting their food particles in the water column and that selection varies between bivalve species. They also observed that 97.5% of small (<5 µm) phytoplankton present is composed of flagellates. They found that Blue Mussel (*Mytilus edulis*) veligers (185 to 260 µm) ingested more algal particles (< 5 µm and 5-15 µm micro-phytoplankton) than did Softshell Clam veligers. Larger Softshell Clam larvae (261-405 µm) ingested significantly more particles < 5 µm than Blue Mussel larvae of similar size. The latter species switch their diet to 15-25 µm algal cells (Raby *et al.*, 1997). The selection of sestonic particles was passive and mostly related to larval mouth size (Raby *et al.*, 1997). The vertical distribution and feeding behaviour of bivalve veligers are usually related to the presence of high food concentrations near the surface. Dobretsov and Miron (2001), for instance, showed that Blue Mussel veligers were close to the water surface where dissolved organic matter (DOM) and phytoplankton concentrations were high. Although there is evidence that bivalve larvae possess amino acid transport mechanisms that allow them to take up dissolved organic matter (DOM), the contribution of this pathway to their nutritional requirements remains unclear (Manahan, 1983). According to Manahan and Crisp (1982), the velum of a bivalve larva is capable of absorbing dissolved nutrients directly from the salt water, which can be of vital importance to the larva when particulate food is scarce and when endogenous reserves are low (Manahan, 1983). Since larvae have a greater absorptive surface area to volume ratio than adults, they have a more rapid weight-specific uptake and faster rate of utilizing absorbed amino acids than do adults (Manahan, 1983). When exposed to relatively high concentrations of amino acids (5.1-7.3 µM), Softshell Clam larvae feeding on phytoplankton seem to increase their survival and biochemical reserves (Gustafson, 1980).

When Softshell Clam larvae approach the pediveliger stage, the degradation of the velum and development of the foot modify feeding behaviour (Bayne, 1965). The uptake of phytoplankton decreases and eventually stops as the larvae become competent to settle. After settlement, the pediveliger starts to feed again at an increasing rate (C. Gionet, pers. comm.). This has been observed in other bivalves having similar life cycles. Dobretsov and Miron (2001), for instance, observed that the concentration of Blue Mussel pediveligers was positively correlated with micro-phytoplankton concentration before settlement but was negatively correlated after settlement.

2.4.2. Juveniles

Once living in the sediments, juvenile Softshell Clams become active suspension filter-feeders. As for most bivalve filter-feeders, Softshell Clams use the cilia in the palleal cavity to create a water current that allows their gills to filter between thirty and sixty times their volume in water per hour (Morton, 1958). Particles in the incoming water flow are retained in mucous strands on the gills. Particle selection by the labial palps based on chemical characteristics and/or volume control mechanisms allows food items to be sent to the mouth for ingestion (Bertness, 1999). Particles not retained for ingestion are rejected as pseudofeces. Juveniles mainly feed on naked flagellates and diatoms. They also feed on bacteria, DOM, and resuspended organic detritus (Abraham and Dillon, 1986; Newell and Hidu, 1986).

2.4.3. Adults

Adult Softshell Clams feed on filamentous algae, diatoms, algal fragments, naked flagellates, dinoflagellates, bacteria, small zooplankton, and detrital particles floating in the water column just above the sediment (Newell and Hidu, 1986; Iversen and Hale, 1992). Matthiessen (1960a) found a significant positive relationship between clam growth and the presence of flagellates in the water column, thus hypothesizing that flagellates were a preferred source of nutritive requirements for adult Softshell Clams. It is estimated that one adult Softshell Clam can filter up to 54 L of water per day (Fisheries and Oceans Canada, 1993).

2.4.4. Physiology

The siphon of the Softshell Clam is divided into two tubes, an incurrent siphon and an excurrent one (Figure 8). A current draws water and suspended particles through the incurrent siphon into the mantle cavity. Gills can retain particles as small as 2 µm (Raby *et al.*, 1997).

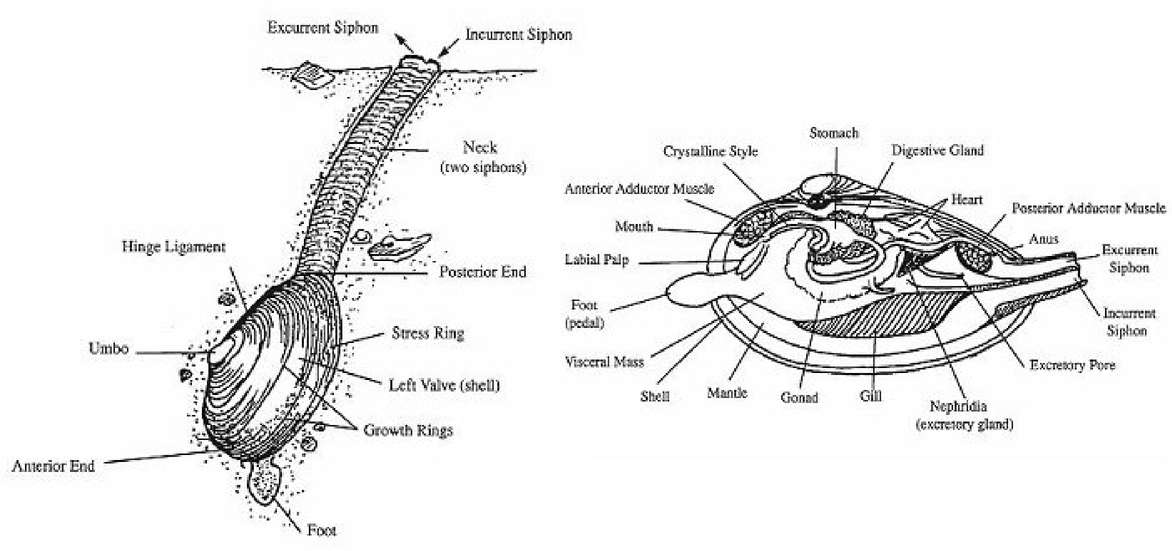

Figure 8: External and internal anatomies of the Softshell Clam (Maine Department of Marine Resources, 2004).

The gills of juvenile and adult clams transport the food particles toward the labial palps and mouth using cilia and mucus (Beninger et al 1997). The labial palps, located at the edge of the mantle, sort food particles via a ciliary mechanism present on the inner face of the palps (Yonge, 1923). When particles are too large, they are carried away by specialized cilia present on the mantle (Beninger et al 1999), and are expelled from the mantle chamber as pseudofeces via the exhalant siphon (Yonge, 1923). Almost the entire alimentary tract of Softshell Clams is ciliated and abundantly covered by mucus secreting glands (Yonge, 1923; Purchon, 1977).

Digestion begins in the stomach where food is further separated into large and small particles. Digestion continues intracellularly in the digestive gland (Newell and Hidu, 1986). The ciliary currents in the stomach allow large or indigestible particles to be carried straight into the intestine. The small particles are carried to the base of a hard plate-like abrasive structure called the gastric shield (Yonge, 1923). Digestive enzymes are released to break down food particles and to facilitate their absorption. The fecal material is released by the anus and is flushed out through the exhalent siphon (Fisheries and Oceans Canada, 1993; Maine Department of Marine Resources, 2004).

2.5. Predation

Cumulative juvenile mortality reported for Softshell Clams between the ages of 3 months to one year has been reported to be in the order of 93 – 100% (Gosselin & Qian, 1997). Predation is believed to play an important role in regulating the populations of infaunal marine bivalves in soft-bottom environments (Beal *et al.*, 2001). This high level of predation is commonly offset by high gamete production in bivalves. In the case of Softshell Clams, it is estimated that the maintenance of a stable population requires the survival to settlement of 40 larvae, out of the average 3 X 10^6 eggs spawned by an average female (Young and Chia, 1985)

Pelagic larvae are food items for a variety of zooplankton predators. Predator types vary with latitude, temperature, salinity and hydrodynamic processes. Hydromedusa, ctenophores (comb jellies) and scyphomedusa (jellyfish) are among the most important predators of bivalve larvae (Kraeuter, 2001; Johnson and Shanks, 2003), including Softshell Clam larvae (Abraham and Dillon, 1986). Larval mortality can also result from predation by copepods, fish larvae, deposit and filter-feeding organisms, including conspecific adults.

Since the larval supply of Softshell Clams varies from year to year (e.g.: Roseberry *et al*., 1991; Leblanc and Miron, 2006), it is believed that predation on their larvae also varies over time. In addition to predation, hydrodynamic processes and postlarval transport significantly influence the local distribution and abundance of Softshell Clam recruits and their predators (Hunt *et al*., 2007). LeBlanc and Miron (2005), for instance, suggested that the concentration of young Softshell Clams at the high intertidal level in the Bay of Fundy may be explained by a lower predation pressure at this level. Hunt and Mullineaux (2002) came to the same conclusion in a similar study off the coast of Massachusetts.

Once Softshell Clam larvae find a suitable substrate for settlement, they remain at the sediment surface and are again subject to intense predation by any organisms feeding there. According to Leavitt (1998), early post-settlement mortality due to predation may reach 80% during the first 100 days of the recruitment period. In field experiments conducted in eastern Maine, netting used to deter predators resulted in more clams being recovered alive after a year in protected vs. unprotected treatments (84% *vs.* 71%) (Beal & Kraus, 2002). The presence of netting resulted in significantly greater (3X) survival of natural recruitment to the area (Beal & Kraus, 2002). Hunt and Mullinaux (2002) suggest that both hydrodynamic transport and predation are responsible for Softshell Clam losses < 2 mm. Predation is the main factor controlling the distribution and abundance of Softshell Clams > 2 mm (Beal *et al.*, 2001; Hunt and Mullinaux, 2002). Population fluxes resulting from high predation rates may result in variable recruitment even with high larval settlement densities (Hunt *et al.*, 2007). In situations where clam beds become depleted, repopulation may be delayed for many years before sufficient larval recruitment and growth re-occurs (Abraham and Dillon, 1986).

Mya arenaria responds to predation cues by burrowing more deeply, suggesting that larger individuals benefit from a spatial refuge that makes them less vulnerable by increasing predator foraging costs (Yamada and Boulding, 1996). However, burial depth affects the clam’s feeding efficiency since the clam siphons must reach the substrate surface to feed on plankton. Therefore, by digging too deep to avoid predators, individual clams have to increase the distance between their siphon and the sediment surface, thus increasing their own energy cost (Whitlow and Dochtermann, 2001).

2.5.1. Birds

Mudflats, shallow embayments, and estuaries provide habitats for Softshell Clams, and therefore feeding grounds for many avian predators such as overwintering waders, waterfowl and shorebirds. When the tide is out, coastal foraging birds are estimated to selectively consume 50 to 70% of the invertebrate populations present in mudflats.

Common Eider Seaducks (*Somateria mollissima*) breed and spend the winter in the south-western Maritimes where they feed on mussels and other shellfish (Erskine, 1992). The diet of the Common Eider varies with age. Young individuals eat small crustaceans. The proportion of bivalves in their diet increases steadily as they get older. White-winged Scoter (*Melanitta fusca deglandi*) forage on marine molluscs (clams, mussels, snails) and crustaceans in inshore waters on their wintering grounds (Boreal Songbird Initiative, 2005). Along the coast, Ring-necked Ducks (*Aythya collaris*), although usually considered to be herbivores, tend to supplement their diets with molluscs and other invertebrates (Erskine, 1992; Morrison, 2000). Willets (*Catoptrophorus semipalmatus*) and Whimbrel *(Numenius phaeopus*) also forage in mudflats and intertidal areas where they probe the sediments for small molluscs (Erskine, 1992; Adams, 2005a,b). Herring Gulls (*Larus argentatus*), Sanderlings (*Calidris alba*) and Spotted Sandpipers (*Actitis macularia*) all commonly feed on molluscs (Cayouette & Grondin, 1972; Erskine, 1992; Adams, 2005c). Small molluscs are part of the Semipalmated Plovers (*Charadrius semipalmatus*) and Ruddy Turnstones (*Arenaria interpres*) diet. Both species can be found on sandy and muddy shores (Cayouette & Grondin, 1972). Lesser Yellowlegs (*Tringa flavipes*) are also found in coastal marshes and mudflats, grabbing prey from shallow water (e.g.: molluscs) (Adams, 2005d).

According to Hicklin (1987), thirty-four species of shorebirds have been recorded foraging in the marshes and mudflats of the upper Bay of Fundy. Among them, the Least Sandpipers (*Calidris minutilla*), the Short-billed Dowitchers (*Limnodromus griseus*), and the Black-bellied Plovers (*Pluvialis squatarola*) pass through the Bay of Fundy and feed during August. Later, the White-rumped Sandpipers (*Calidris fuscicollis*) and the Dunlin (*Calidris alpina*) appear, extending their foraging on coastal flats into October (Hicklin, 1987). In the Kouchibouguac National Park (NB), the American Bald Eagle (*Haliaeetus Leucocephalus*) has also been observed digging and feeding on large Softshell Clams during the summer months (Abgrall, personal observation).

2.5.2. Worms

Predation by various species of worms may be great. Bourque *et al.* (2001), for instance, showed in the laboratory that the nemertean *Cerebratulus lacteus* can predate heavily on Softshell Clams, preferring individuals in the 15-50 mm size classes. Similar observations were made by Rowell and Woo (1990) in a mudflat in NS. The Sandworm *Nereis virens* and the Bloodworm *Glycera dibranchiata* are also predators of juvenile clams (Commito, 1982; Hidu and Newell, 1989). Deposit feeders such as hemichordate worms can ingest young Softshell Clams by accident.

2.5.3. Crustaceans

Shrimps, Rock Crabs, Hermit Crabs and lobsters are highly mobile organisms that can feed on large Softshell Clams (e.g.: Hunt, 2004b). In Maine, the range extension of the invasive Green Crab (*Carcinus maenas*) has been correlated with the gradual decline of Softshell Clam landings (Spear, 1953; Beal, 1994; Beal *et al.*, 2001). The Green Crab has also been identified as a major predator of Softshell Clams in some regions of the Maritimes (Newell and Hidu, 1986; Fisheries and Oceans Canada, 1993; Miron *et al.*, 2005). According to Spear (1953), a single Green Crab is able to eat up to 15 large clams a day. In an enclosure experiment in Pomquet Harbour, NS, Green Crabs significantly reduced the number of small (<17mm) Softshell Clams, removing up to 80% of the small clams in unprotected areas (Floyd and Williams, 2004). In contrast, negligible evidence of Green Crab predation on larger clams was observed, suggesting a size-related refuge. The Blue Crab (*Callinectes sapidus*) (Abraham and Dillon, 1986) and the Horseshoe Crab (*Limulus polyphemus)* (Beal, 1994) are also major Softshell Clam predators on the Atlantic coast of the USA. The Pea Crabs (*Pinnotheres pisum*) are not considered predators but parasites. The crabs measure 1 to 15 mm in diameter and feed on food items collected within the mantle cavity of their Softshell Clam hosts (Bower and McGladdery, 2004).

2.5.4. Fish

During periods of high tide, fish such as rays, flounders, cod, spots, eels and sculpins can eat whole Softshell Clams or sometimes just nip off their siphons (Abraham and Dillon, 1986; Fisheries and Oceans Canada, 1993). The Southern Mummichog (*Fundulus heteroclitus heteroclitus*) is also known to consume Softshell Clams. Kelso (1979), reports predation by mummichog in the order of 500 000 small clams (<12 mm) per km of shoreline per day in Massachusetts. In the Maritimes, the Winter Flounder (*Pseudopleuronectes americanus*) excavates the sediment in search of Softshell Clams (Mark *et al.*, 2003).

2.5.5. Molluscs

The Moon Snail *Euspira heros* preys heavily on Softshell Clams of various sizes (15-51 mm) (Beal, 1994). This naticid gastropod is abundant along the eastern coast of Canada, in NS and NB (e.g.: Miron *et al.*, 2005). According to Edwards and Heubner (1977), *E. heros* can eat 95-100 small clams/year. The clam siphon snails *Boonea* spp. and *Odostomia* spp. are not predators but ectoparasites. These small snails (< 3 mm) attach themselves to the siphon or the mantle margin of the clam, and then penetrate their tissues (Bower *et al.*, 1994). This behaviour may impede the clam feeding (Bower *et al.*, 1994).

2.5.6. Others

The Common Starfish (*Asterias vulgaris*) (Miron *et al.*, 2005) and the Sea Cucumber (Beal *et al.*, 2001) are also known to be Softshell Clam predators. Small terrestrial mammals such as shrews, voles, racoons and moles also utilize the shallow part of the coast and feed on molluscs (Abraham and Dillon, 1986). Humans are a severe predator of Softshell Clams. They also can indirectly kill clams by disturbing sediments during harvesting (Fisheries and Oceans Canada, 1993).

2.6. Competition

2.6.1. Intraspecific

According to Beal *et al.* (2001), competition is less important than predation in regulating Softshell Clam populations. Competition for space is also less important in soft-bottom habitats than in hard-bottom habitats since soft-bottom sediments include a third dimension (Peterson, 1979; Peterson and André, 1980). Intraspecific competition may occur for space between Softshell Clam individuals at locations where high adult densities are found or when predators are absent (André and Rosenberg, 1991; Beal *et al.*, 2001). The intensity of intraspecific competition increases with Softshell Clam density and seems to particularly affect the growth rate and survival of juvenile clams, which are confined to the first cm of the sediment.

Once individuals reach adult size crowding rarely results in mortality (Beal *et al.*, 2001). However, Softshell Clams may respond to intense space competition by allocating resources to shell and soft tissue rather than siphon growth (André and Rosenberg, 1991). Softshell Clams do not usually respond to intraspecific competition by changing burrowing depth. Vertical movements may be observed if oxygen becomes limited in sediments and thus oxygenated sediments become a resource for competition.

Adult bivalves can also have a negative effect on the settlement and survival of conspecific larvae due to their feeding activity. According to André and Rosenberg (1991), adult filter-feeders may ingest larvae while feeding on planktonic organisms and therefore may decrease larval settlement of conspecifics at locations with high concentrations of adults.

2.6.2. Interspecific

There is usually no apparent interspecific competition for space between species of bivalves that occupy different positions in soft-bottom environments (Peterson and André, 1980). However, competition for space can become the primary mechanism of interspecific interaction if the species of bivalves are sharing a similar depth stratum (Peterson and André, 1980). This type of interaction between bivalves does not necessarily result in displacement but can reduce the growth and fecundity of individuals that are too close to each other. If too crowded, interaction between bivalve species can lead to competitive horizontal and vertical displacements which determine the intertidal distribution of different bivalve species.

