
Macoma balthica

Phylum: Mollusca

Class: Bivalvia, Heterodonta, Euheterodonta

Order: Imparidentia, Cardiida

Family: Tellinoidea, Tellinidae, Macominae

Taxonomy: Originally described as a member of the genus *Tellina*, *Macoma balthica* was the name of the Atlantic species. Our west coast clam was originally called *M. inconspicua* (Broderip and Sowerby 1829), but they are now generally considered to be the same species (e.g., Vassallo, 1969, 1971; Haderlie and Abbott 1980). An extensive taxonomic history has yielded many synonyms for *M. balthica*. Some ambiguity exists whether individuals from the southernmost reaches of the distribution on east and west sides of the Atlantic should be considered the same species (Beukema and Meehan 1985) and some researchers (e.g., Meehan 1985; Kamermans et al. 1990; Luttkhuizen et al. 2012; Sanier et al. 2015) consider these allopatric populations to be subspecies (eastern Atlantic *Macoma balthica balthica* and western Atlantic *Macoma balthica rubra*) that have been reproductively isolated for 2–3.5 million years (Luttkhuizen et al. 2012; Saunier et al. 2015). *Macoma petalum* populations in San Francisco Bay, once recognized as distinct species from *M. balthica* (Vainola 2003), are now believed to be genetically identical to *Macoma balthica* (the circum-Arctic species) (Brusati and Grosholz 2007). However, these may yet prove different species and their taxonomy awaits further study (Coan and Valentich-Scott 2007; Brusati and Grosholz 2007). Thus, the description below considers them together as is done in current local intertidal guides (e.g. Coan and Valentich-Scott 2007). (see Vainola 2003 for molecular systematics of *M. balthica* species complex.)

Description

Size: Individuals averaging 30–35 mm in length (Oldroyd 1924), but usually under 30 mm (Coan 1971) and rarely more than 45 mm (Coan 1971; Cardoso et al. 2003). Smallest adults are 2 mm (Caddy 1969). Body proportions are generally 27 in length, 22 in height, and 11 mm in diameter (Oldroyd 1924). The illustrated specimen (from Coos Bay) is 17.5 mm long.

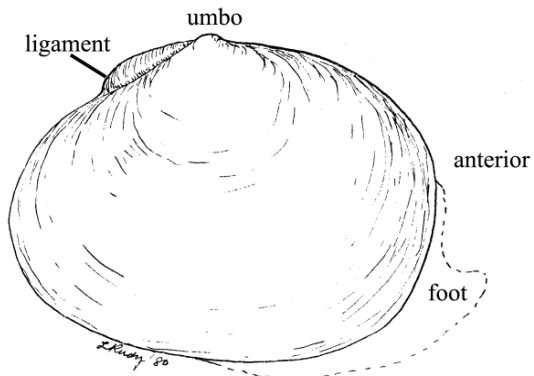
Color: Distinct color is reddish, pale rose or white and is sometimes bluish or yellow (Oldroyd 1924; see Plate 17, Kozloff 1993). Coos Bay specimens are usually pink inside and out, but individuals from British Columbia, Canada can have pink or yellow interiors (Quayle 1970).

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). Among the bivalves, the Heterodonta are characterized by **ctenidia** (or gills) that are eulamellibranchiate, fused mantle margins and the presence of long **siphons**. Veneroid bivalves have well-developed hinge teeth and members of the family Tellinidae have short lateral hinge teeth (when present – see **Possible Misidentifications**), shells with external striations or ribs, and deep pallial sinuses (Coan and Valentich-Scott 2007). When holding closed shell in both hands with the hinged area up and the ligaments toward you, the right valve is in the right hand (Fig. 3) (Keen and Coan 1974).

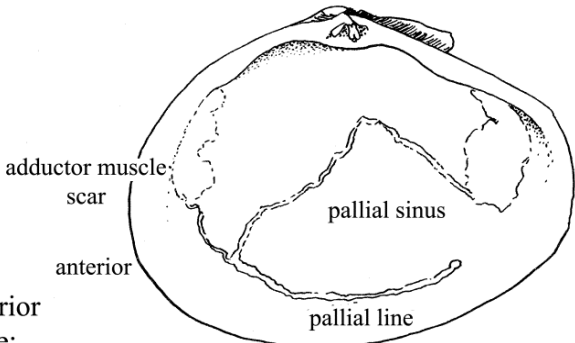
Body:

Color:

