Leukoma staminea

Rock cockle, littleneck clam, hardshell clam or Pacific littleneck

Phylum: Mollusca

Class: Bivalvia, Heterodonta, Euheterodonta

Order: Imparidentia, Venerida

Family: Veneroidea, Veneridae, Chioninae

Taxonomy: Confusion surrounds the appropriate genus for this species. Many species were designated as *Protothaca* (or subspecies thereof, e.g., *Protothaca (Protothaca) staminea,* Kabat and O'Foighil 1987; Lazo 2004), based on shell sculpture, and are likely the same species. Many researchers have thus adopted the older designated name, *Leukoma* (e.g., Groesbeck et al. 2014) for the species described below (see (Coan and Valentich-Scott 2007). However, some local guides (e.g., Brink 2001) and several publications also use *Protothaca staminea*. Other synonyms include *Vererupsis staminea, Protothaca restoriationensis, Paphia staminea* and variations var. *ruderata*, var. *orbella* (Deshayes; Carpenter).

Description

Size: Individuals 2–75 mm in length; average length is 25–50 mm (Ricketts and Calvin 1952; Kozloff 1993). Maximum length of 30.70 mm was reported for specimens collected in Prince William Sound, Alaska (Nickerson 1977).

Color: Overall color is variable. Young specimens often with brown markings like a brown checkerboard pattern on their shell (squares on each valve) (Kozloff 1993). Adults can be uniform brown, pinkish, or orange, with a white interior (Kozloff 1993)

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). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well developed hinge teeth. There are 22 local families, and members of the Veneridae have three cardinal teeth on each valve (see Plate 396H, Coan and Valentich-Scott 2007) (Fig. 2).

Body: (see Fig. 299, Kozloff 1993).

Color:

Interior: The ligament is external and seated on a nymph. The mantle edge is composed of four tentacular folds, the fourth of which is large, glandular and comprised of mucocytes. There is also a large dorsal ridge, which contains mucopolysaccharides and protein-secreting cells (Hillman and Bennett 1979).

Exterior:

Byssus:

Gills:

Shell: The shell is very heavy, *L. staminea* is sometimes called the rock cockle because of its strong radiating ridges (Ricketts and Calvin 1952).

Interior: Shell interior is porcelaneous and the ventral margin is with fine crenulate sculpture (Fig. 2). The muscle scars are almost equal and the pallial line is broken by a deep pallial sinus (Fig. 2). The file-like structure of the inside ventral margin is a distinct feature of this species (Kozloff 1993).

Exterior: The shell shape is sub-oval and heavy. There are numerous, fine, radiating ribs as well as concentric ridges. The radial ribs are more conspicuous for individuals that nestle within rocks, i.e., those found in pholad borings (Coan and Carlton 1975). Specimens often have differing shell shapes based on their different habitats (Fraser and Smith 1928).