Phytoplankton, bacteria and detritus are the main food sources available to soft-bottom communities (Little, 2000). These food sources can be more limiting to deposit-feeders than filter-feeders (Wilson, 1991). The supply of phytoplankton can, however, vary greatly within estuaries (Little, 2000). Depending on their position in the estuary and on local hydrodynamics, filter-feeders can receive different amounts of food particles. These differences in food supply may determine the species' small-scale and large-scale distribution in soft-bottom habitats (Little, 2000).

2.7. Diseases

The most deadly disease in Atlantic Canada for the Softshell Clam is haemocytic neoplasia (Bower, 2005). This disease is also known as disseminated sarcoma or leukemia of Softshell Clams. It is not a human health concern but can cause clam mortalities. Neoplastic haemocytes appear gradually throughout the soft-tissues and their proliferation eventually leads to stasis and organ compression causing death. Its prevalence and effect vary significantly between areas (Bower, 2005). McGladdery *et al*. (2001a,b) showed that an 80 to 95% prevalence of infection was detected in 1999 in various locations in Atlantic Canada in association with Softshell Clam mortalities. However, no mortalities have been associated to this disease in wild Softshell Clam populations from south-eastern Canada for a number of years. According to McGladdery *et al.* (2001a), haemocytic neoplasia may be temperature - related and previously unexposed clam populations may be more susceptible to the disease. Its cause is unknown (Bower, 2005).

Gonadal neoplasia, or germinomas of clams, is also known to cause important mortalities in 2-7 year old Softshell Clams. It has been observed from Penobscot Bay (Maine) to Passamaquoddy Bay (NB) off the Atlantic East coast. As for haemocytic neoplasia, its cause is unknown (Bower, 2001a).

McDowell et al (1999) observed that Softshell Clams exposed to lipophilic organic contaminants in Boston Harbour and other bays had an abbreviated spawning season, a high prevalence of gonadal inflammation, and a higher incidence of haemocytic neoplasia. Their results demonstrate that exposure to chemical contamination can impair *Mya*'s reproductive output and increase its susceptibility to diseases.

3. EASTERN OYSTER [2]

The Eastern Oyster (*Crassostrea virginica,* Gmelin, 1791) is a bivalve mollusc that is generally asymmetrical and pear-shaped varying greatly in size and shape (e.g.: Carriker and Gaffney, 1996). On the outside, the shell is grey with some brown, green and white shades. On the inside, the shell is white except for the muscle scar area which is deep purple (Figure 9).

Figure 9 - Eastern Oyster adult showing an asymmetrical shell and a deep purple muscle scar in addition to shell damage due to boring sponge (Cliona sp.) (Frank, 1998).

Along the coast of NB, Eastern Oyster beds have been an important part of the social and economic development of native and non-native communities for hundreds of years (Milewski and Chapman, 2002). Early records indicate that, in addition to human consumption, Eastern Oysters have been harvested for their shells for the production of lime and for building roads (Milewski and Chapman, 2002). Stafford (1913) mentioned that oyster landings in NB reached an average of about 1 500 000 kg per year from the late 1870s to the early 1910s. This shows that these estuaries were historically characterized by a naturally high abundance of oysters. Estimated landings in NB continued to exceed 1 000 000 kg per year until the arrival of the Malpeque disease in the 1950’s (Fisheries and Oceans Canada, 2001b). Landings hit a historical low of 3 000 kg in 1960. Landings are gradually increasing since the introduction of disease resistant oysters in the late 1950’s and early 1960’s and the development of modern culture techniques in the 1970s (Fisheries and Oceans Canada, 2001b). The mean annual landing of the Eastern Oyster

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[2] Synonyms: American oyster, Virginian oyster, Gulf coast oyster, blue point oyster, blue point, common oyster.

fishery (public beds and private leases) reached 883 600 kg in NB for 2003 (Fisheries and Oceans Canada, 2005a).

3.1. Distribution

The Eastern Oyster is widely distributed along the western Atlantic shores, ranging from northern temperate to sub-tropical environments (Thompson *et al.*, 1996). Along the east coast of North America, they are found in estuaries and coastal areas of reduced salinity, from the Gulf of St. Lawrence to Key Biscayne (Florida). They are also found in the Gulf of Mexico, the Caribbean and off the coast of South America (Brazil, Argentina, and Venezuela). The Eastern Oyster has been introduced on the west coast of North America, Hawaii, Australia, England, and Japan (Carriker and Gaffney, 1996).

Eastern Oysters are mostly found in warm shallow bays and estuaries of the southern and western parts of the Gulf of St. Lawrence, mainly in NB, NS and PEI (Lavoie, 1995). In Quebec, a remnant population from introduced broodstock can be found in the Magdalen Islands in Bassin aux Huître and Clarke’s Bay (Giguère *et al.*, 2007). Except for oyster beds in Cape Breton (Bras d’Or Lake and Mira River), Eel Lake in Southwest Nova and Chedabucto Bay (Ragged Head), there are few natural oyster beds along the Atlantic coast of NS (Lavoie, 1995). In NB, Eastern Oysters are present in the majority of estuaries from the Acadian Peninsula (Caraquet Bay, Lamèque and Miscou islands) to Cap Tourmentin (Neguac, Portage Island, Oak Point, Point aux Carr, Hay Island, Baie du Vin Island, Egg Island, St. Anne Bay, Richibucto, Bouctouche and Cocagne rivers) (Fisheries and Oceans Canada, 2001b; Doiron, 2003). No Eastern Oysters are found in the Bay of Fundy due to low water temperatures that limit oyster reproduction and growth (Fisheries and Oceans Canada, 2003). The northern distribution of the Eastern Oyster in NB used to be more extensive than at present (Ganong, 1899). In the mid-1850s and early 1900s, limited attempts to grow oysters on the Quebec side of Baie des Chaleurs were made (Lavoie, 1995). Eastern Oysters apparently used to be naturally found at the mouth of the Baie des Chaleurs, then called Grand Pabos River (Denys, 1672, cited in Stafford, 1913). According to Denys (1672), Eastern Oysters were also distributed along the southern NS seashore, including Sable Island.

3.2. Life cycle

3.2.1. Gametes and reproduction

Eastern Oysters are dioecious protandrous hermaphrodites (Thompson *et al.*, 1996). They usually start as males and end as females as they grow larger over the years and develop greater energy reserves (e.g.: Thompson *et al.*, 1996). They can have several sex reversals during their lifetime; where there are multiple spawning episodes, they can also alternate sex within a spawning season (Galtsoff, 1964). As for the Softshell Clam, sexual maturity for the Eastern Oyster is related to size rather than age (Osborne, 1999). Gonadal tissues develop 8 to 12 weeks after spat settlement (Eble and Scro, 1996). The size of the gonads varies throughout the year; its development is affected by water temperature, salinity, depth and food supply (Fisheries and Oceans Canada, 2003).

The spawning period of the Eastern Oyster varies with geographic location, beginning earlier in the southern end of the species' distribution (Thompson *et al.*, 1996). In the Maritimes, the spawning season occurs from mid-June to August (Sullivan, 1948). An increase in water temperature prompts a few initial oysters to spawn (ca 20°C), which subsequently communicates an uncontrollable impulse to others (Stafford, 1913). Male and female gametes are released at the same time in the water column in response to a variety of exogenous and endogenous factors (Figure 10) (Giese and Pearse, 1974; Thompson *et al.*, 1996).

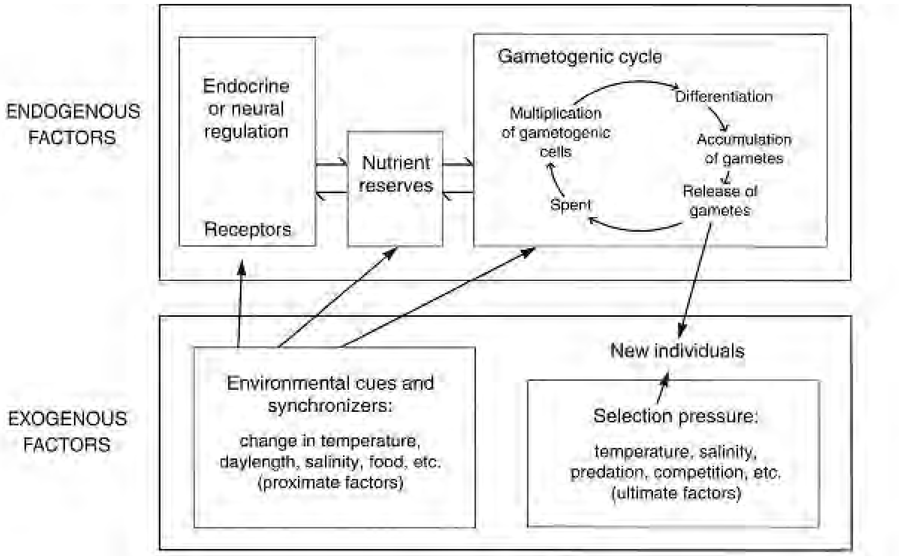


Figure 10: Summary of exogenous and endogenous factors involved in sexual maturity and spawning in the Eastern Oyster Crassostrea virginica (Kennedy, 1996).

According to Thompson *et al.* (1996), Eastern Oyster females can release 5 to 20 millions eggs during a spawning, depending on their weight, nutrient reserves, habitat, and the environmental conditions in which they spawn. Spawning also depends on pheromones, the presence of gametes released by adjacent oysters, and the availability of suitable phytoplankton (Thompson *et al.*, 1996) (see Figure 10). According to Galtsoff (1964), the phytoplankton, which may bear specific chemical cues, can initiate spawning of males. This subsequently induces mass spawning of females. The abundance of phytoplankton is a good predictor of favourable conditions for the oyster larvae that later develop in the water column, making this a more reliable spawning cue for the adult oysters (Starr *et al.*, 1990).

The high reproductive potential of the Eastern Oyster is also related to the fact that sperm can retain its fertilizing capability for 4 to 5 hours after being released (Galtsoff, 1964). Successful fertilization depends on an adequate sex ratio among individuals, the initial density of the oyster broodstock, and the proximity of the individuals, which in turn determines gamete concentration in the water column (Thompson *et al.*, 1996). Galtsoff *et al.* (1930) estimated that in order to maintain itself, a natural oyster reef most have more than 6000 adult individuals per m^2. Recruitment of oysters is enhanced as oyster reefs grow and become larger and more stable, this in part because the high density and close proximity of adults enhances fertilization success (Harris, 2003).

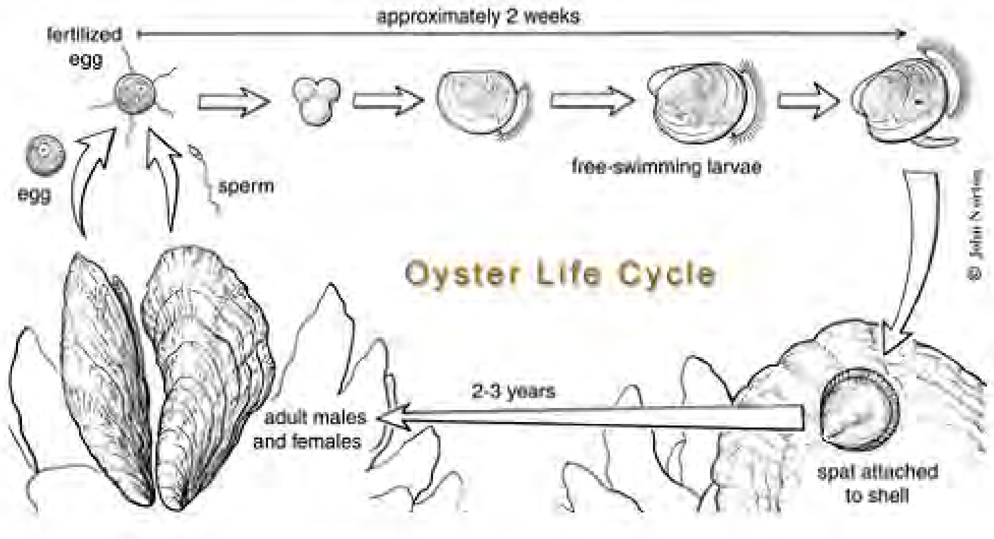


Figure 11: Life cycle of the Eastern Oyster (adapted from North, 2005).

Fertilization occurs shortly after the synchronized spawning (Stephano and Gould, 1988; Thompson *et al.*, 1996). The eggs measure about 50 µm in diameter and, when conditions are favourable, fertilized eggs develop in about 6 hours into free-swimming non-feeding trochophore larvae that depend on their internal yolk supply for energy and survival (Figure 11) (e.g.: Stafford, 1913; Thompson *et al.*, 1996).

After about 24 to 48 hours, the 50 µm trochophore develops into a shelled veliger larva that uses its ciliated velum to swim and to capture food (Figures 11 and 12).

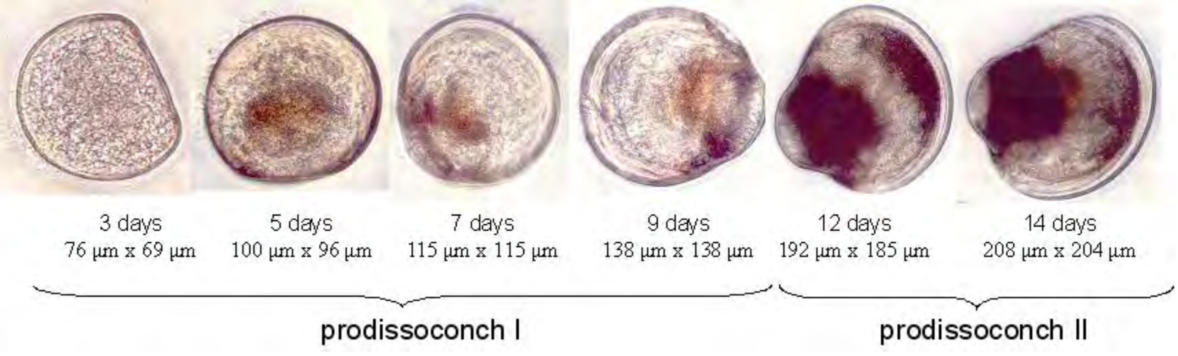


Figure 12: Eastern Oyster veligers at different ages. Veligers can be divided into prodissoconch I and prodissoconch II (Doiron, 1997).

3.2.2. Veligers

Eastern Oyster veligers remain in the plankton for a period of about three weeks before developing into pediveligers. Food supply and temperatures are the main factors affecting the length of their larval period, while salinity and hydrodynamics affect their distribution in the water column (Kennedy, 1996). Veligers show a positive phototaxis that becomes negative with increasing water temperature.

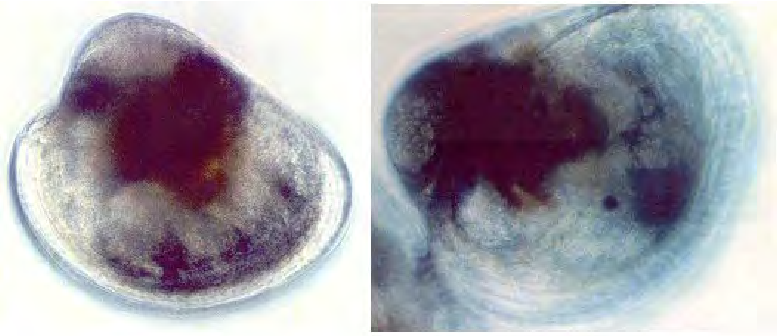
Tidal circulation, wind-driven currents and waves have an important effect on the dispersal of veligers (Kennedy, 1996). Though Eastern Oyster veligers have good swimming capacities they may not be able to swim against currents (Kennedy, 1996). The veligers maintain their location in the water column by migrating to the bottom when the tide is ebbing and to the surface with the incoming tide (Fisheries and Oceans Canada, 1996). This type of vertical movement probably prevents the larvae from being flushed out to deeper and more saline waters. In contrast to Blue Mussel larvae, oyster veligers tend to aggregate above the halocline. Nelson and Perkins (1931) showed that Eastern Oyster veligers move toward the bottom. Once they encounter the halocline, they modify their behaviour and move upward. A similar behaviour was also observed in the hard clam *Mercenaria mercenaria* (Turner and George, 1955). The swimming behaviour of Eastern

Oyster veligers varies as they grow. Young veligers tend to remain near the water surface while old ones are observed throughout the water column (Kennedy, 1996).

Mortality rate is high during the pelagic phase. Only 1% of the veligers reach the metamorphosis stage (Fisheries and Oceans Canada, 1996; Kennedy, 1996). According to Kennedy (1996), this high mortality rate is mostly related to predation, poor food supply, or the poor condition of spawning females that leads to reduced lipid egg contents.

3.2.3. Pediveligers

The veliger develops a paired pigmented structure (eyespots) and a probing larval foot after two or three weeks, depending on food availability and water temperature (Kennedy, 1996; Thompson *et al.*, 1996). At this stage, the larvae are called eyed larvae or pediveligers (Figure 13). They measure about 300 μm. The larvae are heavy enough to sink and are able to use their muscular foot to crawl on the bottom to explore potential settlement sites. Pediveligers are light sensitive. Larval settlement is probably favoured by darkness and partially inhibited by light. This behaviour explains their presence near the bottom (Shumway, 1996). In addition to light, Hidu and Haskin (1971) found that Eastern Oyster pediveligers settled in response to temperature and salinity. Baker (1997) suggested that gravity is a stronger settlement orientation cue than light. This observation, however, does not explain why pediveligers are also able to settle on hard surfaces suspended in the water column (Kennedy, 1996).



16 days
258 μm x 242 μm

19 days
319 μm x 300 μm
(eyed)

Figure 13: Eastern Oyster pediveligers showing the development of the eyespots (Doiron, 1997).

