Mytilus trossulus

The bay mussel

Taxonomy: Confusion has surrounded the taxonomy of Mytilus species because the genus has historically been based on morphological shell characters, which have been shown to be plastic and varies with habitat (e.g. see Growth, Gosling 1992a and b). *Mytilus trossulus* is the species native to the west coast of North America, and was previously confused with *M. edulis*. Thus, in many intertidal guides of the past, (e.g., Kozloff 1993; Ricketts and Calvin 1952; Kabat and O'Foighil 1987; Haderlie and Abbott 1980) *M. edulis* is actually *M. trossulus*. Many of the references to which we refer are for *M*. edulis (and we call *M. trossulus*, for clarity). Mytilus trossulus is a member of the Mytilus edulis species complex, a group of three sibling species (M. trossulus, M. edulis, M. galloprovincialis), recently differentiated using molecular methods (McDonald and Koehn 1988; Gosling 1992a and b; Seed 1992; Geller 2007). The three species can be defined by both molecular and, less easily by, morphological characters (McDonald et al. 1991) (see Range). Additional north Pacific and Arctic synonyms for *M. trossulus* include (but are not limited to): *M. glumeratus*, *M.* pedroanus, M. edulis latissimus, M. edulis kussakini, M. edulis declinis, M. septentrionalis. M. ficus. McDonald and Koehn 1988; Kafanov 1999).

Description

Size: Individual size is about 70–110 mm (Coe 1945; Kozloff 1974; Haderlie and Abbott 1980). Mean dry body weight is 7 grams (Harger 1968).

Color: Blue, violet and white shell with shiny brown-black periostracum. Blue-black color particularly around ventral (posterior) shell margin. Tissues are orangish-tan.

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 Phylum: Mollusca Class: Bivalvia, Pteriomorpha Order: Mytiloida Family: Mytilidae

2007). Mytilids have roughly cylindrical shells and two adductor muscles, with associated scars that are unequal in size (see Plate 395, Coan and Valentich-Scott 2007). Mytilids often use byssal threads to connect them to the substratum (Kozloff 1993). **Body:**

Color:

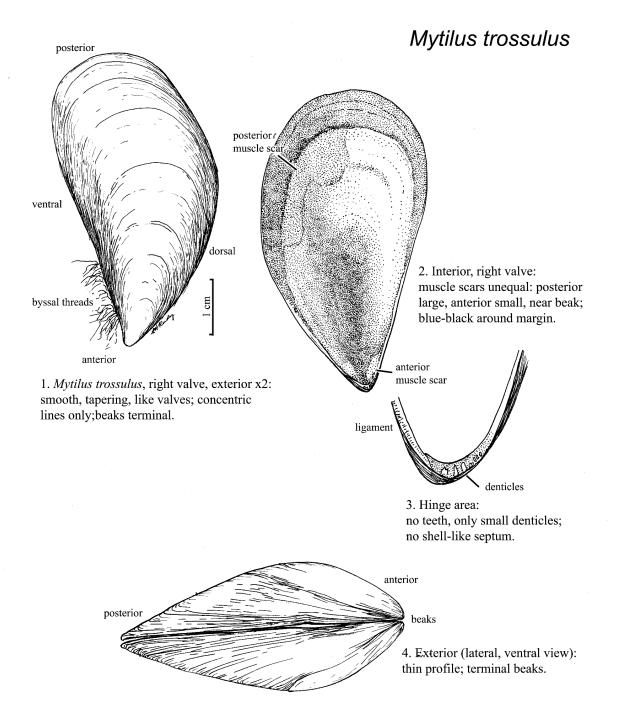
Interior: *Mytilus trossulus* as well as other bivalves can develop hemic neoplasia, a blood cell disorder that is often linked to environmental contaminants (e.g. polycyclic aromatic hydrocarbons, chlorinated hydrocarbons). Up to 30% of *M. trossulus* in Puget Sound, WA were infected. (Krishnakumar et al. 1999). A widely prevelant genus, the physiology of *Mytilus* has been the subject of much research (e.g., Smith 1982).

Exterior: Byssus: Gills:

Shell: Pointed shell, anteriorly, with very broad posterior (Haderlie and Abbott 1980). Individuals that are exposed to more wave action have shells that are thicker and grow more slowly (Haderlie and Abbott 1980).

Interior: Large posterior muscle scar, small anterior scar that is near the beak on the anterior ventral margin (Fig. 2). Pit-like byssal gland is present at the base of foot and produces liquid that hardens into byssal threads which are visible on the ventral shell margin (Fig. 1). Digestion is both intra and extra cellular, and is aided by the crystalline style and associated enzymes (Haderlie and Abbott 1980).

Exterior: Valves of similar morphology, wedge-shaped, and longer than high. Shell regular, smooth, and with concentric growth lines, but no radial ribs (Fig. 1, compare to *Clinocardium nuttallii*, this guide). Fine byssal threads attach to substrate, and beaks (the most prominent point on the shell, or umbo) are anterior and terminal. The shell is made of calcium, which



is absorbed from the surrounding seawater, and precipitated at the shell edge under the periostracum (Haderlie and Abbott 1980).

Hinge: No hinge teeth or chondrophore but small denticles are present near the beak. No shell-like septum (or shelf) at anterior end (Fig. 4).

