Mya arenaria

Soft-shelled clam

Taxonomy: *Mya arenaria* is this species original name and is almost exclusively used currently. However, the taxonomic history of this species includes many synonyms, overlapping descriptions, and/or subspecies (e.g. *Mya hemphilli, Mya arenomya arenaria*, Winckworth 1930; Bernard 1979). The subgenera of *Mya* (*Mya mya, Mya arenomya*) were based on the presence or absence of a subumbonal groove on the left valve and the morphology of the pallial sinus and pallial line (see Bernard 1979).

Description

Size: Individuals range in size from 2–150 mm (Jacobson et al. 1975; Haderlie and Abbott 1980; Kozloff 1993; Maximovich and Guerassimova 2003) and are, on average, 50–100 mm (Fig. 1). Mean weight and length were 74 grams and 8 cm (respectively) in Wexford, Ireland (Cross et al. 2012). Individual weight varies seasonally and is greatest just before spawning and the smallest just after (range, 100–200 mg ash-free dry weight, Wadden Sea, Zwarts 1991).

Color: White with gray or dark, yellowish brown periostracum on shell edges, creating a rough outermost layer. Siphons are dark (Haderlie and Abbott 1980; Kozloff 1993; see Fig. 3, Zhang et al. 2012)

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007).

Body: Body is egg-shaped in outline (Fig. 1; Ricketts and Calvin 1952) (see Fig. 305, Kozloff 1993).

    Color:

    Interior: A crystalline style (consisting of a gelatinous cortex and liquid core, Lawry 1987) resides in a sac lined with cilia. The cilia allow the style to rotate and press against a gastric shield within the stomach, aiding in digestion (Lawry 1987). In *M. arenaria*, the crystalline style can be regenerated after 74 days (Haderlie and Abbott 1980) and may contribute to the clam's ability to live without oxygen for extended periods of time (Ricketts and Calvin 1952). The ligament is white, strong, and entirely internal (Kozloff 1993). Two types of gland cells (bacillary and goblet) comprise the pedal aperture gland or glandular cushion located within the pedal gape. It is situated adjacent to each of the two mantle margins and aids in the formation of pseudofeces from burrow sediments; the structure of these glands may be of phylogenetic relevance (Norenburg and Ferraris 1992).

    Exterior:
   **Byssus:**
    Gills:

Shell: Shell is soft, thin, fragile (hence "soft shell clam", Kozloff 1993; Coan and Valentich-Scott 2007), and composed completely of aragonite (MacDonald and Thomas 1980). The valves have an oval and rounded anterior and a pointed posterior (Kozloff 1993) and gape at each end (Haderlie and Abbott 1980). External shell sculpture is with concentric rings (Fig. 1).
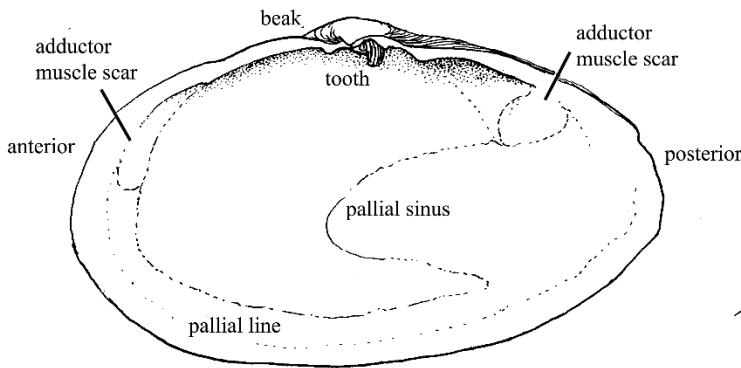
    Interior: Deep pallial sinus and spoon-shaped chondrophore, or triangular projection, is present on the left valve only (Haderlie and Abbott 1980; Kozloff 1993). Left and right adductor muscle scars are the same size but very different in shape (Fig. 2).

    Exterior: Left and right valves are of similar morphology, which is long and egg-shaped, with shells convex, thin and brittle (Fig. 4). Low concentric growth striae on anterior and posterior ends are different: anterior are more blunt and posterior are pointed, but both ends gaping (Packard 1918). Beaks small, bent posteriorly, and slightly anterior of center (Fig. 2).