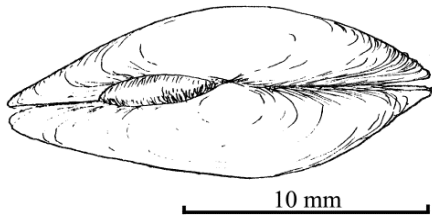
Macoma balthica



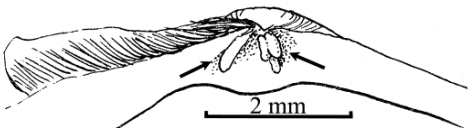
1. *Macoma balthica*, exterior, right valve (L:17.5mm,D:7.5mm,H:14mm) x4: shell regular, oval; valves equal; umbos low, almost central; anterior and posterior ends rounded: no flange, bend or gape; exterior color pink; ligament external, short, strong.



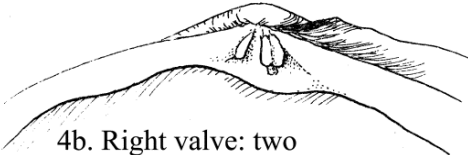
2a. Interior, right valve: pallial line narrow, faint; pallial sinus ends 3/4 of way to anterior adductor muscle scar; sinuses in both valves similar; interior pink.



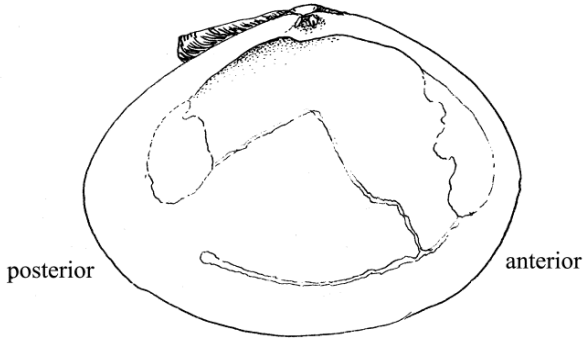
3. (Dorsal view) x4: valves not bent.



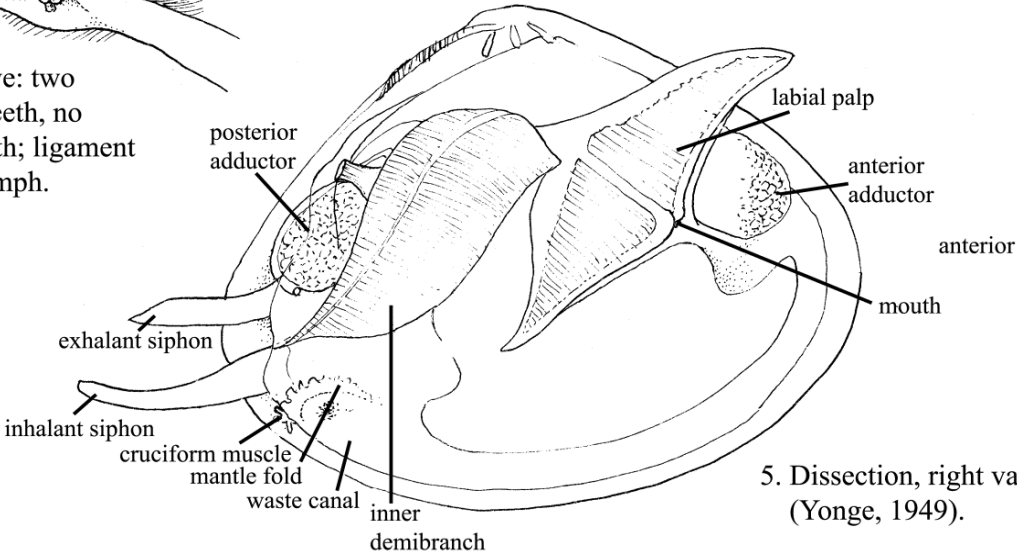
4a. Left valve x12: two cardinal teeth, no lateral teeth.



4b. Right valve: two cardinal teeth, no lateral teeth; ligament not on nymph.



2b. Left valve



5. Dissection, right valve: (Yonge, 1949).

Interior: Ligament is short, but strong, partially sunken, seated on a stout callus (Dunnill and Ellis 1969), but not on a nymph (Tellinidae, Coan and Valentich-Scott 2007).

Exterior:

Byssus:

Gills:

Shell: The shell shape is regularly oval, round, thick, with equal valves, umbos low, almost central, and usually worn (Fig. 1). The dorsal margin is arched, the ventral margin is slightly contracted (Oldroyd 1924), and there is no posterior dorsal flange (posterior to ligament). Valves do not gape (Tellinidae, Keen 1971) and the posterior end is rounded. Shell usually heavy, but bay specimens sometimes thin (Coan 1971).