Substratum exploration is very important for oysters. In contrast to Softshell Clams, settlement on the substratum is permanent. When contact is made with a surface, the pediveliger crawls in a circular path. The movements are more angled if the surface displays enough physical and chemical cues. This, in turn, induces more small - scale exploration (Kennedy, 1996). Among physical and chemical cues, the presence of shell or conspecifics, bacterial surface films, and surface roughness seem to be important stimuli for settlement (Kennedy, 1996). Unattractive surfaces encourage larvae to resume their swimming and explore further. Crisp (1967) and Hidu (1969) have confirmed that Eastern Oyster larvae settle gregariously near adults or newly settled individuals. A protein based component originating from the shell surface may be responsible for this response. The presence of live oysters and oyster shells suggests that the habitat has suitable resources for ensuring growth and survival of the larvae. Over time, this gregarious behaviour results in the formation of large oyster beds or oyster reefs.

Once a suitable surface is found (e.g.: hard surface such as other living oysters, oyster shells, rocks, docks, pilings, and glass bottles), the pediveliger's pedal gland secretes a tiny pool of cement-like adhesive and the oyster turns on its left side. The velum is discarded, the larval foot reabsorbed, and gills start to develop. The left shell is then cemented permanently to the hard surface (Kennedy, 1996; Steward, 1993). The attached larvae are then called spat. The term spat is used to designate small oysters or juveniles and/or post-settlement stages. The process of settling and metamorphosing from a free-swimming to an immobile lifestyle is called spatfall. In contrast to other invertebrate larvae, oyster larvae do not successfully delay settlement. If a suitable settlement surface is not found, the pediveliger sinks to the bottom and dies. Other pediveligers may find solid substrates to settle onto but may encounter poor water quality or inadequate food resources that limit their growth and survival (Kennedy, 1996). In southern U.S. waters, there is a nearly continuous setting of spat during the warm seasons, frequently leading to overcrowding. This, in turn, leads to the formation of thin and elongated oysters (Keith and Anderson, 1995).

3.2.4. Juveniles

Juvenile Eastern Oysters (otherwise known as spat) are mostly male and once they have successfully attached to a hard surface, they begin to grow at the rate of about 2.5 cm/year. Growth rate is influenced by the presence of suitable food and other environmental factors (e.g.: dissolved oxygen concentration). According to Osman and Abbe (1994), low oxygen concentrations significantly decrease the growth of Eastern Oyster spat. As in other bivalves, survival during the early post-settlement life-stage is important to ensure a good recruitment. Spat are especially vulnerable to predators.

Loosanof and Engle (1940) found that spat mortality due to predation ranged between 86 and 100% over a 2 month period in Long Island Sound. The early post settlement stage is critical for oyster culture. In NB, spat collection can occur anywhere between mid-July to mid-August, depending on latitude (Fisheries and Oceans Canada, 2001b). Normally, spat collection occurs earlier in southern areas and later in northern areas.

3.2.5. Adults

Eastern Oysters grow continuously throughout their life. This growth varies seasonally and slows with age and density. In the Maritimes, the growth period occurs from May to late November with a respite around July for spawning. Shell growth usually occurs first. Soft body tissue growth occurs after spawning (Shumway, 1996). It takes 4 to 7 years to reach a commercial size of 76 mm in the Gulf region but only 18 to 24 months in the Gulf of Mexico (Fisheries and Oceans Canada, 2003). In addition to water temperature, growth rates can be affected by food quantity, salinity, and parasites.

The Eastern Oyster usually lives about 25–30 years and reaches a maximum size of 25-30 cm. However, oysters may attain a length greater than 35 cm and live for more than 100 years (Steward, 1993). The oyster's shape depends on the type of substrate on which it originally settled and on crowding if settlement occurs on conspecifics. Settlement on conspecifics is the most common settlement pattern. In crowded conditions, the shells usually develop into more elongated forms. The shape of the oyster shell varies considerably and depends upon growing conditions. The most common growth is the one that produces oyster clusters.

Settlement on conspecifics also leads to clustering. The clusters are formed by successive settlements, one upon another, and each oyster in a cluster is used as a settlement surface by succeeding generations (Keith and Anderson, 1995). The cluster continues to grow and form an oyster bed as new oyster larvae successfully settle and survive to the adult stage. Clusters may reach 30 cm or more in thickness and develop into an important three-dimensional structure called an oyster reef. In this case, only the outermost oysters remain alive as the added weight of additional individuals tends to push the lowermost oysters into the mud where they eventually suffocate. Oyster reefs provide a valuable shelter and habitat for many marine species, such as crustaceans, marine worms, gastropods, bivalves and fish and may prevent coastal erosion by stabilizing the sediments (Milewski and Chapman, 2002).

3.3. Habitat

Eastern Oysters are sessile epibenthic organisms that inhabit dynamic environments such as estuarine and coastal waters (Kennedy, 1996). Hydrodynamic conditions on oyster reefs are especially important to control the dispersal and retention of larvae, suspended food particles and sediment, thereby influencing their recruitment, growth, and survival (Lenihan, 1999). Eastern Oysters are usually unevenly distributed in shallow estuarine waters, but can occur at depths of about 30 meters (NOAA, 2005). In South Carolina, oyster reefs develop in intertidal areas to a depth of about 2-3 meters. There, they form beds that become established on hard substrates where salinities are moderately high and siltation not too excessive (NOAA, 2005). The oyster reefs observed from Cape Fear (North Carolina) to north-eastern Florida may also grow intertidally. In contrast, oyster beds in Chesapeake Bay (Virginia) and Apalachicola Bay (Florida) primarily develop in subtidal areas (NOAA, 2005). In fact, most Eastern Oyster reefs north of Cape Fear are found in subtidal areas and grow on bottoms that are covered with water throughout the tidal cycle (Keith and Anderson, 1995). In the Maritimes, the Eastern Oyster grows in both intertidal and subtidal areas. Those growing in intertidal zones are exposed to freezing air temperatures and ice scouring during the winter months, which may limit their chances of survival (Fisheries and Oceans Canada, 1996).

3.3.1. Substrate

Eastern Oysters settle on stable pebbly or rocky bottoms that are almost free of other fouling organisms. Ultimately, they prefer to settle on conspecifics (MacKenzie, 1996). They can easily be covered with silt and suffocate when they settle on muddy bottoms or hard substrates with high silt deposit (MacKenzie, 1996). According to Jordan *et al.* (1992), large adult oysters can tolerate hypoxic conditions (<2 mg O_2/L) for up to 10 days in 18°C water, and last several weeks without oxygen when water temperature is less than 5°C.

3.3.2. Physico-chemical conditions

Water temperature and salinity are the environmental factors that have the greatest influence on development, feeding, growth, reproduction, survival, and parasite occurrences in Eastern Oysters (Shumway, 1996). The Eastern Oyster is a eurythermal species able to tolerate a wide range of temperatures including freezing ones (Osborne, 1999). They are found abundantly in shallow bays, lagoons, estuaries, and coastal areas, at water temperatures ranging between -2 to 36 ºC (Shumway, 1996; Steward, 1993). The species northern distribution is limited by critical spawning temperatures (10-15 °C in the South and ≥ 20 °C in the North) required for larval development (Thompson *et al.*, 1996; Tyler-Walters, 2003). The optimal temperature for growth and low mortality lies between 20° and 30°C (Shumway, 1996).

The Eastern Oyster can also tolerate a wide range of salinities (0 to 40 ppt). However, they do not tolerate prolonged exposure to fresh water or high salinities. The highest growth and reproductive rates are observed when salinities range from 15 to 30 ppt (Shumway, 1996). Adults are able to spawn at salinities between 5 and 10 ppt (Kennedy, 1996). Low salinities (5-6 ppt) can inhibit gametogenesis (Loosanof, 1953). The preferred salinity range for oysters in the Maritimes lies between 14 and 28 ppt (Doiron, 2003). Their preferred habitats include coastal bays into which many rivers flow, as well as estuaries with brackish waters (Steward, 1993). This preference for low salinities is not in agreement with observations made by Loosanof (1953) which showed that the growth of Chesapeake Bay oysters slows down at 7.5 ppt and stops below 5 ppt. In addition, low salinities appear to slow down Malpeque disease (McGladdery and Bower, 1999) as well as MSX and SSO diseases (Bower, 2007a,b).

3.3.3. Turbidity

Eastern Oysters normally inhabit areas of fairly constant turbidity. Very high deposition rates reduce recruitment, slow growth rates, and increase mortality in most bivalve species (MacKenzie, 1983). The literature, however, offers contrasting information as to the importance of this factor to their life cycle (Shumway, 1996). According to Stern and Stickle (1978) and Shumway (1996), increased concentrations of suspended materials (seston or silt) can induce pumping rate reduction and clog the gills. This may lead to a subsequent reduction of oyster' growth rate and death. Excess sedimentation of biodeposits can also smother and kill both adults and juveniles when it occurs for several days and when the oysters are not able to reopen their valves (Stern and Stickle, 1978; Shumway, 1996). Adult oysters are generally more tolerant to natural estuarine sedimentation rates than are spat. Excess accumulation of sediments can also lead to the burial of juvenile and adult oysters (Galtsoff, 1964). A laboratory study by Ali (1981) showed that Eastern Oysters can survive and grow when exposed to relatively high sediment deposition. Loosanoff and Tommers (1948) also demonstrated that Long Island Sound oysters can ingest small quantities of particles and survive. Loosanoff and Tommers (1948) also observed that the shell movement of Eastern Oysters increased in amplitude in turbid water. These shell movements were mostly associated with the expulsion of large amounts of pseudofeces.

3.3.4. Current

Water currents can have a strong influence on Eastern Oyster populations since they may flush food particles and silt away (Newell and Langdon, 1996). According to Higgins (1980), Eastern Oysters can modulate their feeding activity in response to seston concentration and water flows. Water flows also influence oyster growth as current speed affects the rate of food supply and thus the rate of local food reduction due to oyster feeding (Newell and Langdon, 1996). Lenihan *et al.* (1996) found that the growth of Eastern Oysters under controlled laboratory conditions increases with flow speed (0–10 cm/s) and food concentration.

Hydrodynamics in the vicinity of oyster reefs is complex and may have a general effect on the habitat. Lenihan (1999), for instance, observed that rates of sediment deposition in Neuse River estuary (North Carolina) were seasonally high at the bases of reefs where flow speed was low. He also noticed that more than 90% of the surface area of low reefs was buried after only 16 months of exposure in the estuary, indicating that reef height may control habitat quality indirectly through its effect on flow. Increased turbulence and a reduced benthic boundary layer around reefs is believed to enhance oyster larval settlement as well as that of other epibiota (Harris, 2003)

3.3.5. Ice

Water depth is very important to oyster survival in the Maritimes, especially during the winter months. The formation and movement of the ice cover during the cold months is known to push oysters into the sediment and smother them in silt and decaying organic material. Oysters living in the lower part of the intertidal zone are especially at risk and can be physically damaged or killed by the movement of ice at very low tide (Lavoie, 1995). In addition, ice cover inhibits primary production and can delay the spring phytoplankton bloom, which is essential to promoting bivalve summer growth (Grant and Pilditch, 1996). In their northern range, oyster reefs are normally subtidal, presumably as a result of the negative effects of winter air temperatures and ice scour on oysters that settled intertidally (Kennedy & Sanford, 1999). According to Lavoie (1995), the ideal water depth for the survival of the Eastern Oyster is determined by local ice conditions. This may in part explain why Eastern Oysters are mostly found in subtidal area in northern regions and in intertidal area in southern regions.

3.4. Feeding

Like Softshell Clams and other bivalves, Eastern Oyster larvae and adults obtain food by filtering suspended particles from the water column. The Eastern Oyster has a highly specialized feeding mechanism to capture and process specific food particles since the quality and the quantity of these particles can vary greatly over time within the same habitat (Newell and Langdon, 1996).

3.4.1. Larvae

Similarly to many bivalve species, Eastern Oyster embryos have barely enough protein and lipid reserves in their egg yolk to develop a functional alimentary system. Larvae have to start feeding in the plankton soon in order to grow and survive (Newell and Langdon, 1996). Eastern Oyster veligers use their velum to generate a feeding current and capture food particles (Figure 14). Food is then transported to the mouth by ciliary movement (Newell and Langdon, 1996).

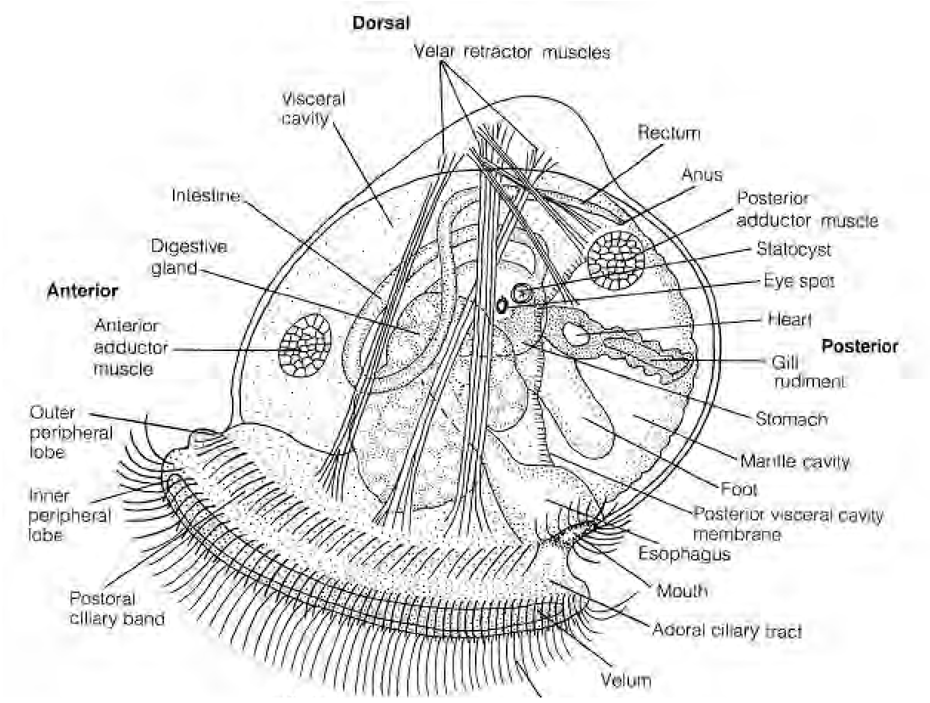


Figure 14: Internal anatomy of an Eastern Oyster prodissoconch II larva (Galtsoff, 1964).

According to Baldwin and Newell (1991), Eastern Oyster larvae are omnivorous and can feed on phytoplankton, heterotrophic bacteria and protozoans that range from 0.2 to 30 μm. These organisms are abundant in estuaries during the summer months and seem to be an adequate diet to support growth, development and metamorphosis (Baldwin *et al*., 1989; Baldwin and Newell, 1991). Active selection of 20 to 30 μm particles was also reported by Baldwin and Newell (1991) and Baldwin (1995) for Chesapeake Bay oysters. These studies also showed that Eastern Oyster larvae can discriminate the nutritional quality of particles and sort particles based on this basis. Larval ingestion rate in the Eastern Oyster is probably regulated by food quantity and quality rather than particle size or abundance. Similarly, Gallager (1988) observed that planktotrophic quahog (*Mercenaria mercenaria*) larvae could reject mineral particles accidentally captured while feeding. According to this study, non-nutritious particles are partially sorted before entering the oesophagus or the stomach, and rejected, while nutritious ones are retained in the stomach and digested.

Baldwin and Newell (1991) observed that the relationship between ingestion rate and food particle concentration follows a Holling's type 3 sigmoid-shaped curve in Eastern Oyster larvae (Figure 15).

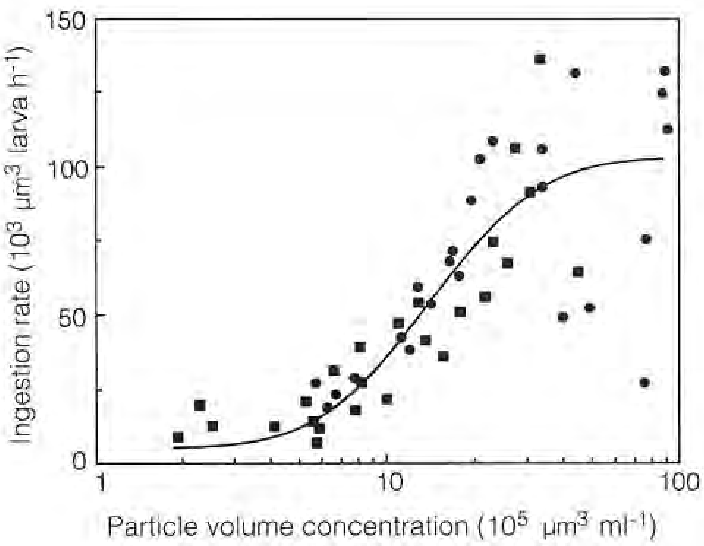


Figure 15: Functional relationship between ingestion rate of Eastern Oyster larvae and particle concentration, in estuarine waters (Baldwin and Newell, 1995).

Selective particle ingestion by oyster larvae suggests that they may switch food types during their development. This kind of behaviour is usually observed when larvae select food type in relation to its abundance. Baldwin and Newell (1995) later observed that Chesapeake Bay Eastern Oyster larvae may feed on larger planktonic particles during a seasonal bloom after feeding on smaller food particles present in the water column prior to the bloom. Small (< 150 μm) and large (> 150 μm) oyster veligers typically feed on particles between 0.5 and 12 μm. Small veligers then switch to 16 μm particles during the phytoplankton bloom, while large veligers feed on 30 μm particles.

3.4.2. Spat

The feeding and alimentary systems of Eastern Oyster pediveliger are reorganized during metamorphosis. The velum is reabsorbed, the mouth re-oriented, and the gills develop as part of the transition from a pelagic to a benthic life (Newell and Langdon, 1996). Eastern Oysters, however, are unable to ingest enough food particles to supply the nutritive elements required for this transformation. The Eastern Oyster ceases to feed and uses lipid reserves stored during the early larval stages. This provides sufficient energy to reorganize the internal anatomy and fully develop its adult feeding structures (Newell and Langdon, 1996). Manahan and Crisp (1982) suggested that the larvae of the oyster *Ostrea edulis* may increase their acquisition of nutrients by epidermal uptake of DOM through their developing gills during the non-feeding period. According to Thompson *et al.* (1996), the growth of juvenile bivalves immediately after metamorphosis is directly correlated with the amount of lipid reserves stored during the larval stages.