Mya arenaria

anterior
(foot)

posterior
(siphons)

2 cm
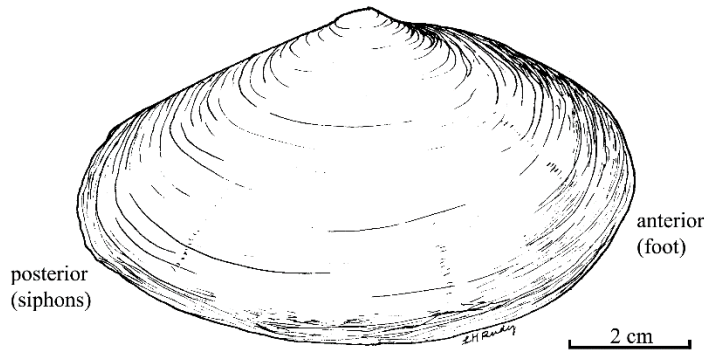
1. *Mya arenaria*, exterior, right valve x1:
shell egg-shaped, thin, brittle; concentric growth rings, small
beaks; both ends rounded, slightly gaping.

beak

adductor
muscle scar

adductor
muscle scar

tooth

anterior

posterior

3. Hinge area, left valve:
chondrophore spoon-shaped.

pallial sinus

a. (Lateral view)

pallial line

b. (Dorsal view)

2. Interior, right valve:
white; muscle scars alike; pallial sinus deep, no
cardinal teeth; ligament completely internal; tooth opposing
chondrophore.

right valve

anterior
(foot)

posterior
(siphons)
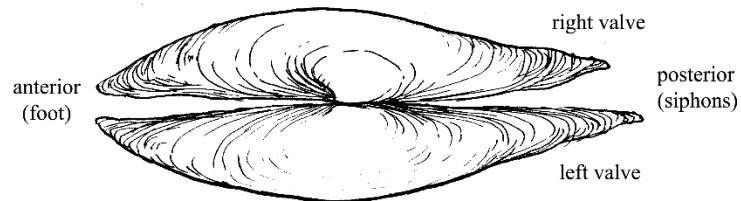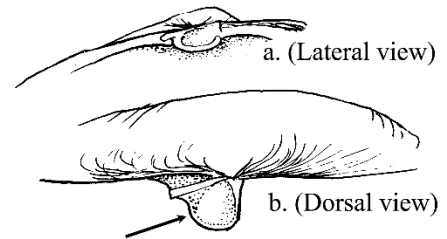
left valve

4. (Dorsal view)

Hinge: Valve areas dissimilar and with spoon-shaped chondrophore in left valve. Right valve is with tooth in opposition to chondrophore (Fig. 3). No hinge plate teeth (cardinal or lateral).
Eyes:
Foot:
Siphons: Long, large siphons are fused, non-retractable (Coan and Valentich-Scott 2007; Tan and Beal 2015), and dark in color (Haderlie and Abbott 1980).
Burrow: Unlike the other local member of the Myidae, *Cryptomya californica* (see description in this guide), *M. arenaria* has long siphons and can be found in relatively deep burrows up to 40 cm (Haderlie and Abbott 1980; Kozloff 1993; Coan and Valentich-Scott 2007; González et al. 2015).

Possible Misidentifications

There are five bivalve subclasses based on morphology and fossil evidence and one of those is the diverse Heterodonta. Recent molecular evidence (18S and 28S rRNA) suggests that the heterodont order Myoida is non monophyletic (Taylor et al. 2007). The family Myidae includes 25–40 species worldwide, which can be divided into groups such as those that are burrowing (*Mya*), those that are attached to shells or stone (*Sphenia*) or those utilizing the burrows of other species (*Cryptomya*, *Paramya*) (Zhang et al. 2012). Characters of the Myidae include a shell that is not cemented to the substratum, valves that are (relatively) morphologically similar, a dorsal margin without ears, a hinge with an internal ligament in a distinct resilifer or chondrophore that is spoon shaped and present on the left valve (Coan and Valentich-Scott 2007). *Cryptomya* species are characterized by hinge without tooth-like process anteriorly on the right valve. *Mya,* on the other hand, have thin shells, gaping anteriorly and posteriorly and commarginal growth lines (Zhang et al. 2012).