Hinge: There are three compressed

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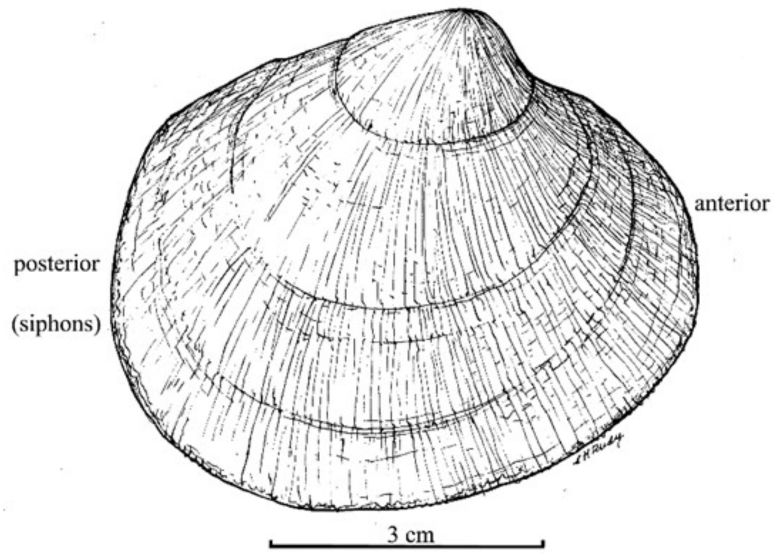
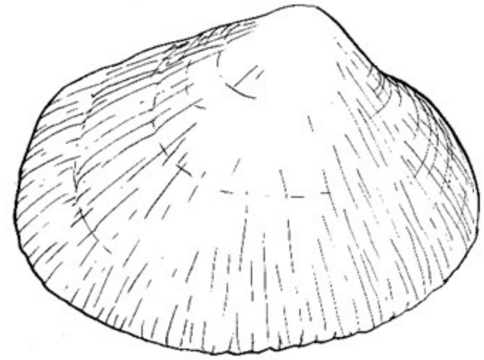
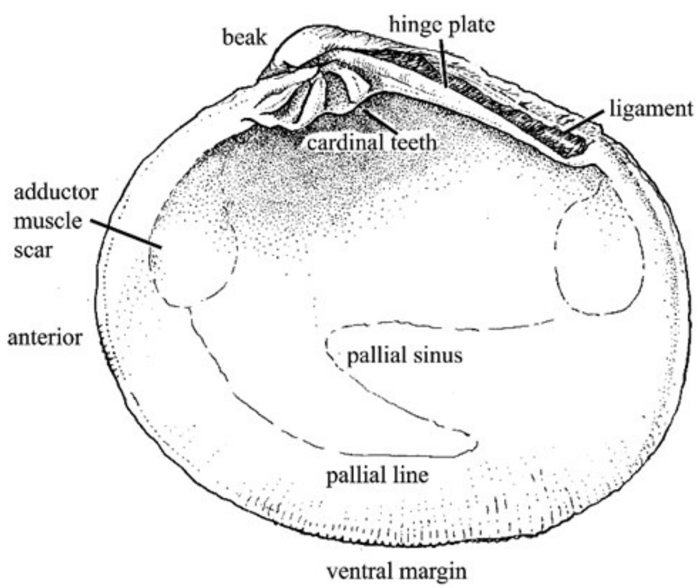


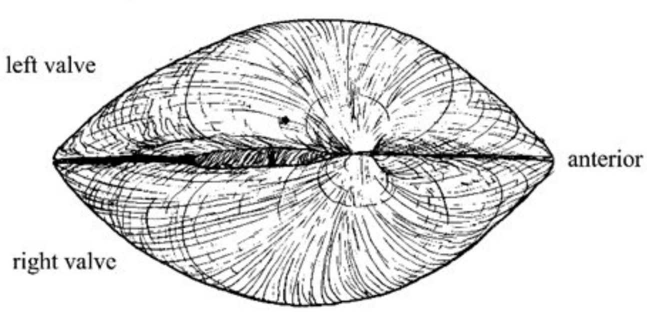
1. *Leukoma staminea*, exterior, right valve x1.5: many fine radiating ribs; concentric ridges also; shell suboval, heavy; posterior rounded.



1a. *Venerupis philippinarum* or *Ruditapes philippinarum (*Adams & Reeve, 1850) x1.5: introduced clam; elongate,strong radial ribs.



2. Interior, right valve: chalky, parcelaneous; ventral margin crenulate; muscle scars subequal; pallial sinus deep; hinge plate angled, ligamental external, on nymph; three cardinal teeth, no lateral teeth.



3. (Dorsal view)

Hiebert, T.C. 2015. *Leukoma staminea. In:* Oregon Estuarine Invertebrates: Rudys' Illustrated Guide to Common Species, 3rd ed. T.C. Hiebert, B.A. Butler and A.L. Shanks (eds.). University of Oregon Libraries and Oregon Institute of Marine Biology, Charleston, OR.

cardinal teeth in the hinge area and no lateral teeth. The hinge plate is wide and set at an angle (Fig. 2).