Interior: Pallial line is narrow and faint. The pallial sinus is large (see Plate 422, Coan and Valentich-Scott 2007) and equal among valves. The sinus ends $\frac{3}{4}$ of the way to anterior adductor muscle scar in both valves (Figs. 2a, 2b), and does not reach the muscle scar (Fig. 2b) (Coan and Valentich-Scott 2007).

Exterior: Periostracum is thin, silky, not shiny (Coan 1971), and a trace is visible only ventrally. Shell sculpture consists of fine concentric growth lines only (Figs. 1, 3) (Dunnill and Ellis 1969).

Hinge: The hinge area has no lateral teeth (*Macoma*, Coan and Valentich-Scott 2007). Two cardinal teeth exist in each valve (Figs. 4a, 4b), one stout, bifid, and the other single and fragile (Dunnill and Ellis 1969).

Eyes:

Foot:

Siphons: The siphons are long, separate, and mobile (Kozloff 1993). Inhalant siphons are four times the shell length, when extended. Exhalant siphons held vertically above surface are 1.5 cm. Siphons bear large palps, for sorting fine particles (Fig. 5) (Yonge 1949). (For diagrams of siphon

development, see Figs. 3, 6, Caddy 1969.)

Burrow:

Possible Misidentifications

Tellinids can be distinguished from other small or young bay clams (i.e., Mactridae: *Tresus*; Veneridae: *Protothaca*, *Saxidomus*; Myidae: *Mya*, *Cryptomya*) an external ligament, an ovate shell, an inconspicuous nymph (or supporting projection for the external ligament), sometimes reddish hue and lateral teeth as well as a shell with ribs or striations (no radial pattern) and shells that never gape. Lateral teeth may or may not be present in the Tellinidae (Coan 1971). Myids have a hinge with a spoon-shaped chondrophore (left valve) and a projecting tooth (right valve) (see *Mya arenaria*, this guide). Venerids have three cardinal teeth in each valve. Mactrids have an internal ligament, A-shaped cardinal teeth, and gaping valves (Coan and Valentich-Scott 2007). The Tellinidae has around 16 species distributed between two genera locally – *Tellina* and *Macoma*. These genera can be differentiated by the hinge teeth, *Tellina* species have a hinge with lateral teeth, while *Macoma* species do not. *Macoma* species have shells that are also more rounded and inflated than *Tellina*, and are smooth, white, often chalky. They are characterized by having a ovate shell consisting of two equal valves, a dark and deciduous periostracum, two cardinal teeth, the absence of lateral teeth and a pallial sinus that is deeper on the left valve (Scott and Blake 1998; Arruda and Domaneschi 2005). *Macoma* species may also have a more northern geographic distribution while *Tellina* are elongate, relatively compressed, conspicuously sculptured, brightly colored, and usually warm water dwellers (Coan 1971). Eleven species in the infaunal genus *Macoma* (Luttikhuisen et al. 2012) are reported locally (although 30 have been identified in the northeastern Pacific, Dunnill and Ellis 1969), but only seven are

described in local keys (e.g. Coan and Valentich-Scott 2007), the four most common species of *Macoma* in our area are *M. balthica*, *M. nasuta*, *M. inquinata*, and *M. secta* (Kabat and O'Foighil 1987).

Two species, *M. secta* and *M. indentata* have a posterior dorsal flange extending from posterior end to the external ligament, this is absent in other *Macoma* species. The former species is called the sand clam and has a quadrate and truncate posterior. The latter is elongate, has a pointed posterior, unique muscle scars, is relatively rare and small (to 2.5 cm) and occurs from Trinidad, California southward. *Macoma secta*, also has a white shell, with a yellowish epidermis. Its right valve is more inflated than the left, and it can be large (to 120 mm) and is more common in clean sand, not in estuarine mud.

The morphology of the pallial sinus differentiates the other species. In species without a posterior dorsal flange, *M. acolasta* and *M. yoldiformis*, the anterior ventral edge of the pallial sinus is detached for a portion of the distance to the posterior adductor muscle scar. *Macoma acolasta* also has a rounded posterior, rather than pointed as in *M. yoldiformis* and is rare, sand-dwelling, and occurs from Bodega Bay, California, southward. *Macoma yoldiformis* is elongate, inflated, and thin, with the pallial sinus detached from the pallial line. Although the range of this clam is from Vancouver south to Baja California, it is not included in Puget Sound or British Columbia work (Dunnill and Ellis 1969). It can be found in silt in low intertidal or protected bays (Coan and Valentich-Scott 2007).