There are only three local myid species including *Platyodon cancellatus*, *Mya arenaria* and *Cryptomya californica* ("the false Mya" see description in this guide). *Platydon cancellatus* can be distinguished from the latter two species because its shells are heavy and with wavy commarginal sculpture and a round anterior. It has a truncate, gaping posterior end covered with periostracum. It also bores into rock and hard clay while *M. arenaria* and *C. californica* burrow into sand or mud. The shells of the two latter species are relatively thin. In *M. arenaria*, the pallial sinus is deep and individuals reach sizes of 150 mm, while in *C. californica* the pallial sinus is shallow, inconspicuous and individuals tend to be smaller (30 mm) (Coan and Valentich-Scott 2007). *Mya arenaria* is found as deep as 40 cm and is not necessarily near *Callianassa californiensis* burrows, where one might find *Cryptomya californica*. The siphons are *M. arenaria* are also longer than those of *C. californica* (see *C. californica*, Figs. 1, 6 in this guide). Additionally, *Sphenia luticola* is a myid species that may occur in our area, but is found offshore in rocks and within kelp holdfasts (Coan and Valentich-Scott 2007). Juvenile *Mya* are not easily distinguished from *Sphenia* species, but *Mya* can be recognized by a large continuous pallial sinus (Coan 1999).

Mya arenaria may be confused with other local common clams, e.g. *Saxidomus*, *Tresus*, *Tellina* or *Macoma* species. These genera do not have an internal ligament or a chondrophore. Small *Tresus* can otherwise be mistaken for *M. arenaria*. Small Tellinid clams have an external ligament without a nymph, and lateral hinge teeth, which *M. arenaria* lack. *Macoma* species (see descriptions in this guide) are very like *Tellina*, but their shells are always a bit flexed, they have no lateral teeth, and no internal coloration. Furthermore, where *M. arenaria* is abundant is in upper reaches of estuaries where salinity is reduced, species in the genera *Saxidomus* and *Tresus* are not usually found.

Ecological Information

Range: Type locality is Europe (Zhang et al. 2012). Current eastern Pacific distribution from Alaska to San Diego, California (Haderlie and Abbott 1980). Current populations introduced from the Atlantic coast with oyster spat in 1874 in San Francisco (Coan and Valentich-Scott 2007), although it appears in the fossil record (Ricketts and Calvin 1971) in California and Vancouver (Packard 1918). However, *M. arenaria* is not represented in local Native American mounds (Kozloff 1993). The palaeontological history of *M. arenaria*

was described by Fujie (1957, 1962), as the species originated in the Pacific in the Miocene, spread to the Atlantic into the Pliocene, became extinct in the Pacific northwest by the Pleistocene was re-established and introduced from Atlantic populations in 1880s and was re-introduced to the eastern Atlantic and Pacific during the Pleistocene (Rasmussen and Heard 1995; Zhang et al. 2012). Following introduction, *M. arenaria* spread northward to Willapa Bay, Washington in 1880 and Alaska in 1950s (Haderlie and Abbott 1980; Ricketts and Calvin 1952). Common on the Atlantic Coast and Europe in areas of low salinity (e.g. Baltic Sea, Kozloff 1993). It has crowded out the native *Macoma* spp. on the Pacific coast in some areas (Keep and Longstreth 1935). In the Cold Temperate Northwest Atlantic biogeographic province, six genetic clusters of *M. arenaria* were observed spanning seven distinct ecoregions. Those to the north were defined by geographic barriers and selection processes and those to the south were likely the result of and increased with geographic distance only (St-Onge et al. 2013).

Local Distribution: Local distribution in Coos and Yaquina Bay as well as the Suislaw, Umpqua, Tillamook, Alsea and Columbia estuaries.

Habitat: Mud and sand of bays with sand, mud, gravel mix (Kozloff 1993; Coan and Valentich-Scott 2007), often in upper reaches where salinity is reduced, but requires complete protection, as it cannot burrow or maintain itself in a shifting substratum (Ricketts and Calvin 1971). Very tolerant of extreme conditions (e.g., anaerobic or foul mud, brackish water, temperatures below freezing, Ricketts and Calvin 1971; Haderlie and Abbott 1980). Can live without oxygen for eight days (Ricketts and Calvin 1952) and it is thought that the shell serves as an alkaline reserve to neutralize lactic acid from anaerobic respiration (Haderlie and Abbott 1980). In a study testing the effects ocean acidification on *M. arenaria*, sedimentary aragonite saturation resulted in a negative relationship with dispersal and a positive relationship with clam burrowing depth (Clements and Hunt 2014). Conversely, increases in proton concentration yielded a negative relationship with burrowing depth

(Clements and Hunt 2014). Thermal stress (e.g., associated with climate change) is accompanied by oxidative stress in marine mollusks, including *M. arenaria,* and leads to the mitochondrial production of reactive oxygen species (Abele et al. 2002). *Mya arenaria* individuals respond to hypoxia by reducing burrow depth and increasing siphon extension (Taylor and Eggleston 2000).