Eyes:

Foot:

Siphons: The siphons are short and fused (Kozloff 1993).

Burrow: *Leukoma staminea* is a poor digger, and thus does not live in sediments that require frequent digging (e.g., those that shift) (Ricketts and Calvin 1952); prefers clay (Ricketts and Calvin 1952). Burrows are less than 20 cm deep (Ricketts and Calvin 1952). Not always buried at all (Dunham et al. 2006). Can move and reburrow using their foot (Shaw 1986). Semi-infaunal to 10 cm in coarse sediment; burrowing rate depends on the sediment size, with faster burrowing in finer sediment (Alexander et al. 1993).

Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth, including most heterodonts. The family Veneridae is characterized by a hinge without lateral teeth, ligament that is entirely external, radial ribs on shell exterior, and three cardinal teeth on each shell valve. There are 12–16 species reported locally in this family within the genera *Nutricola*, *Saxidomus*, and *Leukoma*, with two species in each, and *Gemma gemma*), *Irusella lamellifera*), *Tivela stultorum*, *Venerupis philippinarum*, *Mercenaria mercenaria*, *Callithaca tenerrima*, each with a single species represented locally.

Nutricola species are small, with shells usually less than 10 mm in length. *Gemma gemma* also has a small shell, but it is triangular in shape compared to *Nutricola* species with elongate or oval shells. *Tivela stultorum* also has a triangular shell, but individuals are larger than *G. gemma* and have a smooth shell surface with shiny periostracum. *Nutricola tantilla* has a shell that is white in color and siphons that are fused (or nearly so) at the tips. *Nutricola confusa* has a shell that is purple in color, siphons that bear a conspicuous cleft as well as conspicuous anterior lateral teeth, which are weak in *N. tantilla*.

The remaining species have shells larger than 10 mm in length. Some species have shell sculpturing that is dominated by commarginal ribs with fine radial ridges and others have shells that have radial ridges with inconspicuous, or not predominating, commarginal ribs. Of those in the former category, *I. lamellifera* has widely spaced commarginal lamellae and a shell that is short compared to *M. mercenaria* and *C. tenerrima*. The two latter species have elongated shells, no anterior lateral teeth and valves that do not gape. *Saxidomus* species also have an elongate shell, when compared to *I. lamellifera*, but they possess anterior lateral teeth and valves that are separated by a narrow gape, posteriorly. *Saxidomus nuttalli* and *S. giganteus* can be differentiated as the former species has a elongate and thinner shell as well as a narrow escutcheon (not present in *S. giganteus*). The shell sculpturing in *S. giganteus* also appears smooth as the commarginal ribs are thin, low and tightly spaced, while the opposite is true for *S. nuttalli*.

The venerid species without predominately commarginal ribs include *Ruditapes philippinarum* (Adams & Reeve, 1850) (called *Venerupis philippinarum* in the most recent Light and Smith manual) and members of the genus *Leukoma*. *Leukoma* species differ from *R. philippinarum* by having an inner ventral margin that is not smooth (i.e., inner margin crenulated), a ligament that is not prominent and fused siphons. *Leukoma staminea* has shell sculpturing that is dominated by numerous radiating ribs, with faint commarginal ridges and the opposite is true for its congener (i.e., dominant radiating and commarginal ridges).

A closely related Venerid*, R. philippinarum* (Fig. 1a), has been introduced from Japan, and is common in mud of bays (Coan and Carlton 1975). It is elongate, oval, and has a prominently elevated ligament. Its radial ribs are quite strong and its color pattern distinctive. Its internal ventral margin is smooth, not crenulate, and its pallial sinus only moderately deep. Its internal color is yellowish with a purple stain. It lives at slightly higher elevations than does *L. staminea* and can grow to 50 mm in length (Washington, Haderlie 1980). Other bay clams of the same size and habitat as *L. staminea* lack both its radial and concentric sculpture.