Macoma inquinata, *M. nasuta* and *M. balthica* (see descriptions in this guide) are all species with an anterior ventral edge of pallial sinus that is not detached and they tend to be larger (up to 110 mm) than *M. acolasta* or *M. yoldiformis* (less than 30 mm).

Macoma balthica has a pinkish hue and a pallial sinus that ends $\frac{3}{4}$ of the way to anterior adductor muscle scar and is generally more oval than *M. nasuta* or *M. inquinata* (compare Fig. 1 *M. balthica*, with Fig. 1 *M. nasuta*, this guide) (Kozloff 1993). In *M. inquinata*, the pallial sinus does not reach the ventral end of the anterior adductor muscle and the shell is chalky white with a fibrous olive green periostracum. *Macoma nasuta*, on the other hand, is not as round and heavy as *M. inquinata* and its pallial sinus reaches and joins the anterior adductor scar above its base (left valve). (Its right valve may be more like *M. inquinata*'s). Furthermore, its siphons are orange and its shell posterior is bent to the right. *Macoma inquinata* can also bend slightly posteriorly, and may be confused with the thinner *M. nasuta*, without investigations of the other aforementioned features. (see Plate 422 for diagrams of these distinguishing characteristics in *Macoma*). *Macoma balthica* and *M. inquinata* are generally smaller than *M. nasuta* (up to 5 cm), with mature *Macoma balthica* rarely exceeding 25 mm in length (Dunnill and Ellis 1969), but could be confused with the young of some of these larger clams. Molecular differences have been documented within the *M. balthica* complex (see Vainola 2003) as well as morphological differences between the eastern (*Macoma balthica balthica*) and western (*Macoma balthica rubra*) Atlantic populations or subspecies. In particular, populations from southeastern United States estuaries exhibited larger shells and higher siphon height, which may correspond to deeper burying depths to avoid higher water temperatures in this region (Kamermans et al. 1990).

(The following species may be present locally, but are not included in local dichotomous keys). *Macoma expansa*, is a rare, usually offshore species (to 50 mm) whose pallial sinuses are perpendicular to the pallial

line. *Macoma elimata* is found in 15–476 meters of water. *Macoma incongrua* is a generally northern species which can be found to 33°N latitude, intertidally to 36 meters. It has somewhat inflated valves, is usually 30–40 mm long, and almost round in outline (Dunnill and Ellis 1969). *Macoma calcaria* is found from 35 meters and lower, from 37° northward. Other northern subtidal species include the large *M. brota* and *M. lipara* (Dunnill and Ellis 1969).

Ecological Information

Range: Type locality is the Baltic Sea. *Macoma balthica* is present in the North Pacific and North Atlantic, in both European and North American waters. In Europe, distribution includes the White Sea, Pechora Sea, Wadden Sea, and southern coastal France. North American distribution includes the Gulf of St. Lawrence and Hudson Bay, south to Virginia as well as the Alaskan coast to San Francisco, but rarely further south to San Diego (Coan 1971). This species was possibly introduced to San Francisco from the Atlantic coast (Coan and Valentich-Scott 2007). However, some hybridization between populations has been observed where they meet at the Baltic Sea (Luttikhuisen et al. 2012). Local genetic population structure with depth has been determined in the Gulf of Gdańsk in Poland (Becquet et al. 2013).

Local Distribution: Coos Bay sites at the South Slough channel and airport spoil islands. Oregonian distribution in Siletz, Nestucca, Siuslaw, Netarts, Tillamook Bays and generally all bays within close proximity to the open coast (Hancock 1979; Kozloff 1993).

Habitat: Offshore and bay mud (Kabat and O’Foighil 1987). Often in very fine and sometimes black, foul mud. Currents largely determine distribution, as they affect the settlement of sediment and degree of

shelter. Although coarseness of sediment was found to not be a determining factor in distribution (see Vassalio 1969), individuals may prefer fine sediment, which increases the density of their food supply (e.g., micro-organism populations, Newell 1963).

Macoma balthica recruitment was negatively effected by suction dredging, presumably due to the reduction and subsequent lack of accumulation of fine-grained sediment (Piersma et al. 2001).