Salinity: Tolerates brackish water and reduced salinity, as well as full salt water (Haderlie and Abbott 1980; Kozloff 1993).

Temperature: Range limited to cool areas, although this species can also tolerate temperatures below freezing (Ricketts and Calvin 1952). Eastern Atlantic southern distribution set by critical maximum temperature of 28°C (Rasmussen and Heard 1995).

Tidal Level: Found from 15–40 cm depths in mud habitats (Packard 1918) and intertidal to 20 m (Zhang et al. 2012).

Associates: Commensal pea crabs, *Fabia subquadrata*, *F. concharum*, *Pinnixa fab*a, *P. littoralis* (Ricketts and Calvin 1971; Haderlie and Abbott 1980). Co-occurs with *Macoma balthica* and the lugworm, *Arenicola marina*, in the Wadden Sea (Günther 1992; Strasser et al. 1999). The abundance of *A. marina*, a bioturbator, has a negative effect on recruitment in *M arenaria* (Strasser et al. 1999). Domoic acid (a neurotoxin), released from and ingested with the diatom *Pseudo-nitzschia*, is biodegraded in *M. arenaria* with the help of autochthonous bacteria (Stewart et al. 1998).

Abundance: *Mya arenaria* can be very abundant and often occurs with a patchy distribution (e.g., 177 individuals/m^2, St. Lawrence estuary, Roseberry et al. 1992). Locally abundant in Yaquina, Siuslaw, and Umpqua estuaries, and in some parts of Coos Bay where it is "fairly common" (Haderlie and Abbott 1980). *Mya arenaria* was reported as ubiquitous in northeast and northwest Atlantic (Tan and Beal 2015). In the Wadden Sea, 50 individuals/m^{2}were observed (Strasser et al. 1999; Günther 1992), and up to 1,000 individuals/m^{2}reported in Kandalaksha Bay, White Sea (Maximovich and Guerassimova 2003). This common estuarine species is often used in toxicity and biomarker tests, where effects of tributyltin (TBT) included

masculinizing of females, sex ratios skewed toward male, and delayed male maturation (Gagné et al. 2003).

Life-History Information
Reproduction: Dioecious with, at most, two periods of sexual maturation and spawning, one in the fall (primary maturation period) and one in spring (secondary maturation) (Chesapeake Bay and St. Lawrence estuary, Roseberry et al. 1992). A continuous reproductive period from April to October occurs in New England (Pfitzenmeyer and Shuster 1960). Atlantic species tend to spawn from June to August and eggs 60–80 µm diameter (Haderlie and Abbott 1980). In Cape Cod, gametogenesis began during late winter and spawning was complete by the end of summer (September, Ropes and Stickney 1965). Populations in Wexford, Ireland had sex ratios of 1:1.15 (female to male) and were ripe and spawning in August, completed in November (Cross et al. 2012). Life-history characteristics appeared to correlate along a latitudinal gradient in the northeast coast of the United States: individuals in southern populations grew faster, exhibited greater variation in juvenile mortality, had larger egg sizes (range 25–45 µm), lower egg density (range 495–1,541), decreased longevity (4–15 years), and larger size at maturation (see Table 1, Appeldoorn 1995).   In San Francisco, CA, gametogenesis began in late February and spawning occurred from April to October (Rosenblum and Niesen 1985). Sperm morphology and spermatogenesis of the subspecies *Mya arenaria oonogai* was described by Kim et al. in 2011. In this species, the spermatozoon was approximately 50 µm in length. Disseminated neoplasia, a leukemia-like disease, occurs in the gonadal tissues of *M. arenaria* (Barber 1996; Boettger and Barletta 2015). The frequency of neoplasia increases in spring in Maine (Boettger and Barletta 2015). In 1994 in Whiting Bay, Maine, progressive and potentially lethal gonadal neoplasms were observed in 19% of individuals, involving up to 100% of gonadal follicles. Females were more likely to have neoplasms than males and produced fewer, smaller gametes leading to an overall negative impact on reproductive output (Barber 1996).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the "D" shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.). Young *M. arenaria* larvae (150 µm) have a broadly rounded umbo with a short, sloping posterior (see Fig. 4, Brink 2001). The umbo becomes angled in advanced individuals and the shoulders become straight and steeply sloping. Eventually, the anterior and posterior ends elongate and are pointed and metamorphosis occurs when larvae are 170–230 µm (Chanley and Andrews 1971; Brink 2001). Settlement in the Wadden Sea occurs from May to June (Günther 1992) and in Mill Cove, New Brunswick, when individuals are greater than 500 µm (Morse and Hunt 2013). Settlement may depend on sediment properties (e.g., grain size, presence of sea grasses, Strasser et al. 1999). Juveniles and smaller individuals (< 2 mm) can also be transported hydrodynamically (Hunt and Mullineaux 2002). Maximum transport rates coincided (positive correlation) with peaks in bedload transport: in sheltered sandflats, maximum transport rate was 790 individuals/m/day and in exposed habitats, maximum transport rate increased to 2,600 individuals/m/day (Emerson and Grant 1991). Recruitment is highly variable and based on (among others) predation, temperature, and adult-larval interactions. Some research shows that larvae avoid settlement in areas with high conspecific density (Maximovich and