Ecological Information

Range: Type locality is California (see Orr et al. 2013). Known range extends from the Aleutian Islands in Alaska to the Socorro Islands, Mexico. Previously known varieties of this species were divided into those north of San Francisco: var. *ruderata* (on beaches) and var. *orbella* (in pholad borings). Northern limit is Prince William Sound, Alaska (Feder et al. 1979).

Local Distribution: *Leukoma staminea* is a common clam in most of the larger Northwest estuaries and bays, and around rocky ocean outcroppings.

Habitat: Occurs in coarse sand as well as fine gravel with mud, stones, or shell (Kozloff 1974); seldom found in fine, pure sand (Fraser and Smith 1928). As it is a poor digger, *L. staminea* does not do well in shifting sand, but prefers packed mud, clayey gravel (Ricketts and Calvin 1971). Individuals usually found 3–8 cm below surface, or nestling into sand, rocks, and empty pholad holes (Coan and Valentich-Scott 2007). Both *L. staminea* and *Mytilus edulis* co-occur in Auke Bay, Alaska where their survival is negatively effected by burial depth (as little as 6 cm) and duration by bark chips from a log transferring facility (Freese and O'Clair 1987). A bioindicator species (e.g., Swartz et al. 1979; copper and copper-binding proteins Roesijadi 1980), *Leukoma staminea* survival and growth was also negatively effected by oil from the *Exxon Valdez* oil spill at least 5–6 years following the spill (Fukuyama et al. 2000; Fukuyama et al. 2014). Aside from the negative effect of hydrocarbon accumulation within clam tissues (see Thomas et al. 2007), Fukuyama et al. (2014) suggest that the removal of fine sediment associated with oil spill cleanup had a negative impact on *L. staminea* populations. However, when tested for the accumulation of hydrocarbons from crude oil, *L. staminea* (a suspension feeder) showed less uptake than deposit feeders (e.g., *Macoma inquinata* and *Phascolosoma agassizii*, Roesijadi et al. 1978). Interestingly, *L. staminea* individuals were also more likely to be preyed upon by *Cancer magister* in oiled habitats (Pearson et al. 1981). "Clam gardens", created adjacent to intertidal rock walls constructed by human populations in the Holocene, have four times as many *S. giganteus* and twice as many *L. staminea* individuals as non-walled beaches, and transplanted juveniles of the latter species also grow faster (1.7 times faster) in clam gardens (Groesbeck et al. 2014). Individuals may be both infaunal when found in mud and muddy sand or epifaunal among gravel, the latter habitat yielding the most damaged shells (Lazo 2004). Unlike the co-occurring bivalve, *Macoma balthica*, populations of *L. staminea* in Puget Sound, Washington showed genetic heterogeneity reflecting and potentially caused by the hydrology of the Puget Sound (Parker et al. 2003).

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: Intertidal and subtidal (Hancock et al. 1979); upper 20 cm of cobble, sand and mud (Kabat and O'Foighil 1987). Occurs from below half tide to lowest tideline (Puget Sound, Washington, Kozloff 1974). A range of +1.52 to -0.76 m was reported for individuals in Prince William Sound, Alaska (Nickerson 1977).

Associates: Often found with the cockle, *Clinocardium nuttallii*, and particularly with the butter clam, *Saxidomus giganteus* (Nickerson 1977). Often bored by drilling gastropods (Haderlie 1980). The majority (~70%) of *L. staminea* individuals collected from Cooper's Cove, British Columbia were infested with cysts from an apicomplexan parasite that were 20–150 μm in diameter (Desser and Bower 1997). *Leukoma staminea* and *S. giganteus* co-occur on Kiket Island, Washington, where the greatest diversity and richness of other marine invertebrates are found (Houghton 1977). Co-occurs with other clams (e.g., *Tresus capax* and *T. nuttallii*, Gillispie and Bourne 2004; *Sanguinolaria nuttallii*, Peterson and Andre 1980), but the presence of these species does not seem to effect *L. staminea* abundance (Peterson and Andre 1980). It has been suggested that the non-indigenous manila clam, *Venerupis philippinarum* is out-competing and replacing *L. staminea* in some habitats (British Columbia, Canada, Bendell 2014).