Eyes:

Foot: Foot is reduced and internal. Although individuals are attached to substrate by byssal threads, they are capable of moving. By extending the foot and attaching it to the substrate, they are able to break byssal threads a few at a time and, eventually, detach and move to another location where they use their foot to reattach (Ricketts and Calvin 1952).

Siphons: No siphons, instead there are undulating openings between mantle edges (especially conspicuous along the posterior margin).

Burrow:

Possible Misidentifications

The family Mytilidae is characterized by two adductor muscles and associated scars that are unequal in size; the anterior scars are smaller and near the shell beak (see Plate 395, Coan and Valentich-Scott 2007). Members of this family have cylindrical shells that are dark brown or black that sometimes taper anteriorly, and the two shell valves are of similar morphology. They lack both a chondrophore (e.g., compare to Mya arenaria, this guide) and dorsal margin ears, and the shell is not cemented to the substratum (Coan and Valentich-Scott 2007). There are nearly 20 local species in the family Mytilidae comprising the genera Septifer (S. bifurcatus), Lithophaga (L. plumula), Geukensia (G. demissa), Musculista (M. senhousia), Modiolus (six species) and *Mytilus* (one to four species). Other genera possibly present in the area, but not included in current keys, may include Crenella (C. decussata), Gregariella (G. coarctata), and Solamen (S. columbianum) (Coan and Valentich-Scott 2007).

Genera can be differentiated as follows: *Mytilus* is a cosmopolitan genus with at least four species (Koehn 1991), has shells with beaks at the terminal portion of the anterior end and lack internal septa, while

Septifer species possess an internal septum at their anterior end. All other genera have shells with beaks that are anterior, but not terminal. Of those, Lithophaga plumula individuals are with cylindrical shells and a posterodorsal slope that is rough and with chalky encrustations, while Adula species have a posterodorsal slope without chalky encrustations and, instead, have a thick mat and are sometimes covered with mud or debris. The genera Geukensia, Modiolus, and *Musculista* have shells that are not cylindrical, G. demissa shells have prominent ribs externally and are dark brown or black in color. Modiolus and Musculista species have shells without external ribbing and members of the former genus have periostracial hairs while Musculista do not.

Species in the genus *Mytilus* are difficult to differentiate morphologically. The three local species are *M. californianus*, *M.* trossulus, and M. galloprovincialis (Evans et al. 2010). Mytilus californianus has a shell with radial ribs that are conspicuous, especially near the shell posterior. On the other hand, *M. trossulus*, *M. galloprovincialis* and *M. edulis* all have smooth shells and are lumped into the *M. edulis* species complex. Recent genetic research has shown that the smooth species that is present locally is M. *trossulus*. However, this species overlaps and forms a hybrid with *M. galloprovincialis* to the south in central California. The latter species has also been observed in BC Canada, but their current range includes only central California south to Baia California. Of these three species, only *M. trossulus* is native to the north Pacific, while M. galloprovincialis is native to Europe and M. edulis to the north Atlantic. Mytilus trossulus is often found with Mytilus californianus, the larger, coarser "common mussel" of the West Coast. Internally M. californianus is orange, but the most dependable distinguishing characteristic is the presence of radial ridges in *M. californianus*. When small, the two are more difficult to distinguish, however, M. trossulus has sharper edges, a thinner profile (Fig. 3), finer byssal threads, and more delicate concentric rings than does M. californianus. It also can be found higher in the intertidal zone, in more protected spots, not on exposed rocks with heavy surf and

turbulence. In profile, M. galloprovincialis shells are higher and flatter than *M. trossulus* and the anterior end is beaked in the former species, while it is blunt in the latter. Adductor muscles scars are also different between the two species. The anterior scars are small and round in M. galloprovincialis and narrow to elongate in *M. trossulus* (see Fig. 1.2 Gosling 1992b). Mytilus trossulus is more elongate than *M. edulis*, with which it co-occurs in eastern Newfoundland (Innes and Bates 1999). Few, if any, morphological characters (e.g., shell shape) can be used to reliably differentiate *M. edulis* and *M.* trossulus (McDonald et al. 1991; Seed 1992; Sarver and Foltz 1993). Fortunately, they do not co-occur in Oregon, as they do in the north Atlantic (Varvio et al. 1988; Mallet and Carver 1995; Kafanov 1999; Liu et al. 2011), where less hybridization has been observed between sympatric populations (Toro et al. 2002; Vainola and Strelkov 2011; Tam and Scrosati 2014). Larval characters were proposed for higher-level classification in the Mytilinae by Evseev et al. (2011).

Other rarer mussels include *Modiolus sp.,* the horse mussel, which has external subterminal beaks and is brown and hairy. This species is found in clumps in the mud subtidally. *Septifer bifurcatus* is found under rocks, is black outside, purple within, and with definite radiating ribs and shell-like septum across the anterior end.