3.4.3. Adults

The adult Eastern Oyster is considered to be an active epibenthic suspension filter-feeder that feeds on various sizes of phytoplankton, bacteria, and particles from the surrounding water. Unlike Softshell Clams, the Eastern Oyster cannot move. Its bottom shell is cemented to the substrate and only the top shell can be lifted slightly to allow filtration. Food particles and other particulate matter are drawn into the oyster by the motion of small cilia on the gills. Food particles are retained by the gills, sorted, conducted by ciliary movement of mucus strings to the labial palps, and then to the mouth and stomach. As observed for many other bivalves, Eastern Oysters are able to sort particles by size before ingestion as well as preferentially select organic material for ingestion while rejecting inorganic particles (Newell and Jordan, 1983; Newell and Langdon, 1996).

When water temperature decreases to 4°C*,* the Eastern Oyster opens its shells but stops feeding. The individual thus enters into a dormancy period from December to May. Although the oyster is not filtering, it shows very little weight loss during this period (Steward, 1993). Reduced food intake influences the ability to change sex. This may lead to an excess of males and to an important shift in the sex ratio of the Eastern Oyster population (Thompson *et al.*, 1996). The Eastern Oyster can also refrain from feeding while spawning or after spawning. Individuals then lose weight and need to feed quickly again. Spawning usually occurs during a phytoplankton bloom (Osborne, 1999).

When water conditions are favourable in the Maritimes, the Eastern Oyster feeds almost continuously (Osborne, 1999; Steward, 1993). Oysters appear to increase their feeding rates up to a water temperature of about 26°C. At this temperature, a 10 cm long individual can filter at a rate of 9 to 13 L per hour (Steward, 1993). This feeding rate increase, coupled with an increase in water temperature, usually leads to an increase in feces and pseudofeces production (Figure 16). Conversely, Haven and Morales-Alamo (1966) observed an 85% reduction in weight of biodeposits when water temperature decreased below 6.7°C. Further, when temperature fell below 2.8°C, no measurable quantities of biodeposits were produced.

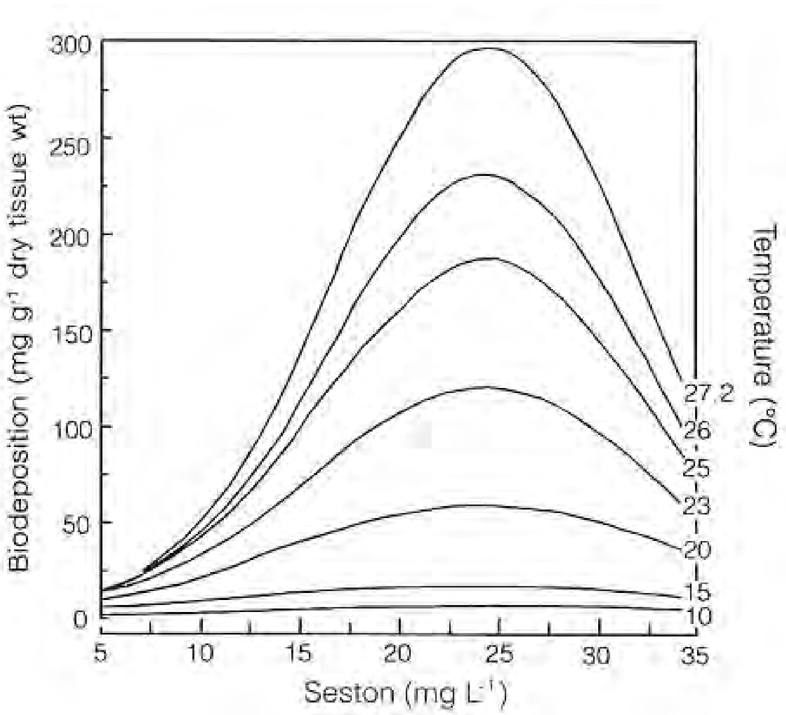


Figure 16: Production of feces and pseudofeces by Eastern Oyster adults in relation to temperature and seston concentration (Jordan, 1987).

Algal cells and fragments in feces and pseudofeces of these oysters consisted mainly of phytoplankton species of the genera *Cyclotella, Peridinium, Prorocentrum, Coccocenieis, Melosira* and *Coscinodiscus*. The smallest algae measured 3 µm and the largest *Nitzschia* measured about 146 µm. The size ranges of algal cells most frequently seen were *Cyclotella*, 10-80 µm; *Peridinium*, 16-32 µm. and *Cocconeis*, 8-30 µm. In laboratory experiments, adult Eastern Oysters presented with inert particles in their mantle cavity ingested the particles smaller than 40 µm in diameter and rejected ones larger than 100 µm (Tamburri & Zimmer-Faust, 1996).

The production of pseudofeces is the major mechanism used by the Eastern Oyster to reject excess amounts or unsuitable filtered particles (Newell and Langdon, 1996). Biodeposits (feces and pseudofeces combined) from oysters sampled in Virginia contained a ratio of 77-91% inorganic matter to about 9-13% organic matter (Haven and Morales-Alamo, 1966).

Feces and pseudofeces sink to the sea bottom or are resuspended and transported by wave action. The deposition of this material by *C. virginica* has been shown to supply a nutritional food source to several deposit-feeders such as *Nereis virens*, *Capitella, capitata* and *Corophium volutator* and it is suggested that this reworked superficial sediment layer may represent a prime food resource for many organisms living in estuaries (Newell, 1979). Through bacterial action, feces and pseudofeces are remineralized into nutrients. Nutrient will eventually be used by phytoplankton cells which will in turn be available for oysters and other pelagic and benthic organisms (Figure 17).

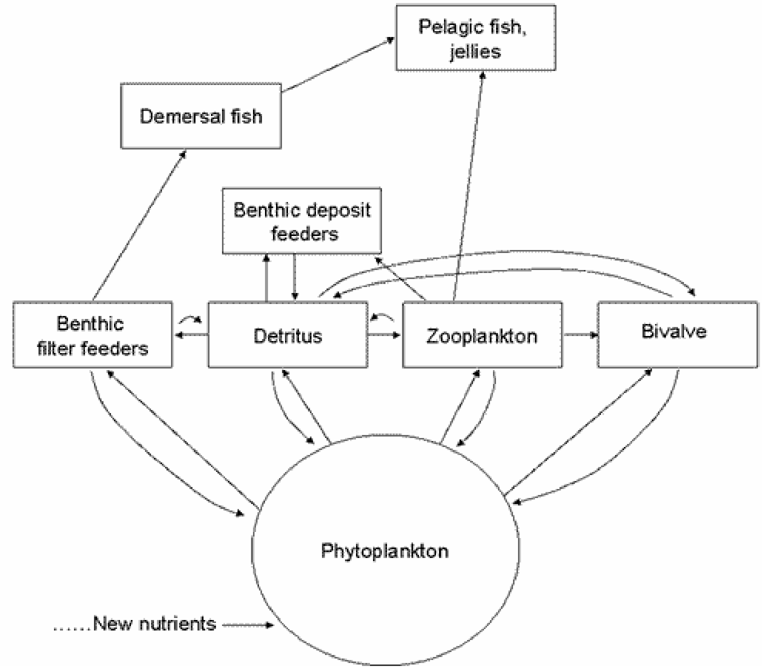


Figure 17: Example of an estuarine food web (Jiang and Knight, 2008).

Depending on the density of oysters and water turbidity, pseudofeces can accumulate on the bottom and modify various benthic characteristics. The ability to filter a large volume of water is important for the Eastern Oyster and other species in estuarine communities. Ulanowicz and Tuttle (1992) suggested that the loss of oyster beds over time in Chesapeake Bay has led to an increase in suspended particles in the water column, which in turn leads to a shift in the food web. Harding (2001) observed that the zooplankton around oyster reefs of the Piankatank River (Virginia) was distributed non-randomly. She similarly suggested that oyster reefs and its associated benthic fauna may influence the composition and abundance of the overlying zooplankton community and indirectly influence the trophic dynamics of the oyster reef community.

3.4.4. Physiology

Once sorted, food particles are directed toward the stomach. Beforehand, small particles are carried to the labial palps and then transferred directly to the mouth with no additional sorting (Figure 18).

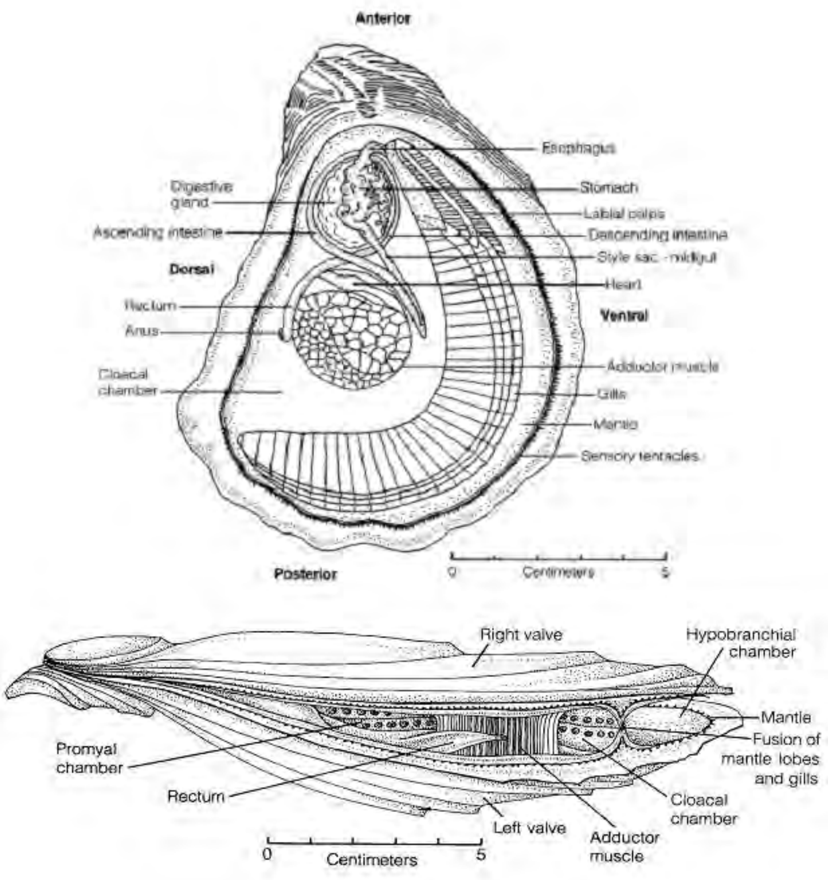


Figure 18: External and internal anatomies of the Eastern Oyster (Galtsoff, 1964).

Large particles are first coated with mucus and then transferred to the labial palps where additional sorting can occur before entering the mouth (Newell and Langdon, 1996).

When seston concentration is very high and gills are clogged, or when silt and other inorganic matter are being ingested, mucus bound particles may be directly sorted and rejected as pseudofeces (Newell and Langdon, 1996). This ability to separate food from silt and other inorganic matter apparently allows Eastern Oysters to survive in turbid estuaries (Keith and Anderson, 1995).

3.5. Predation

According to Galvao *et al.* (1989), ingestion of male Eastern Oyster gametes by heterotrophic microprotozoans and metazoan suspension feeders can rapidly decrease sperm concentration in the water column. This may influence fertilization and larval production. Once fertilized, the eggs and larvae may also be consumed by pelagic predators feeding on the plankton community.

In addition to providing a hard surface for the attachment of many sessile marine organisms, oyster beds and reefs also provide refuges and feeding grounds for various mobile marine organisms such as crustaceans, worms, molluscs and fish (e.g.: White and Wilson, 1996; Milewski and Chapman, 2002). Many predators are found among these organisms, feeding on different sizes of oysters. Eastern Oysters are highly vulnerable to predation since they cannot move and escape. However, large oysters possess a thick shell that is hard to penetrate or to open by predators. The environment in which oysters are found may also be difficult for predators. Intertidal oysters have fewer predators than oysters that grow subtidally (Keith and Anderson, 1995). Similarly, oysters that live in brackish waters tend to have fewer predators than their marine counterparts (White and Wilson, 1996).

3.5.1. Birds

The American oystercatcher (*Haematopus palliates*) is an important predator of Eastern Oysters along the Atlantic coast of North America, from Massachusetts to the lower Florida peninsula. Even though their range has been expanding northward and their presence has been documented as far north as Maine, they are rarely observed in NB (Nol and Humphrey, 1994). In the Maritimes, the Belted Kingfisher (*Ceryle alcyon*) has been reported to feed on clams and oysters when fish are not readily available (Erskine, 1992; Bent, 2006).

3.5.2. Worms

Polyclad turbellarian flatworms such as *Stylochus ellipticus* are common organisms found on oyster beds and reefs along the Atlantic and Gulf coast (Galtsoff, 1964; White and Wilson, 1996). They are observed in PEI and are able to tolerate a wide range of salinities (5 to 27 ppt) and temperatures. They mostly cause mortality among spat but they can kill oysters as large as 6 cm by entering the oyster through its partially gaping valves (White and Wilson, 1996). Newell *et al.* (2000) observed high post-settlement mortality rates of spat < 2.0 mm associated with predation by the juvenile life stage of *S. ellipticus*. They found this predation to be an important source of spat mortality (98%) and a potential factor in the structuring of oyster reefs.

3.5.3. Crustaceans

In NB, the Rock Crab (*Cancer irroratus*) is considered as an important predator of the Eastern Oyster (Doiron, 2003). They use their claws to break the oyster’s shell. Rock Crabs can cause considerable damage among spat and juvenile oysters (Galtsoff, 1964). A laboratory study by Miron *et al.* (2005) showed that Rock Crabs can easily crush or chip oyster shells and feed on oysters smaller than 25 mm. Lobsters (*Homarus americanus*) and mud crabs (*Dyspanopeus sayi*) can also be important marine predators (Doiron, 2003). Fisheries and Oceans Canada (1996) reported that 8 cm lobsters can eat up to 6 oysters (15-25 mm) per day while a 2 cm mud crab can eat about one oyster per day.

Blue Crabs (*C. sapidus*) are not usually found north of Cape Cod. They were however recently observed in Maine and NS following consecutive warm years (Guillory, 2003). The oyster is an important food item of the Blue Crab (Guillory, 2003). Food habit studies, however, have shown that prey species vary greatly in juvenile and adult Blue Crabs, depending upon availability. The Green Crab (*C. maenas*) is another potential predator. The Green Crab was first noticed off the southern shores of PEI in 1997, and has since further extended its range in the southern part of the Northumberland Strait (Audet *et al.*, 2003). Miron *et al.* (2005) observed that Green Crabs in the laboratory can prey heavily on Eastern Oysters smaller than 25 mm.

3.5.4. Fish

Fish are common predators of Eastern Oysters in most northern Atlantic estuaries and bays. Among these are the Sheepsheads (*Archosargus probatocephalus*) found in NS and the Skates (*Raja* spp.) found in the sGSL (White and Wilson, 1996). The Drumfish

(*Pagonias cromis*) is another important predator. They are capable of crushing thick shells and feed on large oysters (≤ 8 cm) (Robins and Ray, 1986; White and Wilson, 1996). They are found from NS to northern Mexico.

3.5.5. Molluscs

Carnivorous snails such as whelks, oyster drills and dogwinkles may feed on oyster spat and juveniles. They inflict severe damage by drilling into their prey. However, most of these predators are unable to survive in brackish water (White and Wilson, 1996). The species *Urosalpinx cinerea* is especially destructive and can inhabit a wide range of different habitats in the intertidal and sublitoral zones along the eastern Canadian shores (White and Wilson, 1996; Gosling, 2003). MacKenzie (1981) showed that *U. cinerea* can become very abundant in Long Island Sound and could kill up to 33% of oyster spat during the summer months.

3.5.6. Others

In the Maritimes, juvenile and adult oysters are preyed heavily upon by the Northern sea star (*Asterias vulgaris*) (Doiron, 2003). Though they move slowly across the bottom, sea stars can cover a few hundred meters in several weeks and cause great damage to oyster populations (MacKenzie, 1970). They are able to open the oyster shells and extend their stomach into a very small opening to digest the oyster (White and Wilson, 1996). Sea anemones, various coelenterates and the boring sponges *Cliona* spp. can also feed on small oysters (White and Wilson, 1996). Humans represent another important predator. In the sGSL, there is a wild fishery in NB, NS and PEI, and contaminated relay fisheries in NS, NB & PEI (Fisheries and Oceans Canada, 1996).

3.6. Competition

The presence of competitors particularly affects Eastern Oyster larvae and juveniles. Food and space competitors can significantly reduce oyster populations through intraspecific and interspecific relationships (White and Wilson, 1996). Eastern Oyster larval settlement tends to occur simultaneously with the settlement of other fouling organisms (Shaw, 1967). Surface area for settlement being limited, competition for space becomes an important source of mortality in natural populations of Eastern Oysters (Osborne, 1999).

3.6.1. Intraspecific

Intraspecific competition can be noticed through the consumption of oyster larvae when they settle near conspecific adults and through space competition when individuals overgrow (White and Wilson, 1996). Young and Chia (1985) note that *C. virginica* veligers have been found in stomachs of adult oysters. If recruitment is great, large Eastern Oyster spat overgrow small neighbouring spat and the latter subsequently die (MacKenzie, 1970). Although mortality occurs, moderate overgrowth by Eastern Oyster spat can be beneficial to the overall population. An oyster reef overcrowded by adults may increase intraspecific competition for food and reduce the fitness of the population (White and Wilson, 1996).

3.6.2. Interspecific

Sessile invertebrates such as ascidians, barnacles and calcareous bryozoans can compete with the Eastern Oyster for space and food and affect their settlement success, post-settlement growth, and survival (Osman *et al.*, 1989; White and Wilson, 1996). Ascidians and bryozoans can prevent oyster larval settlement by covering settlement sites or oyster shells. According to MacKenzie (1970), spat mortality from bryozoan overgrowth can be as high as 8% in some oyster populations (spat < 5 mm). Ascidians are also responsible for important oyster coverage (Galtsoff, 1964). In the Maritimes, the exotic ascidians *Styela clava*, *Ciona intestinalis* and *Molgula manhattensis* have been reported to compete with the Eastern Oysters for food and space in PEI, NS and NB, respectively (Doiron, 2003). Barnacles are also important competitors for food and space and can kill up to 5% of the oysters < 5 mm (MacKenzie, 1970; White and Wilson, 1996). The Blue Mussel is probably the main space and food competitor of the Eastern Oyster in the Maritimes. They can significantly reduce oyster growth (Doiron, 2003; Steward, 1993).