Abundance: *Leukoma staminea* is common; the most abundant clam of the lower intertidal in Puget Sound, Washington (Kozloff 1974). In a Coos Bay estimate (of the genus *Protothaca*) from 1975, Hancock et al., estimated there were 843,000 clams weighting 32.6 metric tons (Hancock et al. 1979). Also common in Tillamook Bay, but the density of individuals is light in Alsea, Siuslaw, and Netarts estuaries (Hancock et al. 1979). Can be very abundant with several individuals in one shovel full, and can even be raked from just under the sediment surface (Kozloff 1993). Individuals sometimes even on top of one another: "2 to 3 shovels full will yield enough clams to feed several hungry people" (Ricketts and Calvin 1952). In British Columbia beaches, assessed in 1993, *L. staminea* density was ranged from 0 to 180 individuals/m^2 (Gillispie and Bourne 2004). In 2006, low densities were reported (presumably due to over harvest) in British Columbia, Canada (up to 7 individuals/m^2, Dunham et al. 2006). Estimates of the total population of *L. staminea* at Chugachik Island, Alaska were determined for 1992, 1995, and 1996 as 7.2, 3.3, and 5.5 million clams, respectively. Of this total, 136,000, 65,000, and 115,000 kg were harvested commercially (Bechtol and Gustafson 1998).

Life-History Information

Reproduction: Dioecious (separate sexes), but some hermaphrodism occurs (Fraser and Smith 1928; Kabat and O'Foighil 1987). Spawning in Oregon occurs from April through August (Robinson and Breese 1982) and in February–March (Puget Sound, Washington and Sydney, British Columbia, Canada, Ricketts and Calvin 1952). Spawning has also been reported from April to September for the Strait of Georgia (Quayle 1943 in Kabat and O'Foighil 1987; Shaw 1986) and in January in Vancouver BC (Fraser 1929). Quayle (1943) reported that females may spawn several times during a season, while males release all gametes at once; while Feder et al. (1979) found females spawn from June–September and males from June–January in Prince William Sound, Alaska. Spawning in response to algal blooms has been reported for this species as well as *Saxidomus giganteus* (Robinson and Breese 1982). Gametes discharged through the siphon during spawning (Shaw 1986).

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). Free-swimming (Brink 2001) veliger larvae of *L. staminea* are found in the plankton after spawning from April to September through October (Strait of Georgia, Quayle 1943 in Kabat and O'Foighil 1987) and February in Vancouver, British Columbia (Kabat and O'Foighil 1987), and from April through October (Broughton Archipelago, British Columbia, Dunham et al. 2006). Ideal conditions for rearing larvae are 10–15˚C at salinities of 32. Larvae can survive at slightly higher temperatures (e.g., 20˚C) at the same salinity but higher temperatures and low salinity (e.g., 27) are lethal (Phibbs 1971). Trochophore larvae are 60–80 µm at 12 hours, straight-hinge veligers at 24 hours. Larvae have a ciliated velum and are 150 µm in length after 1 week, and an umbo when they are 260–280 µm in length at roughly 2 weeks. The total pelagic duration of *L. staminea* is 3 to 4 wks (Shaw 1986). At metamorphosis, larvae are 260–280 µm in length (Gillespie and Kronlund 199).

Juvenile: Gonads are apparent when juveniles are 1 mm in length, but sexes cannot be differentiated until they are 15–30 mm in length, a size reached by 2–3 years (Shaw 1986; Kabat and O'Foighil 1987). Individuals begin spawning after two years.

Longevity: A few individuals over seven years old were observed by Schmidt and Warme (1969). Mortality is greatest before sexual maturity (60%) and in old age (Schmidt and Warme 1969). Few clams are older than ten years (Fraser and Smith 1928), with a maximum age up to 13 (Shaw 1986) or 15 years (Nickerson 1977).