Salinity: Collected at salinities of 30 and also found in brackish water (Vassalio 1969). Individuals found where salinity is as low as 5 (Jansson et al. 2013). Along the York River in the Chesapeake Bay, higher abundance, predation and food availability was found upriver (salinity 5–10) than downriver (salinity 15–19), although recruitment was lowest upriver (Seitz 2011).

Temperature: *Macoma balthica* prefers cold to temperate waters and has a low tolerance to elevated temperatures (Wadden Sea, Beukema et al. 2009). Increases in seawater temperature and mild winters alter the onset of spawning and associated recruitment timing among *Macoma balthica* (Phillipart et al. 2003) and their predators in the Wadden Sea (Dekker and Beukema 2014). Increases in water temperature have also been shown to reduce body mass, which usually decreases in winter, but to a greater degree during mild versus cold winters (Honkoop and Beukema 1997).

Tidal Level: Intertidal and subtidal (Kabat and O’Foighil 1987). Individuals found at + 0.3 m (Coos Bay, Shore Acres) and down to 37 m (Coan 1971). An apparent correlation between clam size and depth distribution was reported, with the smallest animals closest to surface (Vassalio 1969), where distance from surface can be determined by siphon length (Vassalio 1971).

Associates: In San Francisco Bay, California associates include the whelk, *Busycotypus*,

the gastropod *Nassarius*, capitellid and nereid polychaetes, the amphipod, *Ampelisca*, and bivalves, *Gemma* and *Mya* (Vassalio 1969). Individuals are sometimes host to gymnophallid trematode (metacercariae) parasites (e.g. *Gymnophallus somateriae*, *Lacunovermis conspicuus*, *Meiogymnophallus multigemmulus*, Swennen 1969; Ching 1973) as well as a protist parasite, *Perkinsus chesapeaki* (Coss et al. 2001; Burrenson et al. 2005).

Abundance: Adults most abundant in the upper intertidal zone (1.3–2.6 m) (San Francisco Bay, California, Vassalio 1969), where they compose 55% of the total invertebrate community. Density may be determined by currents, fineness of deposits and micro-organism food (Haderlie and Abbott 1980). Individuals not very common in Puget Sound, Washington (Kozloff 1993), but quite common at many stations in Coos Bay, OR. Pelagic larval abundances as high as 12,000 larvae/m³ were reported in the Baltic Sea (Jansson et al. 2013). Larval abundance (determined by single step nested multiplex PCR) in Isefjord, Denmark showed two peaks, one in the July and another at the end of August (Larsen et al. 2007). Juvenile densities of up to 5,000 individuals/m² were reported in June in the Thames estuary, England (Caddy 1969). Adult density correlates with egg size, where populations that are more dense produce smaller eggs (e.g., 224 individuals/m² produce eggs that are 100.5 µm whereas five individuals/m² produce eggs that are 108.5 µm in diameter, Luttikhuizen et al. 2011).

Life-History Information

Reproduction: Reproduction and development has been described for *M. balthica* (Europe, Caddy 1967, 1969; Lammens 1967). Egg size correlates with adult density (see **Abundance**) and ranges from 100.5

–108.5 µm in diameter (Wadden and North Seas, Luttikhuizen et al. 2011). In the Netherlands, oocytes measured 97 µm and spawning occurred in short burst throughout March–April (at 10°C, Caddy 1967). Research on the effects of ocean acidification has found that reduction in pH (e.g. 7.5) negatively effects fertilization, and causes slower growth, and delayed metamorphosis, which occurs at smaller sizes and reduces pelagic survival (Van Colen et al. 2012; Jansson et al. 2013; Jansson et al. 2015).

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 (see Fig. 1, Caddy 1969). 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, Caddy 1969; Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Some bivalve species (e.g. *Mytilus edulis*), including *M. balthica*, have two dispersal periods. The initial larval dispersal and settlement into the benthos, where larvae are 200–500 µm, is followed by potential dispersal from the benthos by thread drifting on long hyaline threads when young clams are 5–12 mm (Beukema and Vlas 1989). In *M. balthica*, advanced veliger larvae have a yellow shell that is 245–350 µm in