Some organisms may release chemicals that can repel oyster settlement or even poison them (White and Wilson, 1996). This is the case for the diatoms *Nitzschia* spp. which releases domoic acid under certain conditions which may repeal larvae and juveniles from settling (Doiron, 2003). Blooms of toxic dinoflagellates can also kill juvenile oysters (Gosselin & Quian, 1997). The exotic green alga *Codium fragile* is commonly found attached to rocks, piers, floating docks and oyster beds in sheltered intertidal and subtidal areas along the northwest Atlantic coast. Commonly known as the oyster thief for its property for dislodging oysters from their habitat, *C. fragile* was first reported in 1957 in Long Island Sound. It reached the east coast of NS in the late 1980s and has since been discovered off the coasts of PEI and NB (Begin and Scheibling, 2003; Fisheries and

Oceans Canada, 2005b) and in the Magdalen Islands (Simard *et al.* 2007). The oyster thief tolerates large variations in salinity and temperature and may colonize a wide range of environments (Begin and Scheibling, 2003). When they attach to oyster beds, they can limit the movement of an oyster's upper shell and impede their filtration (MacKenzie, 1981, Fisheries and Oceans Canada, 2005b). Large oyster thief can create extra drag and become buoyant by trapping gas bubbles, which can dislodge oysters from their substrate and sweep it away (Fisheries and Oceans Canada, 2005b).

3.7. Diseases

A number of micro-organisms are pathogens of oysters. Malpeque disease devastated oyster beds and reefs in PEI (1915-1940), NB, and NS (1954-1957). The multinucleate sphere unknown (MSX) is another deadly disease caused by a micro-organism (*Haplosporidium nelsoni*). The parasite’s current distribution extends from Florida to Maine. Within Canada, MSX has only been detected in oysters from Cape Breton, NS, specifically from the Bras d’Or Lakes (Bower, 2007a) and St-Ann’s Harbour. The initial epizootic event detected in the Bras d’Or Lakes in 2002 was associated with significant mortalities of oysters. MSX has not yet been detected in oyster populations between the southern end of Maine and Bras d'Or Lakes in NS or within Gulf of St.Lawrence. Another *Haplosporidium (H. costale* or SSO) has been found occasionally in the Southern Gulf of St. Lawrence, Atlantic coast of NS, and Bras d'Or Lakes (Bower, 2007b). However, no mortalities were observed with SSO. Other diseases are observed in Atlantic Canada but many are not deadly. The viral gametocytic hypertrophy (VGH) represents a good example. This disease may cause massive gamete hypertrophy, however it has not been associated with mortality (Bower, 2001b).

4. INTERACTIONS BETWEEN WILD *MYA ARENARIA* AND WILD *CRASSOSTREA VIRGINICA*

Molluscs first appeared in the fossil record about 545 million years ago during the early Cambrian period (Bybell, 1999). Most of the modern mollusc groups were present in marine environments by the late Cambrian period (520-505 million years ago). A major radiation of molluscs occurred during the Ordovician period (505-438 million years ago) and thousands of species became widespread during the Mesozoic Era (65 to 251 million years ago) as burrowing species evolved. The Cenozoic period (the last 65 million years) marks the time when molluscan groups, such as marine clams and snails, evolved (Bybell, 1999). Since then, marine clams and snails have represented the dominant groups of hard-shelled marine animals.

Oyster and clam fossils have been found together at an altitude of up to 3000 meters in the mountains, suggesting that they were once parts of the same living marine community. Oyster and clam fossils have also been found in the soft grey marl of New Bern (North Carolina), suggesting that warmer coastal seas were once covering this area and that the two species were part of a living reef (Williams, 2001).

Ray *et al.* (1997) conducted an analysis of benthic invertebrate assemblages and found that habitat-types and/or the presence of certain organisms were closely related. They identified that *M. arenaria*, *C. virginica* and *M. mercenaria* form a characteristic assemblage typical of cool-temperate latitudes along the eastern seaboard. This suggests that the environmental attributes of what they termed ‘virginian’ estuarine habitats tend to generally favour a pattern of co-existence between Softshell Clams, Eastern Oysters and Quahogs under natural settings (Ray *et al.* 1997).

Figure 19 shows an example of oyster and clam co-occurences mapped from field surveys in Great Bay, Little Bay and Oyster River in New Hampshire (Cooperative Institute for Coastal and Estuarine Environmental Technology, 2005).

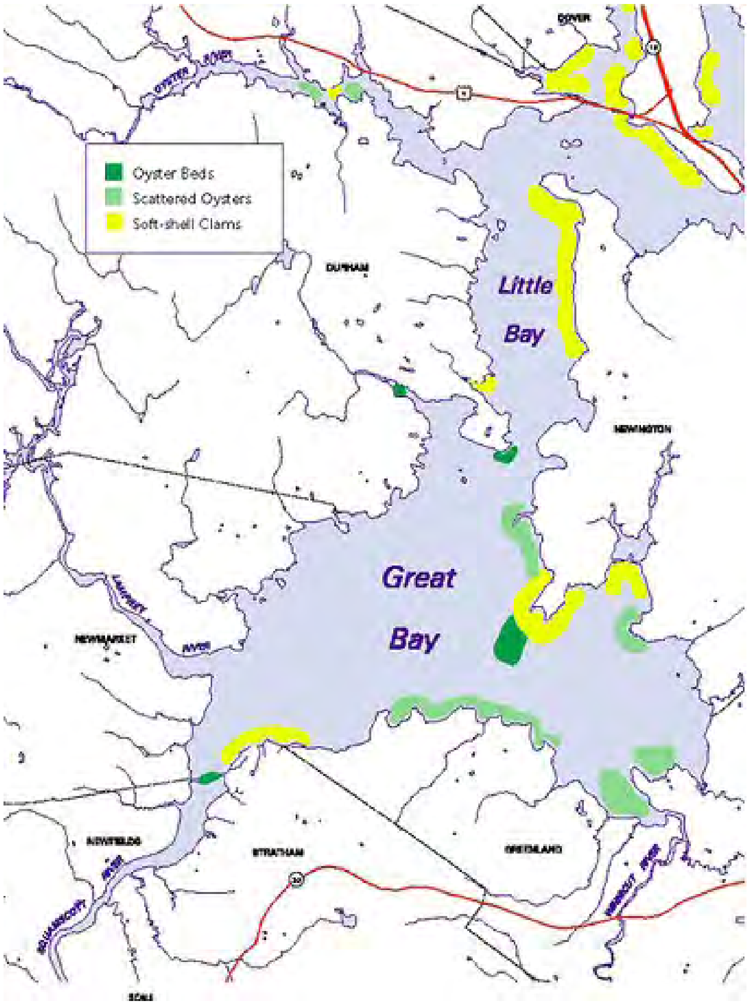


Figure 19: Location of Softshell Clam and Eastern Oyster beds in Great Bay, Little Bay and Oyster River (New Hampshire, USA). The map was developed from data generated by the New Hampshire Fish and Game and scientists from the Jackson Estuarine Laboratory (Cooperative Institute for Coastal and Estuarine Environmental Technology, 2005).

Closer to the sGSL, Figure 20 shows the results of an underwater survey conducted in 1986 in Bouctouche Bay (NB) and illustrates how both species can occupy at times discrete or overlapping habitats within the estuary.

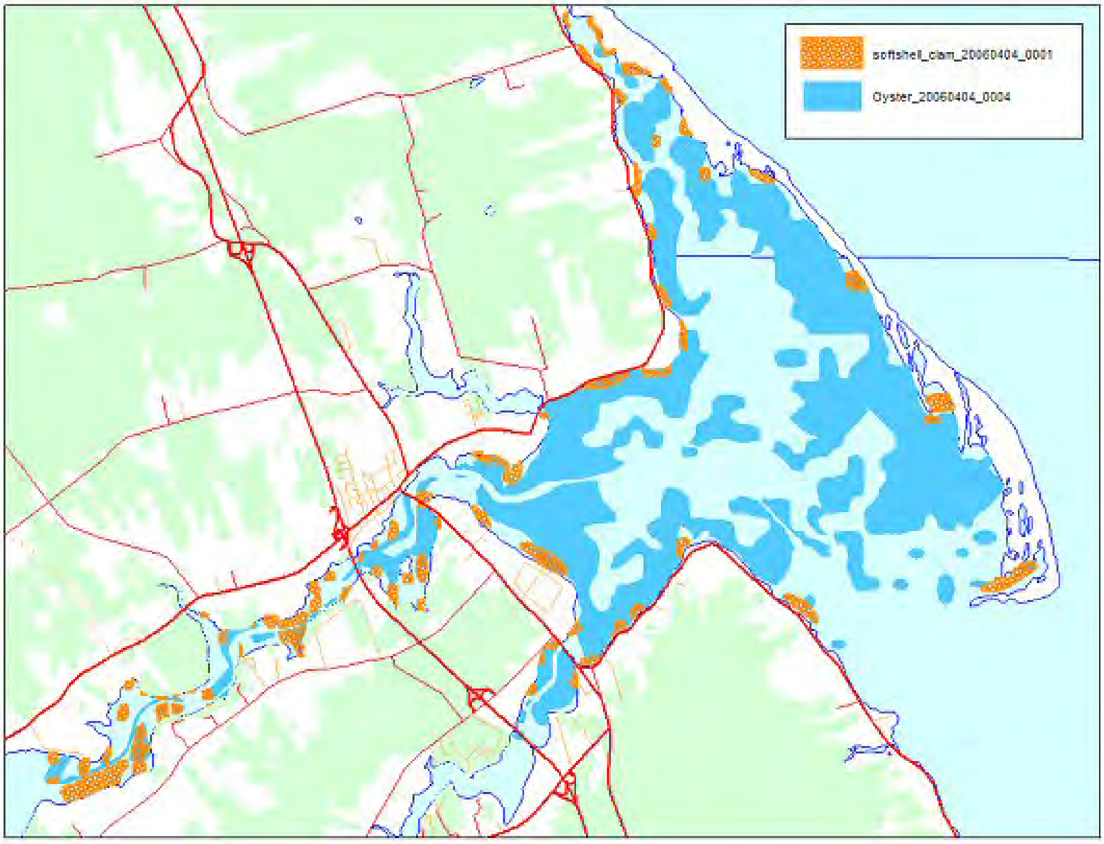


Figure 20: Location of Softshell Clam and Eastern Oyster beds in Bouctouche Bay, New Brunswick, Canada (Senpaq Consultants, 1986).

4.1. Biotic interactions

The biotic relationships between the Eastern Oyster and the soft-shell clam include biological interactions between individuals from the same species (intraspecific interactions) and between individuals of different species (interspecific interactions). While reviewing the evolution of molluscs in fossil records, Stanley (1973) found that, in general, interspecific competition between bivalves has remained weak throughout their evolution. Bivalve species are documented to co-occur within similar habitats, often closely grouped together, with no apparent evidence of narrowing of niche or competitive interactions. Physical disturbances and predation rather than food or space are believed to be the prevalent controls in limiting population densities (Stanley, 1973).

4.1.1. Early stages

The spawning period for the majority of bivalve species found in the Maritimes occurs during the summer months. Aucoin *et al.* (2004) showed that larvae of the Softshell

Clam, Razor Clam (*Ensis directus*), Arctic Rock Borer (*Hiatella arctica*), Surf Clam (*Spisula solidissima*) and Northern Quahog were present between May and July in the Magdalen Islands. Larvae of the sea scallop (*Placopecten magellanicus*), horse mussel (*Modiolus modiolus*) and Eastern Oyster dominate starting in August. Blue Mussel (*M. edulis*) larvae were present all summer. This means that the water column generally contains numerous species of larvae during overlapping periods in the summer.

There are few published reports describing behavioural interactions between larvae from the same species or of different species. According to Young (1995), larvae probably developed mechanisms to locate, collect and handle food to avoid competitors and predators to increase their chance of survival in the water column. In the case of oysters, Figure 21 outlines the complex biotic and abiotic factors that can influence the mortality of pelagic and early benthic stages during different development phases.

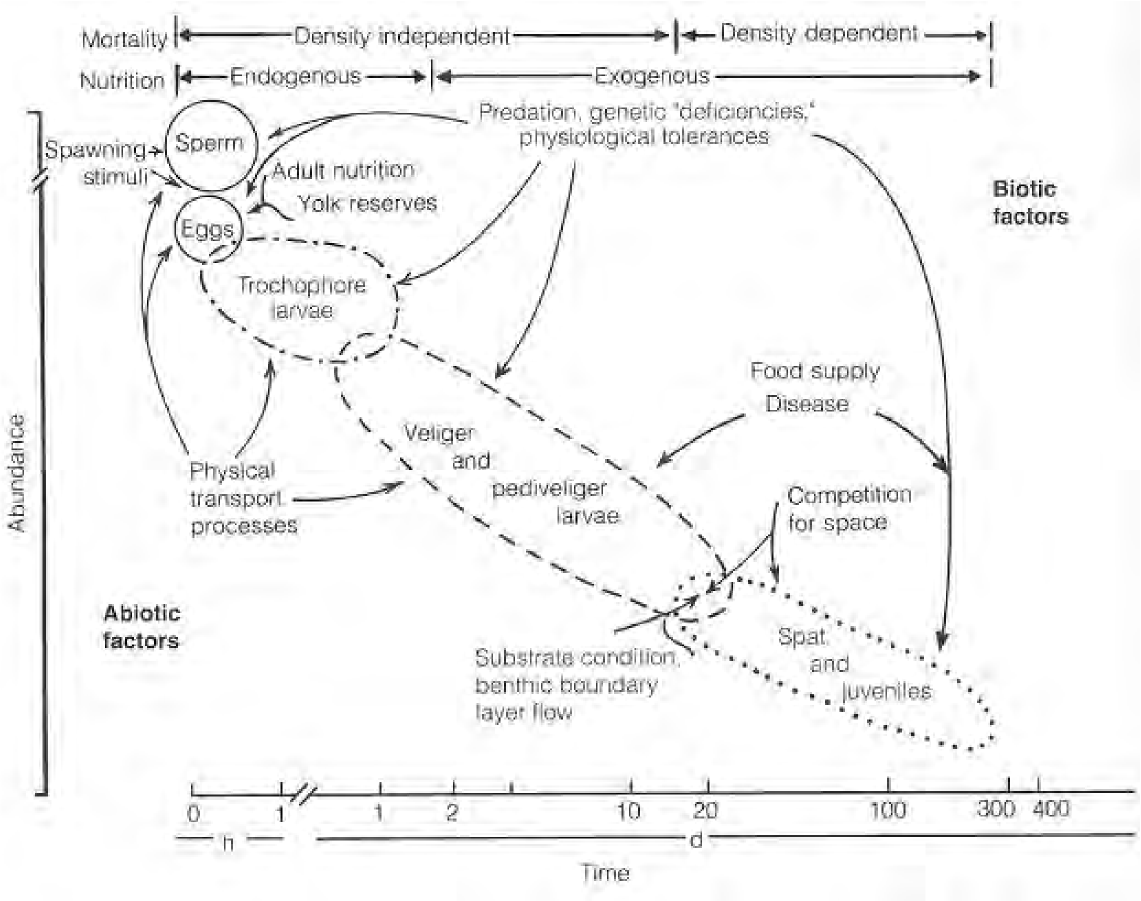


Figure 21: Abiotic and biotic factors influencing the mortality of Eastern Oysters from pelagic to early benthic stages (Kennedy, 1996).

This illustrates that, in contrast to early benthic stages, mortality of pelagic stages of the Eastern Oyster are not density related ; this suggests that food supply in estuarine waters is probably not a source of larval intraspecific or interspecific competition (Kennedy, 1996). In fact, quality of algal biochemical composition, especially that of lipids, rather than quantity, seems to affect larval growth and survival (Boidron-Métairon, 1995).

The relationship between nutrition, larval growth and development does not depend exclusively on food particle abundance or composition but also on its accessibility (size, shape, density) and suitability to the larva’s feeding behaviour. Boidron-Métairon (1995) further suggests that when food is unreliable and individual growth is food limited, starved bivalve larvae can survive for days using endogenous reserves and develop normally when feeding resumes.

Habitat differences can also explain why some bivalve species are more tolerant to lower food concentration than others. His *et al.* (1989) suggested that oceanic mussel larvae tend to be better adapted to low plankton concentrations than estuarine oyster larvae, and that they may feed more successfully on other food sources. Stanley (1973) suggests that bivalves have maintained generalized feeding habits and the ability to withstand long periods of near-starvation as adaptive mechanisms to survive in unpredictable environments. These adaptations and population limitations by predation and stochastic physical disturbances tend to limit intense competition for food between bivalve larvae (*Stanley, 1973*).

A study carried out by Senpaq Consultants and Université de Moncton (1990), showed, for instance, that regular peaks in chlorophyll production are observed during the spring and autumn off the east coast of NB These plankton blooms are particularly apparent in May and from mid-August to late September (Figure 22). One of the characteristics of the southern Gulf of St. Lawrence ecology is its large seasonal increase in planktonic biomass during those periods (Fisheries and Oceans Canada, 2001c). Studies conducted in the Bay of Fundy showed that the cold water diatoms *Skeletonema costatum* (Martin *et al.*, 2001) and *Thalassiosira nordenskioelddi* (Smith *et al.*, 2001) are among the dominant phytoplankton species found in the water column. *S. costatum* (2-21 µm) and *T. nordenskioelddi* (10-50 µm) are found in the diet of most bivalves. According to Raby *et al.* (1994), bivalve larvae of different species tend to feed, at similar sizes, on different particle sizes. Although Softshell Clam and Eastern Oyster larvae ingest food particles of a similar size, the Eastern Oyster may be more selective (Nelson, 1947).