Ecological Information

Range: *Mytilus trossulus* was originally described from Tillamook, OR and Puget Sound, Washington (= "Killimook and Puget Sound, Oregon" McDonald and Koehn 1988; Kafanov 1999), but due to recent understanding of the M. edulis species complex, a neotype designation was suggested from molecularly identified shells by Kafanov (1999). Mytilus trossulus is the native smooth blue mussel from the northeast Pacific and ranges from the Arctic to central California. Also in Hokkaido in the northwest Pacific (Suchanek et al. 1997). Although Mytilus edulis was previously believed to be the predominant species in northern Europe, *M. trossulus* is also widespread there (Vainola and Strelkov 2011). The congeneric species, M. galloprovincialis (the only Mytilus species

to invade new regions, Braby and Somero 2006), is native to Europe but was introduced to the west coast of North America and now has a distribution that overlaps with M. trossulus in central California, and extends south to Baia. California. Where the two species meet, between Monterey and Cape Mendocino, they form a hybrid zone (Braby and Somero 2006). Additional hybrid zones noted between the two species include Whidbey Island, Washington, San Francisco and San Diego Bay, California (Suchanek et al. 1997). The final member of this species complex, *M. edulis*, is native to the north Atlantic (Coan and Valentich-Scott 2007). Mytilus trossulus was previously mistaken for M. edulis before molecular work (McDonald and Koehn 1988; Varvio et al. 1988; McDonald et al. 1991; Vainola and Hvilsorn 1991: Seed 1992: Sarver and Foltz 1993: Geller et al. 1994; Beynon and Skibinski 1996; Burzynski et al. 2003; Wood et al. 2003) revealed the native local species was *M. trossulus* (see **Taxonomy**). Previous descriptions of *M. edulis* include a range from the Bering Sea, Alaska to Mexico (Ricketts and Calvin 1952), but the current distribution of *M. edulis* includes the north Atlantic (where it co-occurs with *M. trossulus*) and in the temperate southern Hemisphere (e.g., Chile). This species complex, including the three species discussed, has been the subject of considerable population genetic research (e.g., Koehn 1991; Riginos and Cunningham 2005), particularly work on hybridization and mitochondrial introgression (from *M. trossulus* into M. galloprovincialis, Geller et al. 1994; Geller 1994; Rawson and Hillbish 1995; Rawson et al. 1996).

Local Distribution: Likely occurs in all Oregon estuaries as well as along the outer coast (with the congener, *M. californianus*). **Habitat:** *Mytilus trossulus* is an extremely adaptable species. Individuals will attach to rock, wood, fiberglass, and firm mud. They prefer pilings in polluted harbors (Ricketts and Calvin 1971) and quiet waters. The congener, *M. californianus*, is more common on open coasts in the rocky intertidal and is well known for its interaction with the sea star, *Pisaster ochraceus* (see description in this guide) and the resulting intertidal vertical zonation; the upper limit is determined by physiological stress of aerial exposure and the lower limit is set by predation from the sea star (Niesen 2007). Mytilus galloprovincialis and *M. trossulus* occur in rocky intertidal habitats, but are limited by stresses (e.g. temperature and predation) that do not affect the thicker-shelled species, *M. californianus*, as greatly (Evans and Somero 2010). Meanwhile, *M. californianus* is competitively excluded by the congeners in bay and estuarine habitats because of a lower tolerance to variable osmotic gradients (Evans and Somero 2010). Mytilus species, including M. trossulus, are indicators of ecosystem health (e.g., lead, Haderlie and Abbott 1980; polycyclic aromatic compounds, Hellou and Law 2003; Turja et al. 2013; Turja et al. 2014; Preece et al. 2015).

Salinity: Mytilus trossulus is better adapted to variable (particularly lower) salinity than other Mytilus species, particularly larval stages, which may facilitate the current geographic distribution of species (see Range) (e.g., M. edulis, M. galloprovincialis, Sarver and Foltz 1993; Qui et al. 2002; Evans and Somero 2010, but see also Gardner and Thompson 2001; Kotta et al. 2015). Mytilus edulis can tolerate lower salinity than can M. californianus (Kozloff 1993). Adults prefer salinities of 2–33. need periods of desiccation and require less oxygenation than does M. californianus. Larvae of M. edulis can't survive at salinities over 45 or under 10 (Field 1922; Qui et al. 2002).

Temperature: Mussels potentially experience maximal thermal stress in intertidal zones due to long periods of aerial exposure and black shells (Hofman and Somaro 1995; Tomanek and Zuzow 2010). Mytilus trossulus is a temperate and coldwater species; it becomes more abundant in the northern reaches of its range (Ricketts and Calvin 1971), where it encounters optimum growth temperature of 10-20°C (Haderlie and Abbott 1980). Mytilus galloprovincialis, on the other hand, is warmadapted due to its native habitat in the Mediterranean Sea (Evans and Somero 2010) and temperature limitation largely contributes to the distribution of these species on the west coast of North America. In fact, Geller et al. (1994) found that M. galloprovincialis was not able to establish

itself in northern regions despite the fact that their larvae were being transported in ballast water from Japan.

Tidal Level: Generally found from mean low to mean higher low, but can occur from -0.3 to +1.5 meters. Subtidal distribution reported to 40 m in bays and sheltered areas (Haderlie and Abbott 1980; e.g., on pilings, Kotta et al. 2015). Also found around (both higher and lower in the intertidal) clumps of *M. californianus* (Ricketts and Calvin 1971; Akester and Martel 2000).