length and is with red umbo and small prodissoconch II (Kabat and O'Foighil 1987; Brink 2001). Veliger shell shape in *M. balthica* is broadly rounded (see Fig. 4, Brink 2001). *Macoma nasuta* and *M. secta* are also known to have free swimming veliger larvae (Marriage 1954; Rae 1978, 1979; Brink 2001). Planktonic duration is probably 2–5 weeks and larvae settle at sizes between 300–330 μm . Significant research has been conducted on recruitment, growth, and general biology of *Macoma balthica* in the Dutch Wadden Sea. These studies found that larval recruitment is most successful in summers following severe winters due to reduced predation pressure from populations negatively influenced by cold temperature (e.g., *Crangon crangon*, *Carcinus maenas*, Beukema et al. 1998; Dekker and Beukema 2014; Dekker and Beukema 2014). Conversely, increases in winter temperatures reduce reproductive output and increase juvenile mortality suggesting that *Macoma balthica* populations will suffer with a warming climate (Wadden Sea, Philippart et al. 2003; Beukema et al. 2009). Highest recruitment was observed after cold winters and recruitment reportedly failed altogether after mild winters in the Wadden Sea (Honkoop et al. 1998) (see also **Temperature**).

Juvenile:

Longevity: Up to 30 years (Cardoso et al. 2003). Five years was reported from Rand Harbor, Massachusetts and up to 25 years in the Gulf of Finland (Gilbert 1973).

Growth Rate: Individual age is often estimated by the external rings on the shell as the rings are produced each winter when growth slows. However, these growth rings are likely overestimates of actual age and, thus, underestimates of growth rates (Cardoso et al. 2003). Seasonal growth was observed in European populations, where growth rate correlates to food supply

(e.g. chlorophyll and unicellular algae) and ranged from 5–7 mm and 10–25 mm/year in the western Wadden Sea (see Fig. 5, Beukema et al. 2002). Growth measured in the same region was 0.009–0.011 mm/day from March through April and reduced to 0.001–0.002 mm/day from July to September (Cardoso et al. 2003). Average maximum length was greater for North American populations than European (Gilbert 1973) and may be evidence for two sibling species (Kamermans et al. 1990). Growth rate depends on season and food availability in San Francisco Bay, California (Thompson and Nichols 1988) and is relatively constant throughout the year in Massachusetts, though slightly accelerated in the summer.

Food: A suspension feeder that also feeds on mud surface bacteria and detritus as well as on planktonic organisms at high tide (Braefield and Newell 1961; Newell 1963; Vassalio 1969; Oldroyd 1924). Thus, *M. balthica* switches between suspension and deposit feeding modes depending on local habitat (Tornroos et al. 2015). Individuals compete for food with the amphipod, *Ampelisca*. Each individual feeds in a 4 cm area (Braefield and Newell 1961) and an increase in individual weight between late winter and early summer is dependent on algal feeding in the Wadden Sea (Beukema et al. 2014).

Predators: Predators include shorebirds (e.g., eiders *Somateria mollissima*, oyster-catchers *Haematopus ostralegus*, red knots *Calidris canutus*, Beukema et al. 2010) and starry flounder (Vassalio 1969; Cardoso et al. 2003). Predators of newly settled spat include, *Ampelisca* (Vassalio 1969) and top down predation on young *M. balthica* by the shrimp, *Crangon crangon* and the shore crab, *Carcinus maenas* have a negative effect on populations (Dekker and Beukema 2014).

Behavior: *Macoma balthica* is essentially static and a slower burrower than some other *Macoma* species (Yonge 1949), requiring 2½

minutes to bury itself (Braefield and Newell 1961). U-shaped tracks in mud suggest movement toward and away from the sun (Braefield and Newell 1961).