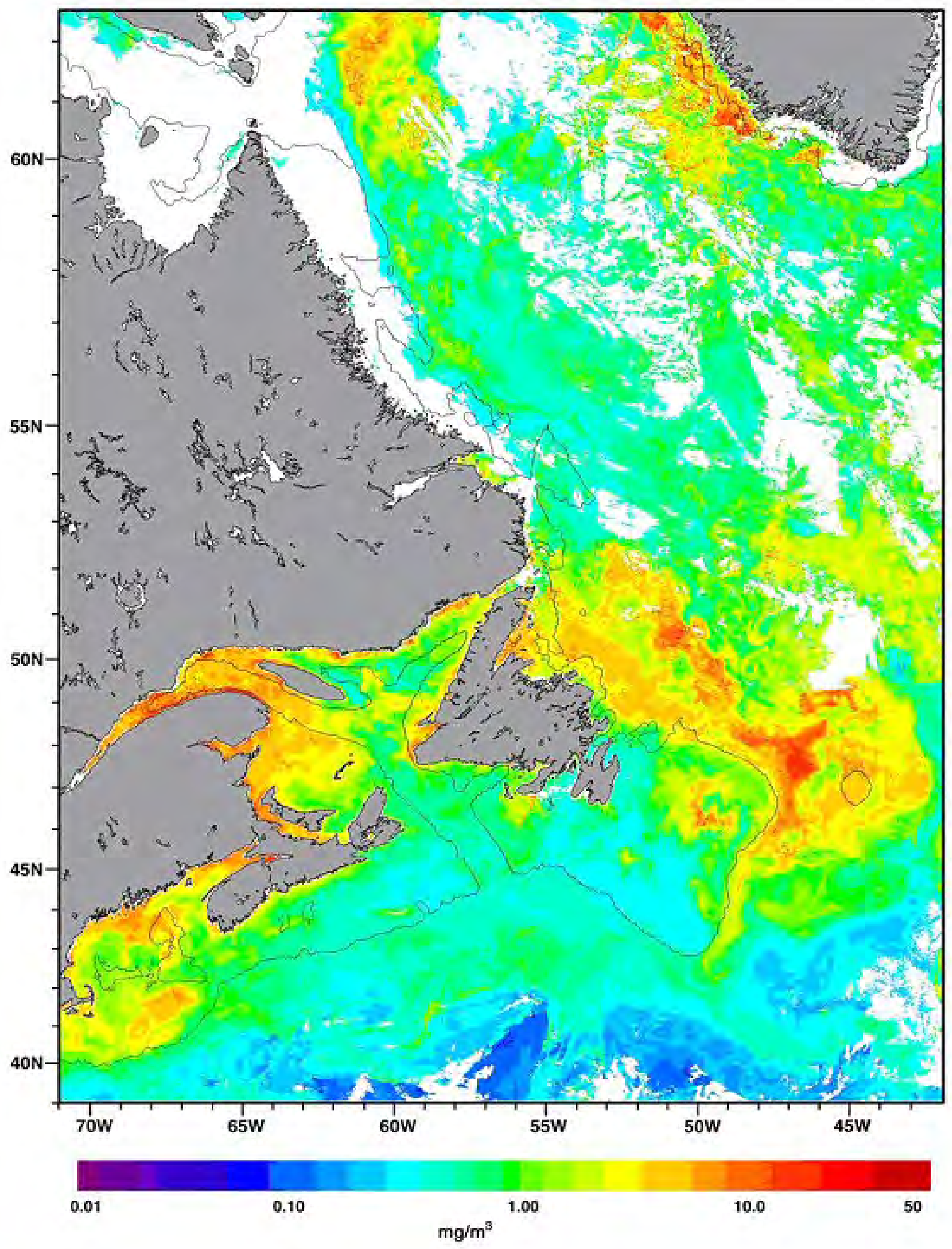


Figure 22: Chlorophyll-a concentration (OC4 algorithm) found along the east coast of Canada in May 2002 (NASA, 2006;** http://oceancolor.gsfc.nasa.gov/**)

A field study of the abundance and occurrence of the pelagic stages of bivalve species in Malpeque Bay (PEI) suggests that Softshell Clam and oyster larvae do not generally co-occur (Figure 23) (Sullivan, 1948). Clam larvae, for instance, are usually dominant in late-June and early July, while oyster larvae are dominant in August. This suggests that the two species may not be directly competing for identical food particles since they are unlikely to be present at the same time or when they are, may not be of the same size.

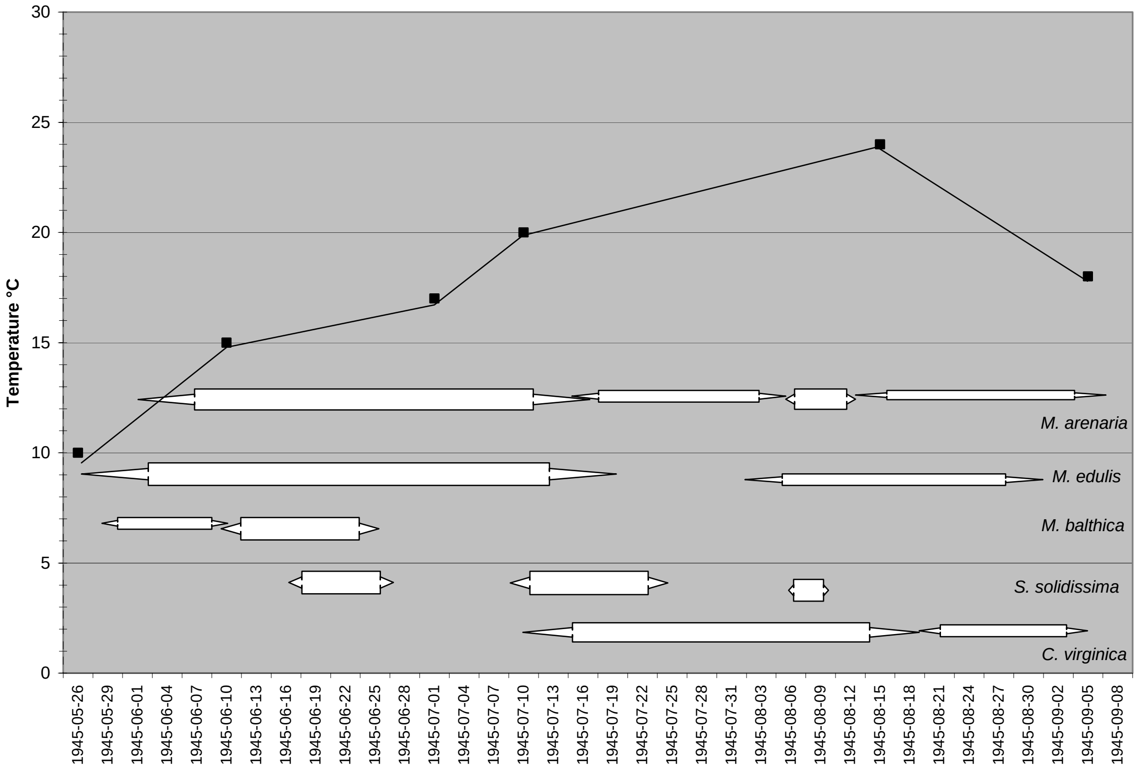


Figure 23 – Example of variation in seasonal occurrence and changing abundance (boxes), relative to water temperature (line), of bivalve larvae present in the water column in Malpeque Bay, PEI in 1945 (replica from Sullivan, 1948)

The vertical distribution profile of estuarine bivalves is influenced by a number of factors during larval life. Initially, it is believed that early-stage larvae of virtually all species swim toward the surface where they encounter the currents which contribute to their dispersal (Young and Chia, 1985). However, late-stage bivalve larvae tend to control their vertical position to enhance their retention within estuaries. They do this by remaining near the bottom during most of the tidal cycle and swimming up in the water column when they detect the higher salinity of the incoming tide (Young and Chia, 1985). In stratified waters, vertical distribution may be limited when larvae are entrapped or favour a position within a specific thermocline or salinity gradient (Young and Chia, 1985). Diel vertical migration patterns are also observed in bivalve larvae (*Young and Chia, 1985*). Thus, a number of behaviours bring larvae to occupy different vertical strata in the water column; this adaptation could serve to spread populations more evenly, or to separate them depending on their size, swimming ability, or photoresponse. This could also serve to limit competition (Young and Chia, 1985).

Recruitment of the Eastern Oyster and the Softshell Clam depends on larval settlement and subsequent post-settlement mortality. Larval settlement for both species involves interactions between the pelagic larvae at the time of settlement, environmental cues, and the substrate. In general, daily mortalities of bivalve larvae are in the order of 10% per day, with an average overall survival rate at settlement of approximately 2% (Young and Chia, 1985). Survivorship of oyster larvae in British Columbia was estimated at less than 2%; Quahog larvae (*M. mercenaria*) at 0 - 2.6% in New Jersey (Young and Chia, 1985). A number of reasons can explain these high rates of planktonic mortality such as inadequate food or temperature conditions, offshore transport, and inability to find adequate substrate. Mortality due to predation is generally considered the most significant factor (Young and Chia, 1985).

The ingestion of free-swimming and settling stages by adult benthic invertebrates has been documented in numerous species (e.g.: review from Mileikovski, 1974; Cowden *et al*., 1984; Hines *et al*., 1989; André *et al*., 1993; Riera and Richard, 1996; Tamburri and Zimmer-Faust, 1996; Pechenik *et al*., 2004). Certain studies suggest that the ingestion of larvae may have an important effect on the population dynamics of benthic species (e.g.: Korringa, 1940; Thorson, 1946; Thorson, 1950; Barnes, 1959; Paine, 1963; Segerstråle, 1973; André *et al*., 1993; Tamburry and Zimmer-Faust, 1996). In a laboratory study, André *et al*. (1993) showed that 75% of bivalve larvae (*Cerastoderma edule*) were captured by adult conspecifics and that mean survival time of the larvae over feeding adults (380 ind m $^{-2}$) was 64 seconds. In the laboratory, a wide range of invertebrate larvae pipetted into the mantle cavity of adult Eastern Oysters were readily consumed and digested, including conspecific veligers (Tamburri & Zimmer-Faust, 1996). The actual impact of the inhalation of larvae by adults on the population dynamics of benthic invertebrates is still poorly understood. Most studies have been done in the laboratory; extrapolation to the field is difficult.

The few field studies available on this impact minimize the role of intraspecific cannibalism (Mileikovsky, 1974) or vary its importance in relation to the density of the filter-feeders (André *et al.*, 1993) and small and large-scale landscape effects (Lindegarth *et al*, 2002). Tamburri *et al*. (2007) surveyed juvenile and adult Pacific Oyster (*C. gigas*) interactions in the field and found that oyster larvae settling in dense intraspecific aggregations were unlikely to be cannibalized. They found that gregarious settlement behaviour was not associated with a greater risk of mortality, but that it had evolved in a number of bivalve species as a means to improve reproductive fitness. Infaunal densities of *Mya* larvae were significantly higher within dense mussel beds than at control sites (Commito, 1987). Young and Chia (1985) have reviewed this question for a number of bivalve species and suggest that a number of complex larval behaviours serve to actually facilitate the retention of larvae in waters near the adult habitat where settlement conditions are more likely to be favourable.

A wide variety of structural, biological and chemical defence mechanisms have been proposed as potential life-history strategies used by bivalves to mediate or reduce predation effects (e.g.: Lucas *et al*., 1979; Stoecker, 1980; Cowden *et al*., 1984, Young and Chia, 1985). Biotic and abiotic elements of particular habitats include spatial and temporal refuges (Seed, 1993); the production of large quantities of gametes to offset predation during the planktonic larval and benthic juvenile stages (Cowden *et al.*, 1984; Stanley, 1973); improved larval fitness and defensive adaptation such as larval shells (Cowden *et al.*, 1984). Behavioural patterns consist of passive and active migration and movement within the water column (Lindegarth et al, 2002), light avoidance, and spawning synchronisation with phytoplankton blooms (Young and Chia, 1985). Even though it has been suggested that predation is a significant source of mortality in bivalve larvae, some experimental manipulations have actually measured low predation rates in studies using natural densities of prey and predators. A study using *Ostrea edulis* suggests that behavioural defence mechanisms may explain the low rate of predation observed (Metaxas & Burdett-Coutts, 2006). Predation on clam and oyster larvae may therefore be differential and not indiscriminate, depending on their respective defence and avoidance mechanisms.

Even when ingested, not all bivalve larvae will die following predation (e.g.: Cowden *et al*., 1984; Pechenik *et al*., 2004). Larvae may resist their passage through the digestive system. According to a study by Baldwin *et al.* (1995), a good proportion of quahog (*M. mercenaria*) larvae that are filtered by oyster adults are rejected alive and bound in pseudofeces. A large proportion of ingested larvae also passed through the adult's gut alive; larvae were again bound in feces. While many of the bound larvae were totally encased in the adult's biodeposit, the authors noticed that some larvae were able to dislodge themselves and escape. Tamburri and Zimmer-Faust (1996) found that there were no effects of capture and release by oysters on the subsequent swimming behaviour of the few larvae that escaped from pseudofeces. Larvae that were not able to free themselves or to open their valves while partially encased, frequently died from starvation or were ingested by other predators or benthic scavengers (Baldwin *et al.*, 1995, Young and Chia, 1985).

Although post-settlement mortality due to predation is likely to be the main factor regulating bivalve population dynamics (Stanley, 1973), it is also likely to vary among species. This is in part because settlement and predator abundance may not occur at the same place and time and partly because larvae of both species are likely to have similar nutritional values. Thus predators are likely to prey randomly on oyster and clam larvae according to their spatial and temporal availability (Gosselin & Qian, 1997). Preferential selection may be made by predators in relation to species and size (Cowden *et al*. 1984). At the time of settlement, oyster larvae (330 μm) are bigger than Softshell Clam larvae (200 μm) and are fixed to the substrate. Unlike oysters however, newly settled clams are able to burrow in the sediment to escape predators.

Intense predation observed at high prey densities may decrease or disappeare at near-natural prey densities (Johnson and Shanks, 2003). High abundance and diversity of plankton may occupy the predator’s foraging time and decrease encounter opportunities, detection, and the capture of specific species of larvae. Nonetheless, levels of mortality to predation in planktonic and juvenile invertebrates are commonly reported to be in the vicinity of 98% (Newell *et al.*, 2000).

4.1.2. Late stages

Eastern Oysters were once abundant and important in maintaining the health of coastal and estuarine ecosystems before a number of factors led to their massive decline throughout their range (Milewski and Chapman, 2002). It has been demonstrated that the degradation of oyster reefs along the North American eastern and western seaboard followed a predictable pattern of gradual exploitation, disease and collapse (Kirby, 2004; Kirby and Miller, 2005) and that this is believed to have had a profound effect on estuarine ecology (Kirby, 2004). The general presumption is that the removal of oysters should result in increased fitness of other bivalves, either through removal of intraspecific and interspecific competition for primary production or for space. Kirby and Miller (2005) used a 300 year time-series on growth rates of molluscs prior to and after the depletion of oyster reefs in Chesapeake Bay to illustrate that improved growth does indeed occur but that this effect is temporary. The loss of oysters appears to result in a short-term enhancement of food supply to other benthic suspension feeders but this effect gradually becomes offset by the establishment of a new trophic equilibrium within the estuary. This equilibrium is characterized by an accumulation of organic matter in the water column, the disappearance of benthic populations, and the dominance of a pelagic food-web dominated by bacteria and gelatinous predators; environmental degradation and eutrophication appear to compound these effects (Kirby and Miller, 2005).

Abundant literature advocates that the Eastern Oyster plays a role as an engineering species in terms of its ability, through feedback mechanisms, to favourably influence the suitability of the environment as habitat for other species. These feedbacks may include influences on sedimentation, inputs of nutrients, and provision the of 3-D habitat (for example, see: Dame *et al.*, 1984; Ray *et al.*, 1997; Coen *et al*., 1999; Coen *et al*., 2006; Lenihan, 1999). These studies look at estuaries where Eastern Oysters were extirpated to demonstrate that their absence has resulted in detrimentally altered phytoplankton concentrations and energy flows. Mass-balance models have been used to illustrate the theoretical effects of restoring oyster biomass to their historical levels. Results suggest a beneficial effect in reducing overabundant phytoplankton production and in increasing benthic primary and secondary productivity (Ulanowicz and Tuttle, 1992). Forecasts of interactions between increased oyster populations and other benthic suspension feeders imply that competition would occur but that it would not threaten their established coexistence (Ulanowicz and Tuttle, 1992).

Interspecific competition for space is unlikely to occur between Eastern Oysters and Softshell Clams as both species rarely settle on the same type of substrate. Oyster reefs however are known to support a number of clam species such as *Macoma* spp., *M. mercenaria* and *M. arenaria* (Ruesink *et al.*, 2005). Softshell Clam juveniles have been observed at high densities within oyster reefs (6,000 ind. m^{-2} in South Carolina, 850 ind. m^{-2} in Georgia) (Bahr and Lanier, 1981) and are considered a species that is commonly associated with oyster reefs (Ray *et al.*, 1997).

Intraspecific competition for space is more likely to occur and affect the recruitment of both species. Eastern Oyster and Softshell Clam larvae face a similar likelihood of being ingested by conspecific or competitor adults when they are ready to settle. Roegner (1991) observed that mortality of newly settled oysters is initially density independent but, as numbers increase, becomes density dependent. This observation suggests that, when the substrate is not limited, there is less intraspecific competition for space at an early stage and post-settlement recruitment may be related to predation. As oyster spat grows, space may become limited and intraspecific competition may thus increase. If there is limited settlement space during spatfall, early mortality and post settlement recruitment is likely to be determined by intraspecific competition for space and subsequent limited growth of oyster spat (Osman *et al.*, 1989). Zajac *et al.* (1989) also suggests that when crowding occurs, competition for food may be the most significant factor influencing growth and survival of oyster spat.

As individuals grow larger and populations get crowded, intraspecific and interspecific competition for food and space becomes more important during the late benthic stages than during the pelagic or early benthic stages (Figure 24). In order to minimize interspecific competition for food and space, bivalves have developed different strategies allowing them to colonize a wide range of habitats and to coexist in similar environments. Primitive bivalves are believed to have first colonized the intertidal and sub-tidal habitats, where they collected food particles directly from the substratum (Purchon, 1977).