Associates: *Mytilus trossulus* can be the dominant member of a diverse community of invertebrates that include the barnacle, Balanus glandula (on mussel shells), nematodes, polychaetes (e.g., sabellid, serpulid, nereid, syllid), nemerteans, flatworms, the limpet *Lottia*, the bryozoan Bugula, anemone Metridium senile, the gastropod Nucella, red algae, tunicates, and hydrozoans (e.g. Phialella fragilis) (Haderlie and Abbott 1980; Niesen 2007; Mills et al. 2007). Some Mytilus trossulus are found in all M. californianus beds, which constitute a well-studied community (Ricketts and Calvin 1971). A blackish little sea cucumber, Cucumaria pseudocurata, is also found in mussel beds (e.g., especially *M. californianus*) (Kozloff 1993). Often occurs in clumps with Septifer bifurcatus nestled in and near the substrate (Haderlie and Abbott 1980). Parasites which can be present in M. trossulus include the copepod Modiolicola gracilis (gills), and Mytilicola orientalis (rectum) (Haderlie and Abbott 1980). Mvtilus species also host pyramidellid and eulimid snails (Kuris 2007) and M. trossulus, specifically, hosts several ciliated protozoans (e.g. Ancistrum mytili, A. caudatum, Crebricoma carinata, Raabella helensis, Landers 2007) as well as the orthonectid, Stoecharthrum fosterae (Kozloff 2007). *Mytilus* species also host commensal pea crabs Fabia subguadrata and Opisthopus transversus (Haderlie and Abbott 1980). *Mytilus trossulus* competes with macrophytes for space in the rocky intertidal (Kotta et al. 2015).

Abundance: Most abundant in northern portion of distribution (e.g. Oregon and Washington, Ricketts and Calvin 1971; Suchanek et al. 1997). A community can re-

establish in three years and is subject to greater fluctuations in numbers than is *M. californianus* (Ricketts and Calvin 1971). Density of *M. trossulus* correlates with habitat, as individuals in very sheltered habitats are large and in low densities where the opposite is true for less sheltered habitats (Tam and Scrosati 2014). Abundance of *Mytilius* spp. larvae, including *M. trossulus*, ranged from over 1,000 to less than 1 individual per cubic meter (Coos Bay, OR, Shanks and Shearmann 2009, 2011) and larval abundances of 2500–4000 individuals per cubic meter have been reported for *M. edulis* (Bay of Fundy and Oslofjord, Bayne 1976).

Life-History Information

Reproduction: Dioecious and free spawning (Field 1922), but hermaphroditism has been observed. Spawning occurs in late fall and winter in central California and November through May in southern California (MacGinitie and MacGinitie 1949; Haderlie and Abbott 1980). Individuals spawn in fall and winter on outer coasts and April-May in Puget Sound, BC, Canada and the San Juan Archipelago. Spawning duration in M. trossulus in the north Atlantic was longer than for *M. edulis*, which spawned for a period of 2–3 weeks in July (Toro et al. 2002). Mytilus californianus, on the other hand, spawns year round in southern California (mostly from Oct-March) and April to May in the San Juan Archipelago (Kabat and O'Foighil 1987). Oocytes are about the same size as M. trossulus at 60 µm and orange in color. Sperm morphology was described by Kafanov and Drozdov (1998); the sperm nucleus is 2 μ m in length, the acrosome 2–5 μ m and the sperm head is flask shaped in *Mytilus* species (see Fig. 2, Kafanov and Drozdov 1998). All three *Mytilus* species exhibit doubly uniparental mitochondrial inheritance, as females inherit mtDNA from their mother only, while males inherit both from mother and father (Rawson and Hillbish 1995; Zbawicka et al. 2007, 2010).

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; Fig. 1, for a generalized life cycle, Brink 2001). For a full description of development in the laboratory see *M. edulis* in Kabat and O'Foighil 1987 (and references therein). Oocytes are 60-65 µm in diameter and surrounded by a thin egg envelope, but no jelly. Development proceeds as follows: 1st polar bodies form at 1 hour post-fertilization, embryos are ciliated and swimming at 6 hours, trochophore larvae at 24 hours. velar lobes and bivalved shell develops at 48 hours, larvae are straight hinge veligers at 42 hours, are at prodissoconch II at 66 hours post fertilization and have a foot (i.e. pediveligers) at 72 hours. (Kabat and O'Foighil 1987). Larvae have a relatively long pelagic duration of four weeks, thus this species has the potential to colonization a wide area and move great distances (Harger 1968). The straight hinge veliger larval stage occurs later in this species than in others, once individuals are 220 µm. At this time the umbo becomes rounded and the anterior lengthens, eventually sloping to a point (see Table 4, Brink 2001). Larval and juvenile morphology for *M. trossulus* were described by Evseev et al. in 2011 (see Fig. 2, Table 1). Larvae that are 270-290 µm have an ovate shell with symmetrical umbo, pointed anterior and rounded posterior. The hinge plate of the provinculum is 5–8 µm in height and includes 8-9 anterior, 15-17 central, and 7-8 posterior teeth and a lensshaped pit ligament. Early juvenile shells are 360–380 µm and the umbo height is greater, anterior margin is broader, and posteroventral margin height increases; the conspicuous central teeth are 10-12 µm in height. Once