Growth Rate: Growth rate and age are determined by examination of rings caused by reduced growth in winter or different growth rates in different localities (but see Berta 1976). Growth is often slow in early years on exposed beaches, due to movement, storms, etc. and becomes more rapid in later years (the opposite may be true for individuals in protected sites). By the end of second year, specimens are 25 mm in length, and the third year, they are 35 mm (Fraser and Smith 1928). Clams were 47–54, 40–45 mm in length were estimated to be 6–8 and 3–7 years old at three sites in the Broughton Archipelago, British Columbia, Canada, respectively (Dunham et al. 2006). At three British Columbia beaches measured in 1993, individuals 25–50 mm in length were 3–7 years old, 30–64 mm were 3–9 years, and 29–46 were 3–8 years old; with individuals reaching 38 mm in length at four years of age (Gillispie and Bourne 2004). Legal catch size is 38 mm in length, which occurs when individuals are approximately 4–5 years old (Bechtol and Gustafson 1998; Gillispie and Bourne 2004). Growth rate decreases as intraspecific density increases (Peterson 1982). A length of 30 mm was achieved in 8 years (see also Fig. 4, Shaw 1986).

Food: A suspension feeder, with short siphons that necessitate feeding close to sediment surface. The ingestion and concentration of toxic algae (e.g., from the genera *Alex-*

andrium, *Gymnodinium*, *Pyrodinium*, Smolowitz and Doucette 1995) leads to paralytic shellfish poisoning, rendering the clams dangerous for human consumption (Ricketts and Calvin 1952).

Predators: Adults are often preyed upon by birds (e.g., diving ducks, Fukuyama et al. 2000), terrestrial animals (Fukuyama et al. 2000), and drilling gastropods (e.g., *Polinices lewisii*, Peitso et al. 1993; Grey et al. 2007), sea stars, fish (siphon nipping, Peterson and Quammen 1982), and see otters (Feder et al. 1979). Crabs, *Cancer productus,* forage for clams in areas where they are most dense (Boulding and Hay 1984; Boulding and Labarbera 1986), the European green crab, *Carcinus maenas* (Curtis et al. 2012), *Cancer magister* (Pearson et al. 1981; Juanes and Hartwick 1990), and *Cancer anthonyi* (Peterson 1983). *Leukoma staminea* is also an intermediate host to the "sporocysts of a Coccidia-like Apicomplexa" (see **Associates**, Desser and Bower 1997). Larvae are prey to planktonic predators and other suspension feeders. Common in coastal middens (~3-9 ka, Takesue and Geen 2004). A commercially harvested species, and populations were dramatically depleted in 1931 (Ricketts and Calvin 1952; Shaw 1986). A harvest as high as over 100,000 kg was reported in 1975 (Broughton Archipelago, British Columbia, Canada, Dunham et al. 2006). (see Bechtol and Gustafson 1998 for commercial summary). After this peak in 1975, landings decreased dramatically.

Behavior: A poor digger, *L. staminea* does not burrow vertically; the siphons and foot are short. Thus individuals remain close to surface of substrate and burrows easily horizontally (personal communication H. Van Veldhuizen).

Bibliography

1. ALEXANDER, R. R., R. J. STANTON, and J. R. DODD. 1993. Influence of sediment grain-size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. Palaios. 8:289-303.
2. BECHTOL, W. R., and R. L. GUSTAFSON. 1998. Abundance, recruitment, and mortality of Pacific littleneck clams *Protothaca staminea* at Chugachik Island, Alaska. Journal of Shellfish Research. 17:1003-1008.
3. BENDELL, L. I. 2014. Evidence for declines in the native *Leukoma staminea* as a result of the intentional introduction of the non-native *Venerupis philippinarum* in coastal British Columbia, Canada. Estuaries and Coasts. 37:369-380.
4. BERTA, A. 1976. An investigation of individual growth and possible age relationships in a population of *Protothaca staminea* (Mollusca: Pelecypoda). Paleobios. 21:1-26.
5. BOULDING, E. G., and T. K. HAY. 1984. Crab response to prey density can result in density-dependent mortality of clams. Canadian Journal of Fisheries and Aquatic Sciences. 41:521-525.
6. BOULDING, E. G., and M. LABARBERA. 1986. Fatigue damage: repeated loading enables crabs to open larger bivalves. Biological Bulletin. 171:538-547.
7. 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.
8. 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.
9. CURTIS, D. L., L. SAUCHYN, L. KEDDY, T. W. THERRIAULT, and C. M. PEARCE.