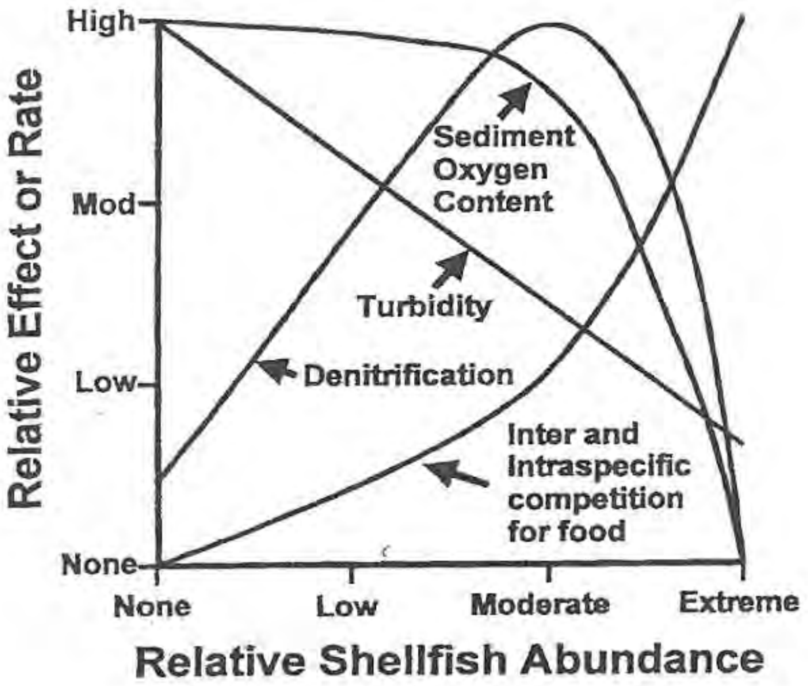


Figure 24: Water column turbidity in relation to relative shellfish abundance in eutrophic coastal waters (Newell, 2004).

The evolution toward filter-feeding rendered bivalves independent from the substratum as a direct source of food and allowed them to diversify into many forms inhabiting various substrates (Purchon, 1977). With the development of filter-feeding mechanisms, bivalves such as the Softshell Clam started to live in the sediment, mostly using the substratum for protection against predation and resuspension (Purchon, 1977). Consequently, such bivalves developed a large muscular foot well adapted for burrowing and a siphon-like structure, allowing them to feed while hidden in the sediment. The establishment of bivalves on hard surfaces required permanent attachment to the substratum and in the case of oysters, allowed them to reach the mid-water column (Purchon, 1977).

Many species of clams can coexist in the Maritimes because each species has specifically adapted to a tidal level and a given depth (Fisheries and Oceans Canada, 1996). Coexistence of bivalves has not required partitioning of food resources or the development of narrow niches in productive estuarine environments (Stanley, 1973). According to the Australasian Water Studies Group (2005), bivalves are able to coexist in such areas because food is not limited. In general, bivalves living in cold temperate environments also adopt a more generalist strategy in order to deal with the winter and its unpredictable conditions.

In the Maritimes, fouling organisms such as barnacles, gastropods, encrusting bryozoans, colonial ascidians and sessile bivalves can compete with the Eastern Oyster for space on hard substrate. Depending on the initial size of the oyster and on the growth rate of competitors, these fouling organisms can overgrow and suffocate oysters (White and Wilson, 1996; Castagna *et al.*, 1996). Barnacles and mussels are the most common competitors found on oyster beds along the western Atlantic and Gulf coasts (White and Wilson, 1996). In addition to competing for space with adult oysters, they affect oyster's recruitment by feeding on settling larvae. Some boring sponges and worms can also weaken oyster shells by their tunnelling (Galtsoff, 1964). Several species of algae can also compete with the oyster for space (Galtsoff, 1964). In the Maritimes, the green algae *Enteromorpha* and *Ulva* are frequently associated with oyster beds and can become important competitors for space if present in great abundance. The green alga *Codium fragile* can cause mortality in oysters when its holdfast becomes extensive and collects silt, thus suffocating the oysters (MacKenzie, 1981).

4.2. Indirect interactions

While biotic interactions may be the best understood and documented causes of mortality in bivalves, other abiotic factors might be equally important in limiting population densities, particularly in intertidal zones where conditions fluctuate to extremes with changing tides and seasons (Gosselin and Quian, 1997). The response of bivalves to environmental disturbances is influenced by the size, age, and ecological complexity of the systems within which they grow and reproduce. These responses reflect the interactions within the ecosystem that are related to productivity, nutrient cycling and physical-chemical processes of energy flow. Filter-feeders assimilate a portion of the filtered material and convey the rest as digested (feces) or undigested (pseudofeces) nitrogen-rich material to the sediments. This material is then available to various benthic organisms (Figure 25) (Baldwin, 1995).

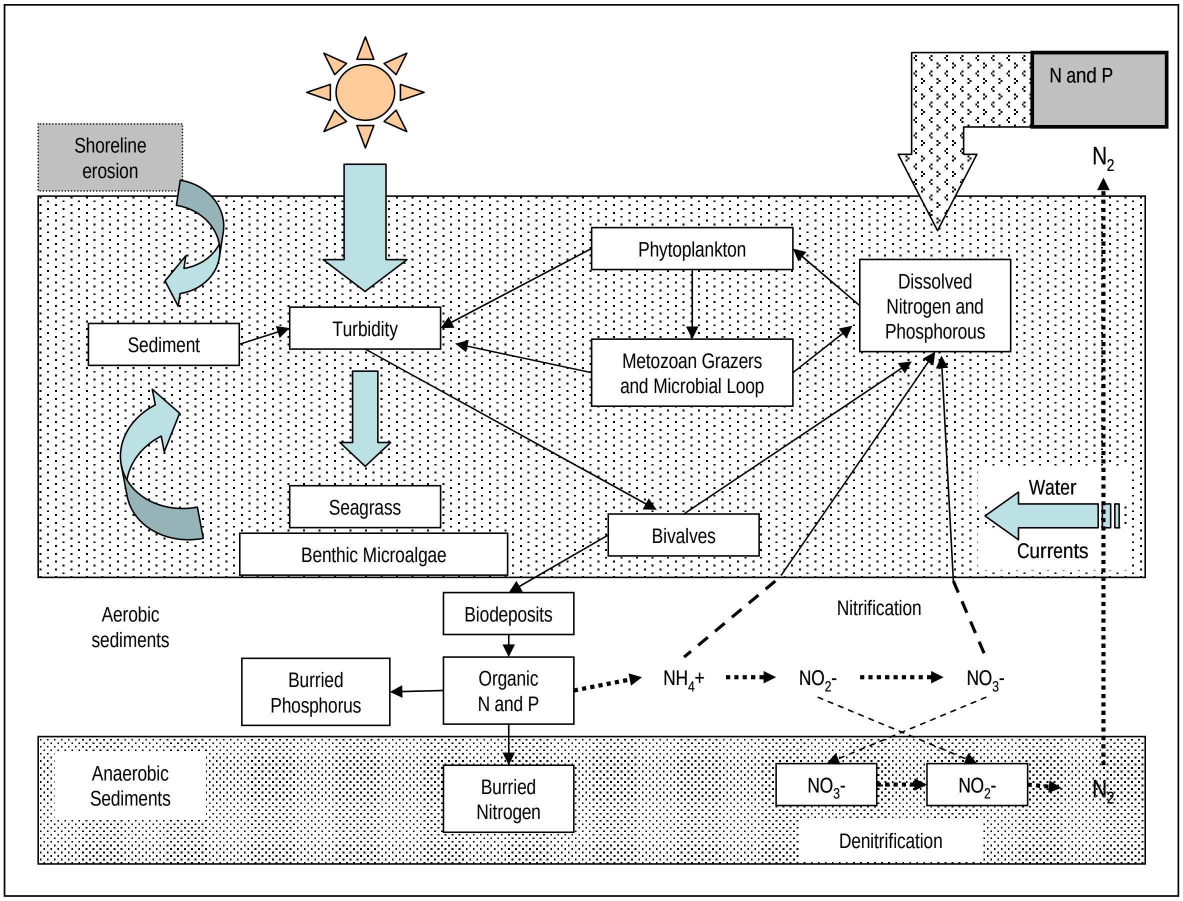


Figure 25: Ecosystem effects of suspension-feeding bivalves in removing organic and inorganic particles from the water column and transferring undigested particles in their biodeposits to the sediment surface. Nitrification occurs within the aerobic sediment layers while denitrification occurs in the underlying anaerobic sediment layers (Newell, 2004).

Bivalve filtration reduces phytoplankton concentration and turbidity and in turn increases light penetration in the water column. This may lead to increased primary production (Newell, 2004). Suspension feeders are therefore important in benthic-pelagic coupling and serve as both a source and a sink of energy in estuarine ecosystems. These filtering and recycling processes are critical to regulating coastal ecosystems. In addition to food and substrate availability and presence of predators and competitors, environmental factors such as water temperature and salinity help to determine the distribution and abundance of different bivalve species and therefore help regulate the benthic-pelagic coupling of estuaries.

Dense bivalve populations, wild or cultured, may modify existing habitat or create new ones through the deposition of organic particulate material on the sea floor or the formation of structurally complex shelled habitats (Working Group on the Application of Genetics in Fisheries and Mariculture, 2003). Bivalves are in fact often considered ecosystem engineers (Gutiérrez *et al.*, 2003). Natural two-dimensional (2-D) and three-dimensional (3-D) structures offer important surface area available for attachment and grazing by other species, and refuges from physical stress (e.g.: currents and waves), predation and competition (Milewski and Chapman, 2002).

Eastern Oysters and Softshell Clams are both active filter-feeders that need a certain flow rate to feed properly. According to Wildish and Saulnier (1993), inhibition of filtration in sea scallops (*Placopecten magellanicus)* may occur when there is no flow velocity, due to the decrease of seston concentration near the inhalant margin. As ambient flow velocity increases, filtration rate tends to increase until it reaches a plateau. The flow velocity can however be too strong and force the scallop to close its valves (Wildish and Saulnier, 1993; Wildish and Kristmanson, 1997). Flow velocity is believed to have similar effects on Eastern Oysters and Softshell Clams. These effects probably vary in relation to seston concentration, water temperature, flow direction, and size of the individual. Although the behavioural response of the Eastern Oyster and the Softshell Clam to high ambient velocities is not known, it is believed that oysters may partially or totally close their mantle and valves to resist the external pressure from flow velocity. Softshell Clams may retract their siphon and remain buried. It is important to note that Eastern Oysters are sessile and cannot orient themselves with the flow direction and velocity, while Softshell Clams can optimize their filtration by orienting themselves in the sediment. Therefore, the feeding, shape and growth rate of the Eastern Oyster may be affected by water movement.

According to Wildish and Kristmanson (1997), the accumulation of suspension feeders can modify small scale hydrodynamic regimes and provide locally higher fluxes of seston to individuals. Oyster reefs represent a good example of this type of suspension feeders in estuarine ecosystems. According to Dame *et al.* (1984) and Dame and Zingmark (1985), oyster reefs consume significant quantities of seston and nitrogen in estuarine ecosystems. They release high rates of ammonia, thus playing an important role in nutrient cycling in North Carolina. The three-dimensional oyster reef structure can significantly alter the hydrodynamics over the oysters on the fringe of reefs; they can also influence the retention of suspended food particles and sediment (Wildish and Kristmanson, 1997). These factors (Figure 26) can affect the settlement and recruitment of Eastern Oysters as well as their growth and survival (Lenihan, 1999).

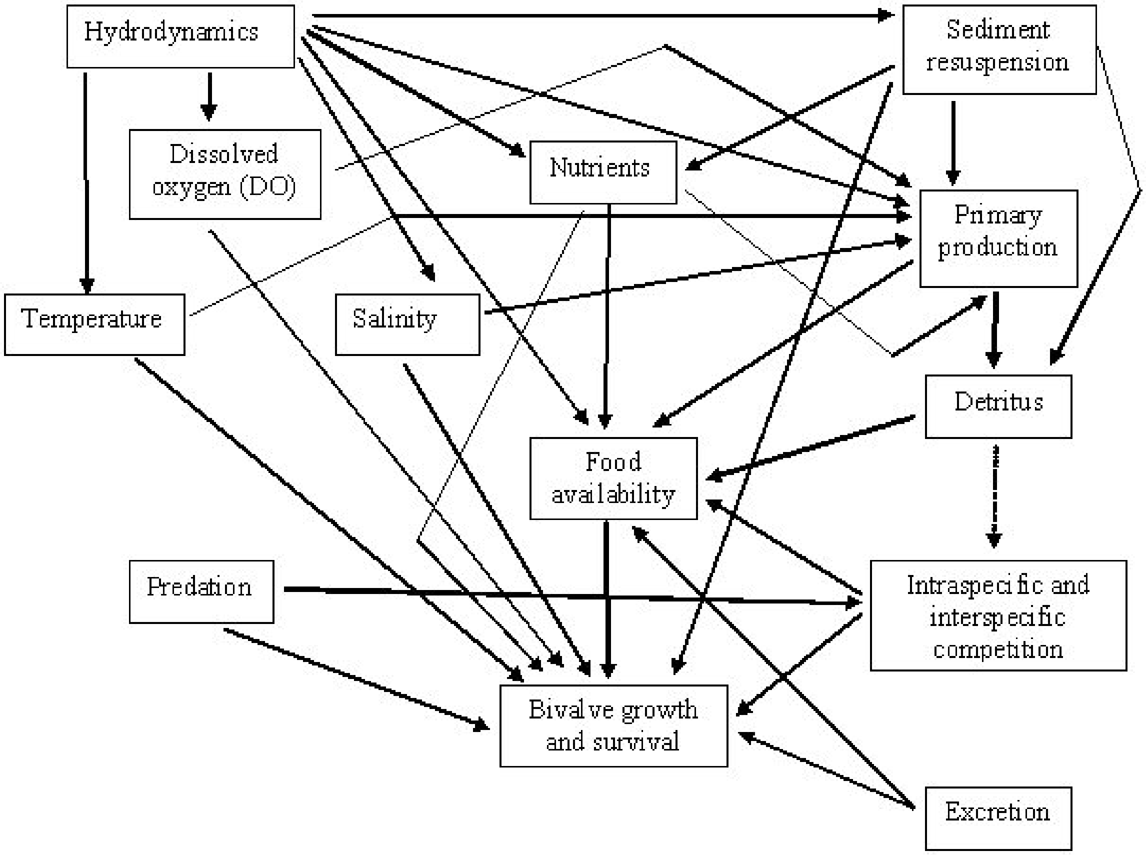


Figure 26: Factors affecting bivalve growth rates (adapted and modified from Spillman, 2003).

5. INTERACTIONS BETWEEN WILD *MYA ARENARIA* AND CULTURED *CRASSOSTREA VIRGINICA*

Many bivalves have a major effect on their environment either directly or indirectly and are thus important ecosystem engineers (Dame 1993; Newell 2004; Dame and Olenin 2005). Similarly, aquaculture of these species may have a considerable effect on the surrounding ecosystems. Although some of the ecological effects provided by bivalves in culture may be desirable, others may potentially be undesirable (McKindsey *et al*., 2006). The goal of this section is not to review the effects of bivalve aquaculture on the ecosystem (on this topic see: Cranford *et al*., 2003; Crawford *et al*., 2003; Newell, 2004; McKindsey *et al*., 2006) but rather to highlight how interspecific interactions may differ between wild Softshell Clams and wild and farmed Eastern Oysters.

One of the major potential drivers of differences in interactions is proximity. Wild oysters and wild clams share the same ecosystem, but usually different habitats, while suspended cultured oysters can share the same habitat as wild clams, although at different depths in the water column. Bivalve aquaculture is believed to have two main effects on pelagic communities, one direct and one indirect. First, as grazers, bivalves can reduce phytoplankton biomass. Second, bivalve aquaculture may also create additional habitat in the water column. These are discussed in the following sections.

5.1. Description of oyster aquaculture in the sGSL

Eastern Oyster culture is not a recent activity in North America. Beginning in 1810, Eastern Oysters were first cultivated in New Jersey in order to rehabilitate over-harvested beds and improve harvests (Lavoie, 1995). Subsequently, oyster culture expanded and eventually reached the Eastern Oysters’ northern distributional limit. In the Maritimes, the first leases for oyster culture were granted by the government of PEI in 1865 (Lavoie, 1995). Although its early history remains incompletly known, it is believed that the first Eastern Oysters were cultured in Bedeque Bay (MacKenzie, 2005). The Bedeque Bay oysters are also believed to be the first oyster group to become resistant to Malpeque disease (Morse, 1971; MacKenzie, 2005). Pollution in Bedeque Bay later led farmers to relocate their activities in Malpeque Bay.

Following the first allocation of leases after Confederation, oyster culture in the Maritimes gained in popularity. For instance, in 1891, a portion of Shediac Bay (NB) was reserved for oyster culture (Stafford, 1913). This did not prevent the serious decline in oyster landings due to overfishing observed in the Maritimes in the early 1900s. Programs were then established to meet market demand and to encourage oyster culture in NB (Stafford, 1913; Milewski and Chapman, 2002). By 1950, NB's production of oysters was still dependent on naturally-produced stocks. A few years later, oyster reefs and beds were affected by Malpeque disease (Morse, 1971; Milewski and Chapman, 2002). Following mortalities greater than 90%, efforts were made to purchase oyster seed, collectors, and equipment to rehabilitate the oyster populations. By the late 1970's, Shediac Bay, Cocagne Harbour, Bouctouche Bay, Richibucto Bay and Bay-du-Vin / Bay Ste-Anne became sites for an experimental program in NB to grow Eastern Oysters using off-bottom culture techniques (Milewski and Chapman, 2002). Since the 1980's, the on-bottom techniques have been mostly replaced by off-bottom culture or suspended techniques.

On-bottom culture techniques used in the Maritimes consist of spreading oyster spat on a suitable substrate for grow-out. In the sGSL, this technique does not involve hatcheries and the spat are directly collected in the water column. Off-bottom culture techniques consist of placing the oyster spat in bags attached to floating lines, fences or other floating structures, to allow oysters to grow in suspension (Lavoie, 1995). Suspended oyster cultures are done in areas with enhanced water circulation to increase the availability of food and oxygen and reduce mortality from predation. Suspended techniques thus tend to produce oysters that grow faster and develop more meat than on-bottom culture techniques (Fisheries and Oceans Canada, 2003).

Off-bottom culture techniques have rapidly evolved in recent years. Total oyster landings (from wild and cultured harvesting) in NB are estimated to have increased from 620 t in 2000 to 2,350 t in 2003 (NB Department of Agriculture, Fisheries and Aquaculture, 2003). The Province of N. B. estimates aquaculture production based on an assessment of the number of growing bags in use. In 2004, for example, the province estimated that 165,000 oyster bags were in production, with an average of 500 oysters per bag, which would have yielded 82.5 million oysters (Government of NB, 2004). Only one fourth of these would have been available for harvest (production time of 4 years), which would amount to 20.6 million harvestable oysters (approximate size of 60 mm). Using a conversion factor of 0.00008 X length in mm X total number as per Comeau *et al.* (2006), suggests that 16,700 tonnes of oysters would have been ready for harvest that year.