400–500 µm, shells are broad and enlarged posteroventrally, the umbo has low shoulders and is subtriangular, the hinge plate height continues to increase and the posterior teeth decrease in number to 5–7. The ligament pit becomes trapezoidal in shape, a lateral tooth develops at each anterior posterior margin, and an external ligament begins to form. At 600–700 µm juvenile teeth appear reduced, there are three teeth at the anterior and posterior margins, and the external ligament is 120–150 µm in length (Evseev et al. 2011). The larvae of *M. californianus* and *M.* trossulus are similar, but can be differentiated by the larvae of the former species having a less conspicuous, flatter umbo, and wider separation between the provinicular lateral teeth (Martel et al. 1999; see Fig. 5, Brink 2001). Larvae settle in summer in southern California, late spring, early summer in Puget Sound, Washington, and in summer on the east coast (Haderlie and Abbott 1980). Some secondary settlement occurs as individuals drift on their byssal threads (Kabat and O'Foighil 1987; Soo and Todd 2014), which allows for dispersal on weak currents (Haderlie and Abbott 1980). This so-called thread drifting has been observed in *Mytilus* spp., including *M. trossulus*, offshore of Coos Bay, OR (Shanks and Shearman 2011). Mytilus californianus larvae are known to settle onto the byssal threads of conspecifics. Post-larval (> 5 mm) settlement in M. trossulus larvae was shown to be related to macroalgal and barnacle cover, water flux, tidal height and flushing time, and reflect the distribution and abundance of adults (Hunt and Scheibling 1996). The upper thermal and desiccation tolerances of larvae 1-2 mm was 34°C and at vapor pressure deficit levels of 1.01 kPa, respectively. The latter factor was more likely to be experienced by mussels at this study site (Barkely Sound, BC, Canada). It has been suggested that larvae settle within filamentous algae then relocate to adult habitats when 2-3 mm, a size at which individuals were more tolerant to desiccation (Jenewein and Gosselin 2013). **Juvenile:** Juvenile size approximately 9–35 mm in length (Akester and Martel 2000). although 'early juvenile' may be as small as 360 µm (see Evseev et al. 2011, above). The posterodorsal margin becomes angular when

shells are 900-1100 µm and at 1500-1700µm the shell is triangular and elongated ventrally, the ligament pit and juvenile teeth are covered by new shell growth and there are four lateral teeth at anterior and posterior margins (Evseev et al. 2011). Differentiating early juveniles in the genus *Mytilus* is challenging and Martel et al. 1999 proposed morphological characters to differentiate M. californianus from the bay mussels (M. trossulus and M. galloprovincialis): M. californianus juveniles have a more posterodrosal apex and a posterior muscle attachment that is larger (for additional characters, see Martel et al. 1999). Longevity: Often the longest lived species in a community (e.g. southern California, Reish and Ayers 1968). Individuals that were 40-50 mm in length were 7-8 years old (Tam and Scrosati 2014).

Growth Rate: Individuals grow fastest early in life (e.g. the first five months, Coe 1945), especially in the second and third months after settling. Growth is also fastest when the water temperature is warmest (July) and dinoflagellate populations are high. Growth slows after 2-3 years (Coe 1945). Following settlement individuals grow 76 mm in the first year and 96 mm after two years (Haderlie and Abbott 1980). Individuals that are highest in the intertidal grow slower than those lower, and those that are continuously submerged are larger and grow faster than those exposed by tides as these individuals grow thick shells and cannot feed continuously. Faster growth is also seen for individuals in shaded areas than those in full sunlight (Haderlie and Abbott 1980). More byssal threads are grown during the night than the day and the number produced correlates with the density of mussels, salinity, and temperature (Haderlie and Abbott 1980). Shell morphology differs with wave exposure: those in wave-exposed habitats had lower shell height and width ratio and a thicker shell, more dysodont teeth, and a thicker hinge ligament (Barkley Sound, BC Canada, see Fig. 2 Akester and Martel 2000). Interestingly, sympatric species show similar shell morphology, which may be due to these environmental factors and phenotypical plasticity, in addition to hybridization (Innes and Bates 1999).

Food: *Mytilus trossulus* is a filter feeder that eats organic detritus (as small as 4–5 µm in size), as well as phyto- or zooplankton (Coe 1945; Lauringson et al. 2014). Feeding is by continual intake of water driven by ciliary currents, and selective feeding with mucus secretions or sheets that cover gills (Fox 1936). Seawater pumping rates measured by Meyhöfer (1985) were approximately 1 liter per hour per gram of individual wet weight in *M. trossulus*. They feed continually when submerged and individuals can sort particles from the water (Haderlie and Abbott 1980). Concentrating some food particles, particularly dinoflagellates (e.g., Gonyaulax catenella), leads to high toxicity in M. trossulus, as well as other filter feeding organisms (e.g, Siliqua patula, see description in this guide), which can be dangerous for human consumption (Haderlie and Abbott 1980).