2012. Prey preferences and relative predation rates of adult European green crabs (*Carcinus maenas*) on various bivalve species in British Columbia, Canada. Canadian Technical Report of Fisheries and Aquatic Sciences. 3014:1-14,III.

10. DESSER, S. S., and S. M. BOWER. 1997. The distribution, prevalence, and morphological features of the cystic stage of an apicomplexan parasite of native littleneck clams (*Protothaca staminea*) in British Columbia. Journal of Parasitology. 83:642-646.
11. DUNHAM, J. S., B. KOKE, G. E. GILLESPIE, and G. MEYER. 2007. An exploratory survey for littleneck clams (*Protothaca staminea*) in the Broughton Archipelago, British Columbia - 2006. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2787:1-33.
12. FEDER, H. M., J. C. HENDEE, P. HOLMES, G. J. MUELLER, and A. J. PAUL. 1979. Examination of reproductive cycle of *Protothaca staminea* using histology, wet weight/dry weight ratios, and condition indexes. Veliger. 22:182-187.
13. FRASER, C. M., and G. M. SMITH. 1928. Notes on the ecology of the little neck clam, *Paphia staminea* Conrad. Transactions of the Royal Society of Canada, Section V, Biological Sciences, Third Series Part 1. XXII:249-269.
14. FREESE, J. L., and C. E. OCLAIR. 1987. Reduced survival and condition of the bivalves *Protothaca staminea* and *Mytilus edulis* buried by decomposig bark. Marine Environmental Research. 23:49-64.
15. FUKUYAMA, A. K., G. SHIGENAKA, and D. A. COATS. 2014. Status of intertidal infaunal communities following the Exxon Valdez oil spill in Prince William Sound, Alaska. Marine Pollution Bulletin. 84:56-69.
16. FUKUYAMA, A. K., G. SHIGENAKA, and R. Z. HOFF. 2000. Effects of residual Exxon Valdez oil on intertidal *Protothaca staminea*: mortality, growth, and bioaccumulation of hydrocarbons in transplanted clams. Marine Pollution Bulletin. 40:1042-1050.
17. GILLESPIE, G. E., and N. F. BOURNE. 2005. Exploratory intertidal bivalve surveys in British Columbia - 2004. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2734:1-144,VIII.
18. GREY, M., P. G. LELIEVRE, and E. G. BOULDING. 2007. Selection for prey shell thickness by the naticid gastropod *Euspira lewisii* (Naticidae) on the bivalve *Protothaca staminea* (Veneridae). Veliger. 48:317-322.
19. GROESBECK, A. S., K. ROWELL, D. L., and A. K. SALOMON. 2014. Ancient clam gardens increased shellfish production: adaptive strategies from the past can inform food security today. Plos One. 9.
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.
21. 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.
22. HILLMAN, R. E., and H. E. BENNETT. 1979. The fourth fold and secretory ridge of the mantle edge of the littleneck clam, *Protothaca staminea*. Proceedings National Shellfisheries Association. 69:195-195.
23. HOUGHTON, J. P. 1977. Age and growth of *Protothaca staminea* and *Saxidomus giganteur* at Kiket Island Washington, USA. Proceedings National Shellfisheries Association. 67:119-119.