Guerassimova 2003, but see Brousseau and Bagilvo 1988; Günter 1992).

Juvenile: Juveniles are typically less than 2–15 mm in length (Strasser et al. 1999; Tan and Beal 2015) and size is generally fixed by epibenthic predators. Sexual maturity occurs when individuals are 25–35 mm in length (Brousseau 1979; Rosenblum and Niesen 1985). Following settlement, significant changes occur in population distributions within the first month, due to post-settlement dispersal and predation (Morse and Hunt 2013). Newly settled individuals and juveniles are prey to a variety of epipenthic predators and their size and abundance is ultimately controlled by predation (Hunt and Mullineaux 2002). Mortality by predation significantly decreases with growth. For example, green crabs (*Carcinus maenas*) reduced 80% of small (<17 mm) *M. arenaria* in caged experiments containing 1–5 crabs in Pompuet Harbour, Nova Scotia (Floyd and Williams 2004). Young *M. arenaria* (< 30 mm) were most susceptible to predation by the snail, *Lanutia heros,* as 3.5% died/year in the first five years (Maine, Commito 1982). Ultimately, size selective feeding leads to overestimated average size measurements among juveniles and fast juvenile growth allows for a size refuge from epibenthic predators (Wadden Sea, Günther 1992). Additionally, juveniles escape predation with severe winters that result in mortality of predators (Günther 1992). Mortality significantly decreased 94 days after settlement (Günther 1992).

Longevity: Up to 28 years (Appeldoorn 1995). A 17 years maximum was reported in Kandalasksha Bay, White Sea (Maximovich and Guerassimova 2003). Over 25 years of monitoring in the White Sea, populations of *M. arenaria* showed alternatively high and low levels of mortality (Table 2, Gerasimova et al. 2015). The authors attributed this variation in mortality to the unstable habitat early in life and intraspecific relationships and competition associated with dense aggregations (Gerasimova et al. 2015).

Growth Rate: Clams as small as 25 mm have been found to have mature gametes (Pfitzenmeyer and Shuster 1965). Individuals approximately 15 mm in length grew 110 µm per day (Günther 1992). Most shell deposition occurred from March to November in Gloucester, MA (Brousseau 1979). Although external growth rings can be conspicuous, they may not be an accurate indicator of clam age and are not always clearly defined. Instead, internal growth lines, which can be seen in thin sections when shells are sliced from the umbo to the ventral margin, reliably indicate growth in late spring months before spawning (Prince Edward Island, MacDonald and Thomas 1980). The neoplastic disease, disseminated neoplasia, which is characterized by excessive and abnormal cell growth is found in *M. arenaria* and appears to be transmitted among populations by horizontal transmission (Carballal et al. 2015).