Predators: Known predators include Pisaster, Nucella, Ancanthina, Ocenebra, Ceratostoma, Cancer antennarius, Pachygrapsus crassipes, Asterias rubens, Cancer irroratus, and Eriocheir sinensis (Newfoundland, Canada, Lowen et al. 2013; Wójcik et a. 2015). Ceratostoma nuttalli bores holes into both *M. californianus* and *M.* trossulus. Other predators include Roperia poulsoni, Nucella canaliculata, and Octopus bimaculoides (Haderlie and Abbott 1980). Mytilus species are also eaten by birds and are used by humans for food and bait. M. trossulus is a farmed species in Europe (Haderlie and Abbott 1980) and was found in archeological sites along the western North American coast (Pleistocene, Coan and Valentich-Scott 2007; Singh and McKechnie 2015). Preferential predation by Nucella limits *M. trossulus* and *M. galloprovincialis* in rocky intertidal zones, as Nucella prefers these species to M. californianus (Evans and Somero 2010).

Behavior: Individuals are more mobile than *M. californianus* and "crawl" to the outer edges of clumps to avoid silt deposition (Harger 1968). Although *M. edulis* tends to aggregate with conspecifics, *M. trossulus* does not (Liu et al. 2011).

Bibliography

- AKESTER, R. J., and A. L. MARTEL. 2000. Shell shape, dysodont tooth morphology, and hinge-ligament thickness in the bay mussel *Mytilus trossulus* correlate with wave exposure. Canadian Journal of Zoology. 78:240-253.
- BAYNE, B. L. 1976. Marine mussels, their ecology and physiology. International Biological Programme. 10:81-120.
- BEYNON, C. M., and D. O. F. SKIBINSKI. 1996. The evolutionary relationships between three species of mussel (*Mytilus*) based on anonymous DNA polymorphisms. Journal of Experimental Marine Biology and Ecology. 203:1-10.
- BRABY, C. E., and G. N. SOMERO. 2006. Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. Marine Biology. 148:1249-1262.
- 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.
- BURZYNSKI, A., M. ZBAWICKA, D. O. F. SKIBINSKI, and R. WENNE. 2003. Evidence for recombination of mtDNA in the marine mussel *Mytilus trossulus* from the Baltic. Molecular Biology and Evolution. 20:388-392.
- COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia. *In:* The Light and Smith manual: intertidal invertebrates from Central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
- 8. COE, W. R. 1945. Nutrition and growth of the California bay-mussel (*Mytilus edulis diegensis*). Journal of Experimental Zoology. 99:1-14.
- 9. EVANS, T. G., and G. N. SOMERO. 2010. Phosphorylation events catalyzed by major cell signaling proteins differ in response to thermal and osmotic stress among native (*Mytilus californianus* and *Mytilus*

trossulus) and invasive (*Mytilus galloprovincialis*) species of mussels. Physiological and Biochemical Zoology. 83:984-996.

- EVSEEV, G. A., N. K. KOLOTUKHINA, and V. A. KULIKOVA. 2011. Morphological structures of the shell of *Mytilus trossulus* and *Crenomytilus grayanus* in early ontogenesis and their importance in the taxonomy of Mytilinae (Bivalvia: Mytilidae). Journal of the Marine Biological Association of the United Kingdom. 91:1655-1664.
- 11. FIELD, I. A. 1922. Biology and economic value of the sea mussel *Mytilus edulis*. Bulletin of the United States Bureau of Fisheries. 38:127-259.
- 12. FOX, D. L. 1936. The habitat and food of the California sea mussel. 4:1-64.
- GARDNER, J. P. A., and R. J. THOMPSON. 2001. The effects of coastal and estuarine conditions on the physiology and survivorship of the mussels *Mytilus edulis*, *M. trossulus* and their hybrids. Journal of Experimental Marine Biology and Ecology. 265:119-140.
- GELLER, J. B. 1994. Marine biological invasions as models of dispersal: tracking secondary spread and introgressive gene flow. California Cooperative Oceanic Fisheries Investigations Reports. 35:68-72.
- 15. —. 2007. Molecular identification, p. 32-36. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
- 16. GELLER, J. B., J. T. CARLTON, and D. A. POWERS. 1994. PCR-based detection of mtDNA haplotypes of native and invading mussels on the northeastern Pacific coast: latitudinal pattern of invasion. Marine Biology Marine Biology. 119:243-249.
- 17. GOSLING, E. M. 1992a. Genetics of *Mytilus*. Developments in Aquaculture and Fisheries Science. 25:309-382.
- 18. —. 1992b. Systematics and geographic distribution of *Mytilus*.

Developments in Aquaculture and Fisheries Science. 25:1-20.

- 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.
- 20. HARGER, J. R. E. 1968. The role of behavior traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. Veliger. 11:45-49.
- HELLOU, J., and R. J. LAW. 2003. Stress on stress response of wild mussels, *Mytilus edulis* and *Mytilus trossulus*, as an indicator of ecosystem health. Environmental Pollution. 126:407-416.
- 22. HOFMANN, G. E., and G. N. SOMERO. 1995. Evidence for protein damage at environmental temperatures: seasonal changes in levels of ubiquitin conjugates and HSP70 in the intertidal mussel *Mytilus trossulus*. Journal of Experimental Biology. 198:1509-1518.
- HUNT, H. L., and R. E. SCHEIBLING. 1996. Physical and biological factors influencing mussel (*Mytilus trossulus*, *M. edulis*) settlement on a waveexposed rocky shore. Marine Ecology Progress Series. 142:135-145.
- INNES, D. J., and J. A. BATES. 1999. Morphological variation of *Mytilus edulis* and *Mytilus trossulus* in eastern Newfoundland. Marine Biology. 133:691-699.
- 25. JENEWEIN, B. T., and L. A. GOSSELIN. 2013. Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: effects of desiccation and heat on juvenile mortality. Marine Ecology Progress Series. 481:147-159.
- 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.