24. JUANES, F., and E. B. HARTWICK. 1990. Prey size selection in Dungeness Crabs: the effect of claw damage. Ecology. 71:744-758.
25. 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.
26. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
27. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
28. LAZO, D. G. 2004. Bivalve taphonomy: testing the effect of life habits on the shell condition of the littleneck clam *Protothaca staminea* (Mollusca : Bivalvia). Palaios. 19:451-459.
29. NICKERSON, R. B. 1977. A study of the littleneck clam *Protothaca staminea* and the butter clam *Saxidomus giganteu*s in a habitat permitting coexistence, Prince William Sound, Alaska USA. Proceedings National Shellfisheries Association. 67:85-102.
30. ORR, J. W., D. T. DRUMM, R. VAN SYOC, K. P. MASLENIKOV, T. W. PIETSCH, D. E. STEVENSON, and R. R. LAUTH. 2013. An annotated checklist of bottom-trawled macroinvertebrates of Alaska, with an evaluation of identifications in the Alaska Fisheries Science Center Bottom-Trawl Survey Database. NPRB Project 1016 Final Report. North Pacific Research Board, Alaska.
31. PARKER, M. S., P. A. JUMARS, and L. L. LECLAIR. 2003. Population genetics of two bivalve species (*Protothaca staminea* and *Macoma balthica*) in Puget Sound, Washington. Journal of Shellfish Research. 22:681-688.
32. PEARSON, W. H., D. L. WOODRUFF, P. C. SUGARMAN, and B. L. OLLA. 1981. Effects of oiled sediment on predation on the littleneck clam, *Protothaca staminea*, by the Dungeness Cra, *Cancer magister*. Estuarine Coastal and Shelf Science. 13:445-454.
33. PEITSO, E., E. HUI, B. HARTWICK, and N. BOURNE. 1994. Predation by the naticid gastropod *Polinices lewisii* (Gould) on littleneck clams, *Protothaca staminea* (Conrad) in British Columbia. Canadian Journal of Zoology. 72:319-325.
34. PETERSON, C. H. 1982. The importance of predation and intraspecific and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecological Monographs. 52:437-475.
35. —. 1983. Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* and *Cancer anthonyi* (Rathbun). Journal of Experimental Marine Biology and Ecology. 68:145-158.
36. PETERSON, C. H., and S. V. ANDRE. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. Ecology. 61:129-139.
37. PETERSON, C. H., and M. L. QUAMMEN. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). Journal of Experimental Marine Biology and Ecology. 63:249-268.
38. 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.
39. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
40. ROESIJADI, G. 1980. Influence of copper on the clam *Protothaca staminea*: effects on gills and occurrence of copper-binding proteins. Biological Bulletin. 158:233-247.
41. ROESIJADI, G., J. W. ANDERSON, and J. W. BLAYLOCK. 1978. Uptake of hydrocarbons from marine sediments contaminated with Prudhoe Bay crude oil: influence of feeding type of test species and availability of polycyclic aromatic hydrocarbons. Journal of the Fisheries Research Board of Canada. 35:608-614.
42. SCHMIDT, R. R., and J. E. WARME. 1969. Population charactersitics of *Protothaca staminea* (Conrad) from Magu Lagoon, California. Veliger. 12:193-199.
43. SHAW, W. N. 1986. Species profiles, life histories and environmental requirements of coastal fishes and invertebrates: Pacific Southwest common littleneck clam *Protothaca staminea*. U.S. Fish and Wildlife Service Biological Report:I-VI, 1-11.
44. SWARTZ, R. C., W. A. DEBEN, and F. A. COLE. 1979. Bioassay for the toxicity of sediment to marine marcrobenthos. Journal Water Pollution Control Federation. 51:944-950.
45. TAKESUE, R. K., and A. VAN GEEN. 2004. Mg/Ca, Sr/Ca, and stable isotopes in modern and Holocene *Protothaca staminea* shells from a northern California coastal upwelling region. Geochimica et Cosmochimica Acta. 68:3845-3861.
46. THOMAS, R. E., M. LINDEBERG, P. M. HARRIS, and S. D. RICE. 2007. Induction of DNA strand breaks in the mussel (*Mytilus trossulus*) and clam (*Protothaca staminea*) following chronic field exposure to polycyclic aromatic hydrocarbons from the Exxon Valdez spill. Marine Pollution Bulletin. 54:726-732.

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