Food: A suspension and filter feeder (Tan and Beal 2015), *M. arenaria* takes up oxygen, food, algae, and detritus containing iron (Fe) and other trace metals (González et al. 2015) by filtering seawater. Compared to other filter feeders, *M. arenaria* may have a low filtration rate (Jorgensen 1966 in Vincent et al. 1988). Individuals can adapt to varying algal concentrations; a low concentration leads to a reduced siphon opening and valve gape, which can occur after several hours of reduced concentrations, while an increase in algal concentration leads to siphon opening within 5–20 min (Riisgard et al. 2003).

Predators: Shorebirds (e.g., sea gulls), sea otters eat exposed adults and larvae are preyed upon by planktonic predators and suspension feeders. Adults are prey to infaunal predators (e.g., gastropods, nemerteans) and juveniles live so close to the sediment surface that their siphons are often nipped off by crustaceans and fish (Tan and Beal 2015). Additional predators include fish, shrimp, sandworms, crabs (e.g., the green crab, *Carcinus maenas*, Wong 2013; Morse and Hunt 2013; Tan and Beal 2015, the blue crab (*C. sapidus*, Taylor and Eggleston 2000), snails (Cross et al. 2012), the stingray, *Dasyatis sabina* (Rasmussen and Heard 1995), and *Nereis virens* (Morse and Hunt 2013). Predation by *Polinices duplicatus*, increased with temperature, with individuals ingesting as many as 96 *Mya arenaria/*snail/year (Edwards and Huebner 1977). *Carcinus maenas* (green crab) populations decrease populations of *M.*

arenaria and survival of clams was seven times greater when predation by green crabs was experimentally removed (Maine, Tan and Beal 2015). Also a commercially important species. In eastern Canada (e.g., Nova Scotia, New Brunswick) the fishery landed 4,500 tons in 1986 and 3,000 tons in 1988 (Aramaratunga and Misra 1989). Predators of newly settled larvae also include adults of the same species. There is a negative relationship between adult density and newly settled larvae in both *Cerastoderma edule* (40% mortality) and *M. arenaria* (20% mortality) (André and Rosenberg 1991).
Behavior: In the presence of predators, individuals increase their burial depth and reduce growth (Tan and Beal 2015). Preferred orientation is perpendicular to the principle component of current direction. This allows siphons to be in line with the current and, presumably, avoids inhalant exhalant contamination (Vincent et al. 1988).

Bibliography

1. ABELE, D., K. HEISE, H. O. PORTNER, and S. PUNTARULO. 2002. Temperature-dependence of mitochondrial function and production of reactive oxygen species in the intertidal mud clam *Mya arenaria*. Journal of Experimental Biology. 205:1831-1841.
2. AMARATUNGA, T., and R. K. MISRA. 1989. Identification of soft-shell clam (*Mya arenaria* Linnaeus, 1758) stocks in eastern Canada based on multivariate morphometric analysis. Journal of Shellfish Research. 8:391-398.
3. ANDRE, C., and R. ROSENBERG. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. Marine Ecology Progress Series. 71:227-234.
4. APPELDOORN, R. S. 1995. Covariation in life-history parameters of soft-shell clams (*Mya arenaria*) along a latitudinal gradient. ICES Marine Science Symposia. 199:19-25.
5. BARBER, B. J. 1996. Effects of gonadal neoplasms on oogenesis in softshell clams, *Mya arenaria*. Journal of Invertebrate Pathology. 67:161-168.
6. BERNARD, F. R. 1979. Identification of living *Mya* (Bivalvia: Myoida). Venus: the Japanese Journal of Malacology. 38:185-204.
7. BOETTGER, S. A., and A. T. BARLETTA. 2015. Effect of reproductive effort on neoplasia development in the soft-shell clam, *Mya arenaria*. Integrative and Comparative Biology. 55:E17-E17.
8. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In:* Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. BROUSSEAU, D. J. 1979. Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. Marine Biology. 51:221-227.
10. BROUSSEAU, D. J., and J. A. BAGLIVO. 1988. Life tables for two field populations of soft-shell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound. Fishery Bulletin. 86:567-579.
11. CARBALLAL, M. L., B. J. BARBER, D. IGLESIAS, and A. VILLALBA. 2015. Neoplastic diseases of marine bivalves. Journal of Invertebrate Pathology. 131:83-106.
12. CHANLEY, P. E., and J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. Malacologia. 11:45-119.
13. CLEMENTS, J. C., and H. L. HUNT. 2014. Influence of sediment acidification and water flow on sediment acceptance and dispersal of juvenile soft-shell clams (*Mya arenaria* L.). Journal of Experimental Marine Biology and Ecology. 453:62-69.
14. COAN, E. V. 1999. The eastern Pacific species of *Sphenia* (Bivalvia: Myidae). Nautilus. 113:103-120.
15. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.