Bibliography

1. ARRUDA, E. P., and O. DOMANESCHI. 2005. New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from southeastern Brazil, and with description of its gross anatomy. *Zootaxa*:13-22.
2. BECQUET, V., R. LASOTA, E. PANTE, A. SOKOLOWSKI, M. WOLOWICZ, and P. GARCIA. 2013. Effects of fine-scale environmental heterogeneity on local genetic structure in *Macoma balthica* from the Gulf of Gdask (southern Baltic Sea). *Hydrobiologia*. 714:61-70.
3. BEUKEMA, J. J., G. C. CADEE, and R. DEKKER. 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *Journal of Sea Research*. 48:111-125.
4. BEUKEMA, J. J., G. C. CADEE, R. DEKKER, and C. J. M. PHILIPPART. 2014. Annual and spatial variability in gains of body weight in *Macoma balthica* (L.): Relationships with food supply and water temperature. *Journal of Experimental Marine Biology and Ecology*. 457:105-112.
5. BEUKEMA, J. J., and R. DEKKER. 2014. Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Marine Ecology Progress Series*. 513:1-15.
6. BEUKEMA, J. J., R. DEKKER, and J. M. JANSEN. 2009. Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Marine Ecology Progress Series*. 384:135-145.
7. BEUKEMA, J. J., R. DEKKER, and C. J. M. PHILIPPART. 2010. Long-term variability in bivalve recruitment, mortality, and growth and their contribution to fluctuations in food stocks of shellfish-eating birds. *Marine Ecology Progress Series*. 414:117-130.
8. BEUKEMA, J. J., and J. DEVLAS. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Marine Ecology Progress Series*. 52:193-200.
9. BEUKEMA, J. J., P. J. C. HONKOOP, and R. DEKKER. 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia*. 375-76:23-34.
10. BEUKEMA, J. J., and B. W. MEEHAN. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Marine Biology*. 90:27-33.
11. BRAEFIELD, A. E., and G. E. NEWELL. 1961. The behaviour of *Macoma balthica* (L.). *Journal of the Marine Biological Association of the United Kingdom*. 41:81-87.
12. 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.
13. BRODERIP, W. J., and G. B. SOWERBY. 1829. Observations on new or interesting mollusca contained, for the most part, in the Museum of the Zoological Society. *Zoological Journal*. 4:359-379.
14. BRUSATI, E. D., and E. D. GROSHOLZ. 2007. Effect of native and invasive cordgrass on *Macoma petalum* density, growth, and isotopic signatures. *Estuarine Coastal and Shelf Science*. 71:517-522.
15. BURRESON, E. M., K. S. REECE, and C. F. DUNGAN. 2005. Molecular, morphological, and experimental evidence support the synonymy of *Perkinsus chesapeaki*

- and *Perkinsus andrewsi*. Journal of Eukaryotic Microbiology. 52:258-270.
16. CADDY, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). Canadian Journal of Zoology. 45:955-965.
 - 17.—. 1969. Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata). Canadian Journal of Zoology. 47:609-617.
 18. CARDOSO, J. F. M. F., S. SANTOS, J. I. J. WITTE, R. WITBAARD, H. W. VAN DER VEER, and J. P. MACHADO. 2013. Validation of the seasonality in growth lines in the shell of *Macoma balthica* using stable isotopes and trace elements. Journal of Sea Research. 82:93-102.
 19. CHING, H. L. 1973. Description of *Gymnophallus somateriae* (Levinsen, 1881) from *Macoma inconspicua* and diving ducks from Vancouver, Canada. Canadian Journal of Zoology. 51:801-806.
 20. COAN, E. V. 1971. The Northwest American Tellinidae. California Malacozoological Society, Berkeley.
 21. 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.
 22. COSS, C. A., J. A. F. ROBLEDO, G. M. RUIZ, and G. R. VASTA. 2001. Description of *Perkinsus andrewsi* n. sp isolated from the baltic clam (*Macoma balthica*) by characterization of the ribosomal RNA locus, and development of a species-specific PCR-based diagnostic assay. Journal of Eukaryotic Microbiology. 48:52-61.
 23. DEKKER, R., and J. J. BEUKEMA. 2014. Phenology of abundance of bivalve spat and of their epibenthic predators: limited evidence for mismatches after cold winters. Marine Ecology Progress Series. 513:17-27.
 24. DUNNILL, R. M., and D. V. ELLIS. 1969. Recent species of the genus *Macoma* (Pelecypoda) in British Columbia. National Museum of Canada, National Historical Papers. 45:1-34.
 25. GILBERT, M. A. 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). Biological Bulletin. 145:119-126.
 26. 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.
 27. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBART, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
 28. HONKkoop, P. J. C., and J. J. BEUKEMA. 1997. Loss of body mass in winter in three intertidal bivalve species: An experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. Journal of Experimental Marine Biology and Ecology. 212:277-297.
 29. HONKkoop, P. J. C., J. VAN DER MEER, J. J. BEUKEMA, and D. KWAST. 1998. Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*? Marine Ecology Progress Series. 164:229-235.
 30. JANSSON, A., J. NORKKO, S. DUPONT, and A. NORKKO. 2015. Growth and survival in a changing environment: Combined effects of moderate hypoxia and low pH on juvenile bivalve *Macoma balthica*. Journal of Sea Research. 102:41-47.
 31. JANSSON, A., J. NORKKO, and A. NORKKO. 2013. Effects of reduced pH on