- KAFANOV, A. I. 1999. Some nomenclatural problems in *Mytilus edulis* (Linnaeus, 1758) group (Bivalvia: Mytilidae). Bulletin of the Institute of Malacology Tokyo. 3:103-114.
- KAFANOV, A. I., and A. L. DROZDOV. 1998. Comparative sperm morphology and phylogenetic classification of recent Mytiloidea (Bivalvia). Malacologia. 39:129-139.
- 29. KOEHN, R. K. 1991. The genetics and taxonomy of species in the genus *Mytilus*. Aquaculture. 94:125-145.
- 30. KOTTA, J., K. OGANJAN, V. LAURINGSON, M. PAERNOJA, A. KAASIK, L. ROHTLA, I. KOTTA, and H. ORAV-KOTTA. 2015. Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. Plos One. 10.
- 31. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
- 32. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
- —. 2007. Orthonectida, p. 203-205. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
- 34. KRISHNAKUMAR, P. K., E. CASILLAS, R. G. SNIDER, A. N. KAGLEY, and U. VARANASI. 1999. Environmental contaminants and the prevalence of hemic neoplasia (leukemia) in the common mussel (*Mytilus edulis* complex) from Puget sound, Washington, USA. Journal of Invertebrate Pathology. 73:135-146.
- 35. KURIS, A. M. 2007. Intertidal parasites and commensals, p. 24-27. *In:* The Light and Smith manual: intertidal invertebrates from central California to

Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.

- LANDERS, S. C. 2007. Symbiotic and attached ciliated protozoans, p. 70-80. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. C. Carlton (ed.). University of California Press, Berkeley.
- LAURINGSON, V., J. KOTTA, H. ORAV-KOTTA, and K. KALJURAND.
 2014. Diet of mussels *Mytilus trossulus* and *Dreissena polymorpha* in a brackish nontidal environment. Marine Ecology. 35:56-66.
- LIU, G., E. STAPLETON, D. INNES, and R. THOMPSON. 2011.
 Aggregational behavior of the blue mussels *Mytilus edulis* and *Mytilus trossulus*: a potential pre-zygotic reproductive isolation mechanism. Marine Ecology. 32:480-487.
- LOWEN, J. B., D. J. INNES, and R. J. THOMPSON. 2013. Predator-induced defenses differ between sympatric *Mytilus edulis* and *M. trossulus*. Marine Ecology Progress Series. 475:135-143.
- 40. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
- 41. MALLET, A. L., and C. E. CARVER. 1995. Comparative growth and survival patterns of *Mytilus trossulus* and *Mytilus edulis* in Atlantic Canada. Canadian Journal of Fisheries and Aquatic Sciences. 52:1873-1880.
- 42. MARTEL, A. L., C. ROBLES, K. BECKENBACH, and M. J. SMITH. 1999. Distinguishing early juveniles of Eastern Pacific mussels (*Mytilus* spp.) using morphology and genomic DNA. Invertebrate Biology. 118:149-164.
- 43. MCDONALD, J. H., and R. K. KOEHN. 1988. The mussels *Mytilus* galloprovincialis and *Mytilus trossulus* on the Pacific coast of North America. Marine Biology. 99:111-118.
- 44. MCDONALD, J. H., R. SEED, and R. K. KOEHN. 1991. Allozymes and morphometric characters of three species of *Mytilus* in the northern and

southern hemispheres. Marine Biology. 111:323-333.

- 45. MEYHOFER, E. 1985. Comparative pumping rates in suspension feeding bivalves. Marine Biology. 85:137-142.
- 46. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, and C. HAND. 2007. Hydrozoa: polyps, hydromedusae, and siphonophora, p. 118-168. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. C. Carlton (ed.). University of California Press, Berkeley.
- 47. NIESEN, T. M. 2007. Intertidal habitats and marine biogeography of the Oregonian Province, p. 3-17. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
- PREECE, E. P., B. C. MOORE, and F. J. HARDY. 2015. Transfer of microcystin from freshwater lakes to Puget Sound, WA and toxin accumulation in marine mussels (*Mytilus trossulus*). Ecotoxicology and Environmental Safety. 122:98-105.
- 49. QIU, J. W., R. TREMBLAY, and E. BOURGET. 2002. Ontogenetic changes in hyposaline tolerance in the mussels *Mytilus edulis* and *M. trossulus*: implications for distribution. Marine Ecology Progress Series. 228:143-152.
- 50. RAWSON, P. D., and T. J. HILBISH. 1995. Evolutionary relationships among the male and female mitochondrial-dna lineages in the I species complex. Molecular Biology and Evolution. 12:893-901.
- 51. RAWSON, P. D., K. L. JOYNER, K. MEETZE, and T. J. HILBISH. 1996. Evidence for intragenic recombination within a novel genetic marker that distinguishes mussels in the *Mytilus edulis* species complex. Heredity. 77:599-607.
- 52. REISH, D. J., and J. L. AYERS, JR. 1968. Studies on the *Mutilus edulis* community in Alamitos Bay, California. Veliger. 11:250-255.