16. COMMITO, J. A. 1982. Effects of *Lunatia heros* predation on the population dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. Marine Biology. 69:187-193.

17. CROSS, M. E., S. LYNCH, A. WHITAKER, R. M. O' RIORDAN, and S. C. CULLOTY. 2012. The reproductive biology of the softshell clam, *Mya arenaria*, in Ireland, and the possible impacts of climate variability. Journal of Marine Biology. 2012:1-9.

18. EDWARDS, D. C., and J. D. HUEBNER. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. Ecology. 58:1218-1236.

19. EMERSON, C. W., and J. GRANT. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnology and Oceanography. 36:1288-1300.

20. FLOYD, T., and J. WILLIAMS. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the Southern Gulf of St. Lawrence. Journal of Shellfish Research. 23:457-462.

21. FUJIE, T. 1957. On the myarian pelecypods of Japan. Part I: Summary of the study of the genus *Mya* from Hokkaido. Journal of the Faculty of Science Hokkaido University Geology. 9:381-413.

22. —. 1962. On the myarian pelecypods of Japan. Part II: Geological and geographical distribution of fossil and recent species, genus *Mya*. Journal of the Faculty of Science Hokkaido University Geology. 11:399-430.

23. GAGNE, F., C. BLAISE, J. PELLERIN, E. PELLETIER, M. DOUVILLE, S. GAUTHIER-CLERC, and L. VIGLINO. 2003. Sex alteration in soft-shell clams (*Mya arenaria*) in an intertidal zone of the Saint Lawrence River (Quebec, Canada). Comparative Biochemistry and Physiology: C-Toxicology & Pharmacology. 134:189-198.

24. GERASIMOVA, A. V., N. V. MAXIMOVICH, and N. A. FILIPPOVA. 2015. Cohort life tables for a population of the soft-shell clam, *Mya arenaria* L., in the White Sea. Helgoland Marine Research. 69:147-158.

25. GONZALEZ, P. M., D. ABELE, and S. PUNTARULO. 2015. Oxidative status of respiratory tissues of the bivalve *Mya arenaria* after exposure to excess dissolved iron. Marine and Freshwater Behaviour and Physiology. 48:103-116.

26. GUNTHER, C. P. 1992. Settlement and recruitment of *Mya arenaria* (L.) in the Wadden Sea. Journal of Experimental Marine Biology and Ecology. 159:203-215.

27. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In:* Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.

28. HUNT, H. L., and L. S. MULLINEAUX. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). Limnology and Oceanography. 47:151-164.

29. JACOBSON, R. W., P. HEIKKILA, and K. S. HILDERBRAND. 1975. Oregon's captivating clams. Oregon State University Extension Service, Sea Grant Marine Advisory Program, and Oregon Dept. of Fish and Wildlife, Corvallis, Or.

30. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In:* Reproduction and development of marine invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.

31. KEEP, J., and J. LONGSTRETH. 1935. West coast shells: a description in familiar terms of the principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra.

Stanford University Press, Stanford, CA.

32. KIM, J., J. CHUNG, and Y. PARK. 2011. Ultrastructures of germ cells during spermatogenesis and taxonomic values in sperm morphology in male *Mya arenaria* oonogai (Heterodonta: Myidae). Korean Journal of Malacology. 27:377-386.

33. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.

34. LAWRY, E. V. 1987. *Cryptomya californica* (Conrad, 1837): observations on its habitat, behavior, anatomy, and physiology. Veliger. 30:46-54.

35. MACDONALD, B. A., and M. L. H. THOMAS. 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. Marine Biology. 58:105-109.

36. MAXIMOVICH, N. V., and A. V. GUERASSIMOVA. 2003. Life history characteristics of the clam *Mya arenaria* in the White Sea. Helgoland Marine Research. 57:91-99.