Comeau *et al.* (2006) conducted a comprehensive aerial and boat survey of oyster production in NB and concluded that 1,249 tonnes of oysters (all sizes included) were under cultivation in 2005. The discrepancy in production estimates between the three main sources of information (producers, government officials and sales slips) illustrates how difficult it is to gauge actual production. Comeau *et al.* (2006) estimated that the total actual production of oysters was 679 t from aquaculture and 75 t from commercial harvest, for a total landing of 754 t. Estimates for PEI and NS oyster landings were 2,849 t and 232 t, respectively (Fisheries and Oceans Canada, 2006). For comparison, a conservative estimate of the biomass of oysters in natural populations in the sGSL before Malpeque disease is in the range of 175,000 t (Bastien-Daigle *et al.,* 2007).

Comeau *et al.* (2006) calculated that the average density of oysters grown in NB is approximately 2 t ha^{-1} yr^{-1} (wet weight, shell included). This calculation is based on the total surface area of the leased area, which appears to be the standard used to report densities elsewhere. This is roughly equivalent to densities one fifth that is produced with *C. gigas* in Thau Lagoon, France, at 10 t ha^{-1} yr^{-1} (Mazouni, 2004). In terms of number of bags used per surface area, Comeau *et al.* (2006) reports densities of 691 bags per hectare in NB as compared to 4,943 bags per hectare in Normandie (France).

Other countries use techniques that can lead to very intensive oyster cultures. For instance, in other temperate systems, Tasmania (Australia) uses oyster growing densities that approach 20 t ha^{-1} yr^{-1} (Crawford, 2003). In semi-tropical and tropical systems, Chinese farmers used the stone-bridge method in the southern part of Fujian. There, oyster production (*C. rivularis*) varies between 30 and 80 t ha^{-1} yr^{-1} (FAO, 1988). The stake method used in the northern and eastern parts of Fujian, a technique adapted to soft-bottom environments, yields between 60 to 110 t ha^{-1} yr^{-1} of cultured oysters (Lovatelli, 1988). Although yields are generally considered limited in their usefulness as indicators of growing densities, mainly because of the differences in reporting methodology, conversion to common units, differences in species and techniques used, etc. this rapid comparison illustrates that oyster growing densities used in the sGSL can be considered to represents low intensity productions (Comeau *et al*, 2006).

5.2. Description of clam aquaculture in the sGSL

At the moment, the only area where clam aquaculture is practised is in Prince Edward Island and, more recently, in the Îles-de-la-Madeleine, Quebec. Clam culture is based primarily on the transfer of young clams to private seeding sites. Since this is still considered in its development phase there are limited references available on densities and techniques used. Therefore, no description of clam aquaculture interactions can be made at this point.

5.3. Biotic interactions

Biotic interactions between cultured oysters and natural populations of Softshell Clams are expected to be similar to those outlined in the preceding section. Anticipated differences with aquaculture are likely to be related to the concentration of size - specific oysters found in a given area at a given time. Under natural conditions, juvenile and adult oysters typically live at high densities in reef populations that vary between a few hundred to a few thousand individuals of all sizes per square meter, plus associated macrofauna. On the south Atlantic coast, Bahr & Lanier (1981, cited in Zimmer-Faust & Tamburri, 1994) report a mean frequency of 15,000 ind. m^{-2} on reefs extending over 10,000 m^2. Similar estimates of densities on intact oyster reefs in sGSL are not available, but Comeau *et al.* (2006) calculates that densities on northern Atlantic oyster reefs would be approximately 124 kg m^{-2}. Unfortunately, intact oyster reefs with these densities are no longer the dominant feature of sGSL estuarine ecoystems (Milewski and Chapman, 2002).

By comparison, densities of oysters in suspended culture (estimated using the surface area of each bag, not that of the lease area), average 7.27 kg m^{-2} (Comeau *et al*, 2006). Although the contexts is very different, in that suspended oysters grow faster, produce more biodeposits and are removed quickly, this represents densities an order of magnitude less than what what historically found on oyster reefs. Thus the biotic interactions between *M. arenaria* and cultured *C. virginica* should not entail concentrations of oysters greater than those encountered in wild populations.

5.3.1. Early stages

In theory, the spawning period of off-bottom cultured oysters could precede wild oyster populations because of warmer water surface temperatures. However, because of the typical shallow depths of sGSL bays and estuaries, tides and/or wind-driven events often mix the water column which is likely to minimise these differences. There is no indication in the literature that the growth and/or behaviour of larvae reared from cultured oysters differ from that of larvae reared from wild oysters.

Genetic differences between naturally occurring and cultured oyster populations have not been investigated. In the sGSL, all oyster spats are collected directly from a number of wild harvesting sites. Because of this natural recruitment, any potential genetic differences are not expected to be significant.

While the preferred culture technique is increasingly off-bottom, there is limited information on whether the spatial aspect of rearing oysters closer to the water surface will significantly increase overall Softshell Clam larvae mortalities. Softshell Clam veligers are observed throughout the water column while pediveligers are most likely to be found close to the benthos (Young and Chia, 1985). A recent study conducted in NB confirms that concentrations of bivalve larvae in the water column do not differ significantly between the surface and bottom. Early indications of that study, however, show that the total frequency of ingested bivalve larvae (unspecified species) was significantly higher in the stomachs of oysters growing at the surface than in oysters growing near the bottom, for about half of the samples. That difference was only significant during specific time-periods but was quite important (Elise Mayrand and collaborator, personal communication).

5.3.2. Late stages

Suspension filter-feeders feed on various sizes of plankton, bacteria, and detritus from the surrounding water. As a result, bivalves can capture conspecific larvae as well as various other larval species while feeding. There is no indication in the literature that the feeding behaviour of a cultured oyster is different from wild oyster except for the fact that they have optimal access to food sources, both in quantity and quality, and that the food sources are located at different depths in the water column.

In the wild, evidence that suspension-feeding bivalves populations fluctuate with food supply is limited (Stanley, 1973). According to Landry *et al.* (2006) any herbivorous bivalve species may reduce the phytoplankton biomass that may affect the productivity of other grazing species. However, Riera et al. (2002) found that co-occurring suspension-feeding invertebrates may feed either on similar or different components of the suspended particulate organic matter (POM). This was due in part to the preferential utilisation of different food size classes and to the ability of oysters (*C. gigas*) to select for specific components within the available POM. This ability of suspension-feeding invertebrates to utilise different segments of available nutrients may reduce the overall competition for food (Riera et al. 2002).

Pietros and Rice (2003) simulated oyster aquaculture in a microcosm study and found that particulate organic matter (POM) and chlorophyll-*a* content did not decrease significantly, in spite of the oysters actual high phytoplankton clearance rate. This indicated that phytoplankton uptake of nutrient and subsequent regeneration occurred faster than filtration by oysters. Oysters were also found to selectively feed on *Skeletonema costratum* but that they had little overall effect on phytoplankton species composition and sedimentation rates (*Pietros and Rice, 2003*).

It is likely that off-bottom tables overlap during the ice-free months with Softshell Clam habitats when they are located in the intertidal zone (Doiron, 2003). This could have an effect, such as increase local competition for food. Tables are raised above the substrate to allow water circulation around the bags. However, off-bottom culture techniques in subtidal areas are now the preferred choice for the aquaculture industry. Thus, this habitat overlap effect is presently minimal in most areas.

5.4. Indirect interactions

Bivalves serve as key agents in benthic-pelagic coupling because they feed on seston and transfer undigested organic and inorganic material in their mucus-bound feces and pseudofeces (bio-depositions) to the sediment surface (Dame and Olenin, 2005). Thus, bivalves can also have an effect on water turbidity which in turn will affect the production of phytoplankton and benthic plants. Shifts in benthic community structure and functioning due to bio-deposition, physical alterations, and the presence of fouling organisms have been noted in proximity to bivalve aquaculture operations, however, the extent of these changes are variable. Preliminary data suggest that bivalve aquaculture may increase coastal secondary productivity by creating additional habitat in the water column for some pelagic species benefiting from food availability or predator avoidance (Landry *et al*., 2006), although this cannot be applied to Softshell Clams, since it is a benthic species. Peterson, Grabowski and Powers (2003) have estimated that the restoration of natural oyster reefs and associated ecosystem services would result in production of fish and large mobile crustaceans, but there is no mention of benefits to other bivalves.

5.4.1. Early stages

It is unclear how aquaculture infrastructure may influence local hydrodynamics which could influence larval feeding and settlement behavior. Undisturbed subtidal oyster reefs are described as mounds of living and dead oysters fastened together and gradually growing vertically and laterally to finally reach the form of a flat platform breaking the water’s surface (Kennedy & Sanford, 1999). In cross-section, these beds would have included a thin layer of densely packed living oysters (10 m^{-2} to 1,000 m^{-2}, DeAlteris, 1988) and associated fauna located at or near the surface, sitting on top of varying layers of building material (shell, rocks, mud, etc). This distribution in the water column is believed to benefit the oyster by reducing exposure to hypoxic or anoxic water conditions, breaking the boundary layer flow, and enhancing food capture, gamete fecundation, and larval transport (DeAlteris, 1988; Kennedy, 1999). In contrast, off-bottom oyster aquaculture equipment would only occupy the top segment of the water column and allow movement of water underneath. Thus, off-bottom aquaculture techniques only appear to partially replicate conditions found within oyster reefs.

Similarly to a natural reef, the floating structures used in aquaculture can also provide new settlement sites for various organisms. Although this is generally limited by cleaning bags, aquaculture infrastructures may attract fish and other potential predators, and locally increase biodiversity. It is generally recognized as a benefit of aquaculture that sessile organisms usually found in hard-bottom habitats may be observed on structures installed in a soft-bottom environment (McKindsey *et al*, 2006) although this may not always be the case, such as in certain bays of the sGSL where invasive tunicates completely foul aquaculture gear. The floating structures may also provide a refuge from pelagic predators to planktonic larvae and create local hydrodynamic processes that allow better nutrient exchanges (Whiteley, 2005). A number of bivalve species, including *M. arenaria*, use floating bags for settling. Although mussels would remain attached, it is likely that clams and other non-attached species eventually fall to the benthic environment or fall prey to larger predators.

5.4.2. Late stages

Large production of bio-deposits could increase the nutrient input in the benthic community under and near culture sites. High deposit rates on the seabed could affect the diversity of the benthic communities and eliminate species sensitive to organic enrichment or smothering (Newell, 2004). This could ultimately affect various biological and chemical processes of the benthic community and modify the food web. The relationship between the Softshell Clam and other invertebrate species could then be modified. Cranford *et al.* (2003) suggested that the carrying capacity of a water system is regulated to a large extend by water motion and mixing. It is thus important to look at oceanographic parameters of the water system that support potential interactions between cultivated and wild bivalves. In intensively cultured systems, filter-feeders could increase sedimentation of fine suspended particles and modify energy flow in the ecosystem.

Intensive sedimentation under or near culture infrastructure could influence the feeding behaviour of other filter-feeders. Intensive sedimentation could also bury organisms that are not mobile. Intensive sedimentation could finally have an effect on settlement if bio-deposits and subsequent degradation modify benthic sediment quality. All these effects could influence Softshell Clams at the individual and population scale. Haven and Morales-Alamo (1966) reported that a one-acre oyster reef could produce 981 kg of biodeposits per week and estimated a biodeposition rate of 7.58 t for an acre of oysters during an eleven day period. However, there is no indication in the literature or from visual observation that the culture of Eastern Oysters in the sGSL has such an effect (Comeau *et al.*, 2006). Information on the quantity of biodeposits and siltation currently produced on average under and near oyster aquaculture tables indicates that deposition of organic sediments is rapidly remobilized by wind-driven events and ice scour and that in the course of a year, no overall deposition can be detected (Mallet *et al.,* 2006).

Recycling of biodeposits by benthic deposit feeders could also explain why they do not tend to accumulate. In Newfoundland, the organic material contained within biodeposits of horse mussels (*Modiolus modiolus*) has been found to provide a source of energy rich matter and to be rapidly recycled (Navarro & Thompson, 1997). A monitoring of a *C. gigas* aquaculture site in operation since 1934 in California attempted to measure if pseudofeces from suspended oyster culture contributes to the deposition of organic matter below the structures. The amount of organic matter resulting from eelgrass decomposition was found to be a far greater contributor to organic deposition, making any significant inputs from the oysters undetectable in that study (Elliot-Fisk *et al.*, 2005). In this example, eelgrass meadows were described as abundant and dense.

Crustaceans, fish and other predators can benefit from cultured bivalves and attached epibiont fall-offs (e.g.: Lopez-Jamar *et al.*, 1984; Freire *et al.*, 1990). This food availability could increase the abundance of predators on and near aquaculture operations thus potentially increasing predation pressure on adjacent Softshell Clam beds. However, the overall effect of aquaculture activities on predator densities and feeding behavior is unclear; some studies suggest aggregation of predators while others do not. In studies with increased predator densities, it is unclear if this is due to the aggregation of existing populations or an actual increase in the number of individuals (Landry *et al*., 2006). In Western Canada, Kirk *et al.* (2007) have documented that predators like sea duck exploit and benefit from the novel prey resource growing on oyster aquaculture equipment.

5.5. Summary of potential interactions

Table 1 summarizes the information about the habitat requirements of both species discussed earlier in the text.

Table 1 – Summary of habitat requirements for both species

	Mya arenaria	*Crassostrea virginica*
Habitat	Soft substrate	Hard substrate
	Endobenthique	Sessile epibenthic
	Intertidal – shallow subtidal	Mainly subtidal
Feeding method	Suspension-feeder	Suspension-feeder
Salinities (optimal)		
• Larvae	16 - 32 ppt	17.5 – 33 ppt
• Juveniles	15 - 20 ppt	n/a
• Adults	10 - 35 ppt	14 – 28 ppt
Salinities (lethal)		
• Adults	< 5 ppt	< 5 ppt
Temperatures (optimal)		
• Larvae	18 – 22 °C	19 – 30.5 °C
• Juveniles	12 – 19 °C	n/a
• Spawning	15 – 21 °C	≥20 °C
• Growth	20 – 30°C	20 – 30°C
Temperatures (lethal)		
• Adults	< -2 °C - > 28 °C	< -2 °C – > 36 °C
Size @ sexual maturity	35 – 40 mm	25 mm
Lifespan (average)	10 – 12 years	25 – 30 years
Lifespan (maximum)	> 25 years	> 100 years
Size (average)	10 – 15 cm	12 – 18 cm
Size (maximum)	15 cm	> 35 cm

Overall, our review shows that the species share similar diet (particle sizes and types of food). This was documented for individuals of both species for the veliger, juvenile and adult stages, but Eastern Oyster pediveligers do not feed. Spawning occurs during different period of the year; early summer for the Softshell Clam and late summer for the Eastern Oyster. The difference in the spawning period is likely to minimize competition for food between veligers of different species. If veligers of both species are present in the water column at the same time, Softshell Clam larvae will usually be older, thus bigger than Eastern Oyster larvae. The difference in larval size is likely to minimize potential food competition since potential food particle size increases with increasing larval size. Potential food competition in juveniles and adults is minimized by the fact that both species have evolved mechanisms and strategies that optimize their co-existence.

Predation is an important population regulator in benthic communities. It is probably one of the main factors driving the population dynamics of both species. Both species are likely to share similar predators during their pelagic phases. Other filter-feeders may also act as non-selective predators. Filter-feeders are known to inhale larvae as they swim and explore potential settlement sites.

Filter-feeders are also known to produce, depending on their density, large amounts of biodeposits that may accumulate on the seafloor. Excessive accumulation may impede the feeding and settlement of invertebrate species including Softshell Clams. In the sGSL, these accumulations have been shown to be rapidly resuspended and dispersed during wind-driven events and ice scour (Mallet *et al,* 2006).

The technique used to rear oysters close to the water surface can create a potential overlap of oysters with clam habitats. However, this pattern can also be found in nature, with random patterns of co-existence in certain regions of estuaries. Inhalation of Softshell Clam larvae by oysters is unlikely to be more significant at that position in the water column since Softshell Clam veligers are observed throughout the water column while pediveligers are most likely to be found close to the bottom. The hydrodynamic conditions around aquaculture infrastructures are likely to be modified and could have localised effects on larvae transport and/or movement. In dynamic estuarine environment, particle transport is unlikely to be altered enough to modify the feeding and the settlement behaviour of the Softshell Clam.

6. CONCLUSION

Archaeological and historical evidence shows that Softshell Clams (*Mya arenaria*) and Eastern Oysters (*Crassostrea virginica*) have coexisted in temperate estuaries of the eastern seaboard and the southern Gulf of St. Lawrence since the last glacial period. Both species are filter-feeders that are commonly associated with temperate estuaries characteristic of the Virginian ecozone. The objective of this literature review was to summarize the biological and ecological characteristics of both species to outline potential interactions between wild populations. This was done to identify potential interactions between cultured Eastern Oysters and natural Softshell Clam populations. To our knowledge, very few specific laboratory or field studies have specifically addressed interactions between these two species.

This literature review covered the biology of Softshell Clams and Eastern Oysters as well as their known and potential interactions. Although further field and laboratory studies would certainly contribute to a better understanding of potential interactions between these populations, their historic coexistence appears to be well established in nature. There is no published information currently available that would suggest that their interspecific relationship is likely to be significantly altered in the present culture setting.

The scale and intensity of current oyster farming activities in the region is considered to be relatively low when compared to other parts of the world. Should this change in the future, an ecological risk assessment should be completed in order to direct scientific research about these populations as well as measuring potential cumulative effects.

Furthermore, this literature review identified gaps in our understanding of the effects of other anthropogenic activities on these interspecific interactions. Although they were not considered in the terms of reference of this particular review, studies on the cumulative impacts of various human activities, in particular fisheries, habitat alteration and diseases, could be extremely useful in gaining a better understanding of the stressors currently affecting both populations.

Future studies focusing on the interactions between cultured oysters and natural Softshell Clam populations should also consider the physical processes that govern water circulation and transport of particles, including food particles and waste products.

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