- Macoma balthica* larvae from a system with naturally fluctuating pH dynamics. PLoS ONE. 8:1-7.
32. 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.
 33. KAMERMANS, P., H. W. VAN DER VEER, J. I. J. WITTE, and E. J. ADRIANS. 1999. Morphological differences in *Macoma balthica* (Bivalvia, Tellinacea) from a Dutch and three southeastern United States estuaries. *Journal of Sea Research*. 41:213-224.
 34. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
 35. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 36. 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.
 37. LAMMENS, J. J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Netherlands Journal of Sea Research*. 3:315-382.
 38. LARSEN, J. B., M. E. FRISCHER, K. W. OCKELMANN, L. J. RASMUSSEN, and B. W. HANSEN. 2007. Temporal occurrence of planktotrophic bivalve larvae identified morphologically and by single step nested multiplex PCR. *Journal of Plankton Research*. 29:423-436.
 39. LUTTIKHUIZEN, P. C., J. DRENT, K. T. C. A. PEIJNENBURG, H. W. VAN DER VEER, and K. JOHANNESSON. 2012. Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. *Molecular Ecology*. 21:3048-3061.
 40. LUTTIKHUIZEN, P. C., P. J. C. HONK-OOP, and J. DRENT. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology*. 396:156-161.
 41. MARRIAGE, L. D. 1954. The bay clams of Oregon. Contribution No. 20. Fish Commission of Oregon, s.l.
 42. MEEHAN, B. W. 1985. Genetic comparison of *Macoma balthica* (Bivalvia, Tellinidae) from the eastern and western north Atlantic Ocean. *Marine Ecology Progress Series*. 22:69-76.
 43. NEWELL, R. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London*. 144:25-45.
 44. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
 45. PHILIPPART, C. J. M., H. M. VAN AKEN, J. J. BEUKEMA, O. G. BOS, G. C. CADEE, and R. DEKKER. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography*. 48:2171-2185.
 46. PIERSMA, T., A. KOOLHAAS, A. DEKINGA, J. J. BEUKEMA, R. DEKKER, and K. ESSINK. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology*. 38:976-990.
 47. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
 48. RAE, J. G. 1979. Population dynamics of

- two sympatric species of *Macoma* (Mollusca, Bivalvia). *Veliger*. 21:384-399.
49. SAUNIER, A., P. GARCIA, V. BECQUET, N. MARSAUD, F. ESCUDIE, and E. PANTE. 2014. Mitochondrial genomes of the Baltic clam *Macoma balthica* (Bivalvia: Tellinidae): setting the stage for studying mito-nuclear incompatibilities. *BMC Evolutionary Biology*. 14:259.
 50. SCOTT, P. V., and J. A. BLAKE. 1998. The Mollusca Part 1: the Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel*, vol. 8. Santa Barbara Museum of Natural History, Santa Barbara, CA.
 51. SEITZ, R. D. 2011. Gradient effects on structuring of soft-bottom benthic infauna: *Macoma balthica* and predation, recruitment, and food availability. *Journal of Experimental Marine Biology and Ecology*. 409:114-122.
 52. SWENNEN, C. 1969. Crawling-tracks of trematode infected *Macoma balthica* (L.). *Netherlands Journal of Sea Research*. 4:376-379.
 53. THOMPSON, J. K., and F. H. NICHOLS. 1988. Food availability controls seasonal cycle of growth in *Macoma balthica* (L.) in San Francisco Bay, California. *Journal of Experimental Marine Biology and Ecology*. 116:43-61.
 54. TORNROOS, A., M. C. NORDSTROM, K. AARNIO, and E. BONSDORFF. 2015. Environmental context and trophic trait plasticity in a key species, the tellinid clam *Macoma balthica* L. *Journal of Experimental Marine Biology and Ecology*. 472:32-40.
 55. VAINOLA, R. 2003. Repeated trans-Arctic invasions in littoral bivalves: molecular zoogeography of the *Macoma balthica* complex. *Marine Biology*. 143:935-946.
 56. VAN COLEN, C., E. DEBUSSCHERE, U. BRAECKMAN, D. VAN GANSBEKE, and M. VINCX. 2012. The early life history of the clam *Macoma balthica* in a high CO₂ world. *Plos One*. 7.
 57. VASSALLO, M. T. 1969. The ecology of *Macoma inconspicua* (Broderip and Sowerby, 1829) in central San Francisco Bay. Part 1. The vertical distribution of the *Macoma* community. *Veliger*. 11:223-234.
 58. —. 1971. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1829) in central San Francisco Bay. Part 2. Stratification of the *Macoma* community within the substrate. *Veliger*. 13:279-285.
 59. YONGE, C. M. 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamelibranchia. *Transactions of the Royal Society of London, Series B*. 234:29-76.

Updated 2015

T.C. Hiebert and K. Meyer