37. MORSE, B. L., and H. L. HUNT. 2013. Impact of settlement and early post-settlement events on the spatial distribution of juvenile *Mya arenaria* on an intertidal shore. Journal of Experimental Marine Biology and Ecology. 448:57-65.

38. NORENBURG, J. L., and J. D. FERRARIS. 1990. Cytomorphology of the pedal aperture glands of *Mya arenaria* L. (Mollusca, Bivalvia). Canadian Journal of Zoology. 68:1137-1144.

39. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. Zoology. 14:199-452.

40. PFITZENMEYER, H. T., and C. N. SHUSTER. 1960. A partial bibliography of the softshell clam *Mya arenaria* Linnaeus. Maryland Department of Research and Education, Chesapeake Biological Laboratories, Solomons, MD.

41. RASMUSSEN, E., and R. W. HEARD. 1995. Observations on extant populations of the softshell clam, *Mya arenaria* Linne, 1758 (Bivalvia: Myidae), from Georgia (USA) estuarine habitats. Gulf Research Reports. 9:85-96.

42. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.

43. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.

44. RIISGARD, H. U., C. KITTNER, and D. F. SEERUP. 2003. Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration. Journal of Experimental Marine Biology and Ecology. 284:105-127.

45. ROPES, J. W., and A. P. STICKNEY. 1965. Reproductive cycle of *Mya arenaria* in New England. Biological Bulletin. 128:315-327.

46. ROSEBERRY, L., B. VINCENT, and C. LEMAIRE. 1991. Growth and reproduction of *Mya arenaria* in their intertidal zone of the Saint Lawrence Estuary. Canadian Journal of Zoology. 69:724-732.

47. ROSENBLUM, S. E., and T. M. NIESEN. 1985. The spawning cycle of soft-shell clam, *Mya arenaria*, in San Francisco Bay. Fishery Bulletin. 83:403-412.

48. ST-ONGE, P., J. SEVIGNY, C. STRASSER, and R. TREMBLAY. 2013. Strong population differentiation of softshell clams (*Mya arenaria*) sampled across seven biogeographic marine ecoregions: possible selection and isolation by distance. Marine Biology. 160:1065-1081.

49. STEWART, J. E., L. J. MARKS, M. W. GILGAN, E. PFEIFFER, and B. M. ZWICKER. 1998. Microbial utilization of the neurotoxin domoic acid: blue mussels (*Mytilus edulis*) and soft shell

clams (*Mya arenaria*) as sources of the microorganisms. Canadian Journal of Microbiology. 44:456-464.

50. STRASSER, M., M. WALENSKY, and K. REISE. 1999. Juvenile-adult distribution of the bivalve *Mya arenaria* on intertidal flats in the Wadden Sea: why are there so few year classes? Helgoland Marine Research. 53:45-55.

51. TAN, E. B. P., and B. F. BEAL. 2015. Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA. Journal of Experimental Marine Biology and Ecology. 462:62-73.

52. TAYLOR, D. L., and D. B. EGGLESTON. 2000. Effects of hypoxia on an estuarine predator-prey interaction: foraging behavior and mutual interference in the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*. Marine Ecology Progress Series. 196:221-237.

53. TAYLOR, J. D., S. T. WILLIAMS, E. A. GLOVER, and P. DYAL. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. Zoologica Scripta. 36:587-606.

54. VINCENT, B., G. DESROSIERS, and Y. GRATTON. 1988. Orientation of the infaunal bivalve *Mya arenaria* (L.) in relation to local current direction on a tidal flat. Journal of Experimental Marine Biology and Ecology. 124:205-214.

55. WINCKWORTH, R. 1930. Notes on nomenclature. 5. Some new names for British marine bivalves. Proceedings of the Malacological Society of London. 19:14-15.

56. WONG, M. C. 2013. Green crab (*Carcinus maenas* Linnaeus, 1758) foraging on soft-shell clams (*Mya arenaria* Linnaeus, 1758) across seagrass complexity: Behavioural mechanisms and a new habitat complexity index. Journal of Experimental Marine Biology and Ecology. 446:139-150.

57. ZHANG, J., F. XU, and R. LIU. 2012. The Myidae (Mollusca, Bivalvia) from Chinese waters with description of a new species. Zootaxa:39-60.

58. ZWARTS, L. 1991. Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. Netherlands Journal of Sea Research. 28:231-245.