- 53. 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.
- 54. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
- 55. RIGINOS, C., and C. W. CUNNINGHAM. 2005. Local adaptation and species segregation in two mussel (*Mytilus edulis x Mytilus trossulus*) hybrid zones. Molecular Ecology. 14:381-400.
- SARVER, S. K., and D. W. FOLTZ. 1993. Genetic population structure of a species complex of blue mussels (*Mytilus* spp.). Marine Biology. 117:105-112.
- 57. SEED, R. 1992. Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. American Malacological Bulletin. 9:123-137.
- 58. SHANKS, A. L., and R. K. SHEARMAN. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. Marine Ecology Progress Series. 385:189-204.
- 59. —. 2011. Thread-drifting juvenile Mytilus spp. in continental shelf waters off Coos Bay, Oregon, USA. Marine Ecology Progress Series. 427:105-115.
- SINGH, G. G., and I. MCKECHNIE.
 2015. Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America. Journal of Archaeological Science. 58:175-183.
- 61. SMITH, J. R. 1982. A survey of endogenous dopamine and serotonin in ciliated and nervous tissues of five species of marine bivalves, with evidence for specific, high-affinity dopamine-receptors in ciliated tissue

of *Mytilus californianus*. Comparative Biochemistry and Physiology C: Toxicology & Pharmacology. 71:57-61.

- 62. SOO, P., and P. A. TODD. 2014. The behaviour of giant clams (Bivalvia: Cardiidae: Tridacninae). Marine Biology. 161:2699-2717.
- SUCHANEK, T. H., J. B. GELLER, B. R. KREISER, and J. B. MITTON.
 1997. Zoogeographic distributions of the sibling species *Mytilus galloprovincialis* and *M. trossulus* (Bivalvia: Mytilidae) and their hybrids in the north Pacific. Biological Bulletin.
 193:187-194.
- TAM, J. C., and R. A. SCROSATI. 2014. Distribution of cryptic mussel species (*Mytilus edulis* and *M. trossulus*) along wave exposure gradients on northwest Atlantic rocky shores. Marine Biology Research. 10:51-60.
- TOMANEK, L., and M. J. ZUZOW.
 2010. The proteomic response of the mussel congeners *Mytilus* galloprovincialis and *M. trossulus* to acute heat stress: implications for thermal tolerance limits and metabolic costs of thermal stress. Journal of Experimental Biology. 213:3559-3574.
- 66. TORO, J. E., R. J. THOMPSON, and D. J. INNES. 2002. Reproductive isolation and reproductive output in two sympatric mussel species (*Mytilus edulis*, *M. trossulus*) and their hybrids from Newfoundland. Marine Biology. 141:897-909.
- TURJA, R., N. HOEHER, P. SNOEIJS, J. BARSIENE, L. BUTRIMAVICIENE, T. KUZNETSOVA, S. V. KHOLODKEVICH, M. H. DEVIER, H. BUDZINSKI, and K. K. LEHTONEN. 2014. A multibiomarker approach to the assessment of pollution impacts in two Baltic Sea coastal areas in Sweden using caged mussels (*Mytilus trossulus*). Science of the Total Environment. 473:398-409.
- 68. TURJA, R., A. SOIRINSUO, H. BUDZINSKI, M. H. DEVIER, and K. K. LEHTONEN. 2013. Biomarker responses and accumulation of

hazardous substances in mussels (*Mytilus trossulus*) transplanted along a pollution gradient close to an oil terminal in the Gulf of Finland (Baltic Sea). Comparative Biochemistry and Physiology C: Toxicology & Pharmacology. 157:80-92.

- 69. VAINOLA, R., and M. M. HVILSOM. 1991. Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (Mytilidae, Mollusca). Biological Journal of the Linnean Society. 43:127-148.
- VAINOLA, R., and P. STRELKOV.
 2011. *Mytilus trossulus* in Northern Europe. Marine Biology. 158:817-833.
- VARVIO, S. L., R. K. KOEHN, and R. VAINOLA. 1988. Evolutionary genetics of the *Mytilus edulis* complex in the North Atlantic region. Marine Biology. 98:51-60.
- WOJCIK, D., M. NORMANT, B. DMOCHOWSKA, and A. FOWLER.
 2015. Impact of Chinese mitten crab *Eriocheir sinensis* on blue mussel *Mytilus edulis trossulus* laboratory studies of claw strength, handling behavior, consumption rate, and size selective predation. Oceanologia.
 57:263-270.
- 73. WOOD, A. R., A. R. BEAUMONT, D. O. F. SKIBINSKI, and G. TURNER. 2003. Analysis of a nuclear-DNA marker for species identification of adults and larvae in the *Mytilus edulis* complex. Journal of Molluscan Studies. 69:61-66.
- 74. ZBAWICKA, M., A. BURZYNSKI, D. SKIBINSKI, and R. WENNE. 2010. Scottish *Mytilus trossulus* mussels retain ancestral mitochondrial DNA: complete sequences of male and female mtDNA genomes. Gene. 456:45-53.
- 75. ZBAWICKA, M., A. BURZYNSKI, and R. WENNE. 2007. Complete sequences of mitochondrial genomes from the Baltic mussel *Mytilus trossulus*. Gene. 406:191-198.