
Balanus glandula

Acorn barnacle

Phylum: Arthropoda, Crustacea

Class: Multicrustacea, Hexanauplia, Thecostraca, Cirripedia

Order: Thoracica, Sessilia, Balanomorpha

Family: Balanoidea, Balanidae, Balaninae

Description

Size: Up to 3 cm in diameter, but usually less than 1.5 cm (Ricketts and Calvin 1971; Kozloff 1993).

Color: Shell usually white, often irregular and color varies with state of erosion. Cirri are black and white (see Plate 11, Kozloff 1993).

General Morphology: Members of the Cirripedia, or barnacles, can be recognized by their feathery thoracic limbs (called cirri) that are used for feeding. There are six pairs of cirri in *B. glandula* (Fig. 1). Sessile barnacles are surrounded by a **shell** that is composed of a flat **basis** attached to the substratum, a **wall** formed by several articulated **plates** (six in *Balanus* species, Fig. 3) and movable **opercular valves** including **terga** and **scuta** (Newman 2007) (Figs. 2, 4, 5).

Shell:

Shape: Shell surrounding the barnacle body is pyramidal in shape (see Fig. 99, Kozloff 1993) (Fig. 2).

Basis: Calcareous and flat, attached to hard substrate, rendering *B. glandula* a sessile, or attached barnacle (Balanomorpha).

Wall: Formed by the six plates (Fig. 2) and composed of irregular, vertical, filled tubes, giving the exterior the appearance of rough ribbing.

Longitudinal Tubes: Only present in immature individuals (Newman 2007).

Plates: Calcareous, nearly conical and columnar. Six in family Balanidae. Each plate is composed of parietes (exposed triangular part) (Figs. 3a, 3b), alae

(the plate overlapping plate edges) and radii (the plate edge marked off from the parietes by a definite change in direction of growth lines) (Fig. 3b) (Newman 2007). The plates themselves include the carina, the carinolateral plates and the compound rostrum (Fig. 3).

Opercular Valves: Valves consist of two pairs of movable plates inside the wall, which close the aperture: the tergum and the scutum (Figs. 3a, 4, 5).

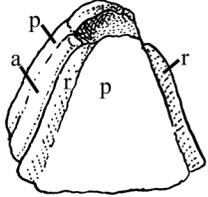
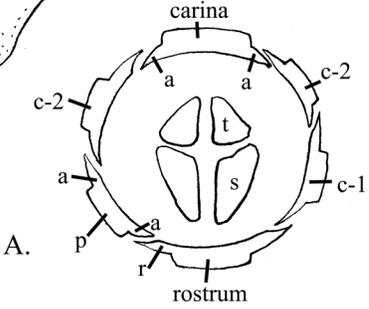
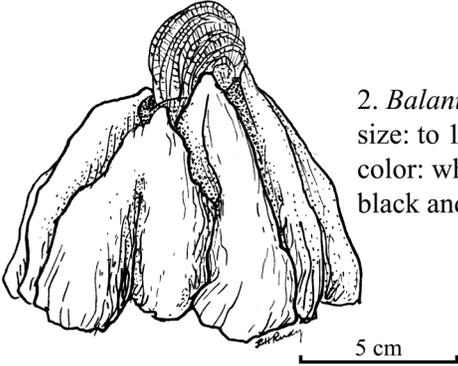
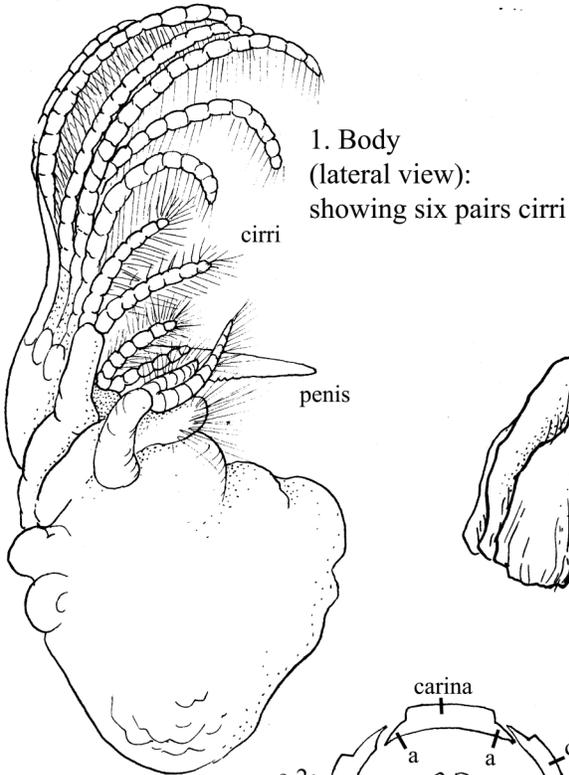
Scuta: The scuta have pits on either side of a short adductor ridge (Fig. 5), fine growth ridges, and a prominent articular ridge.

Terga: The terga are the upper, smaller plate pair and each tergum has a short spur at its base (Fig. 4), deep crests for depressor muscles, a prominent articular ridge, and an articular furrow (Pilsbry 1916).

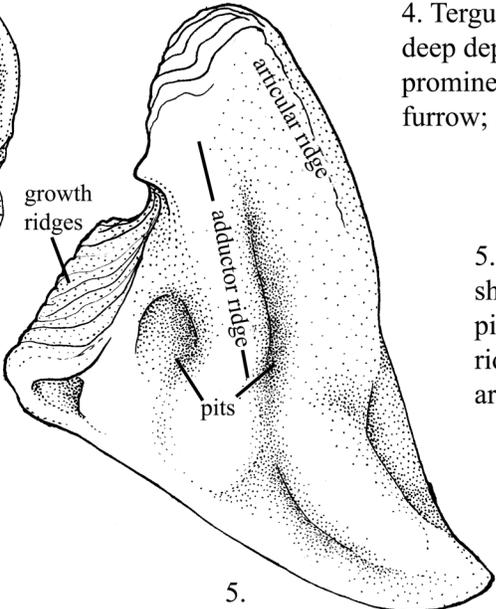
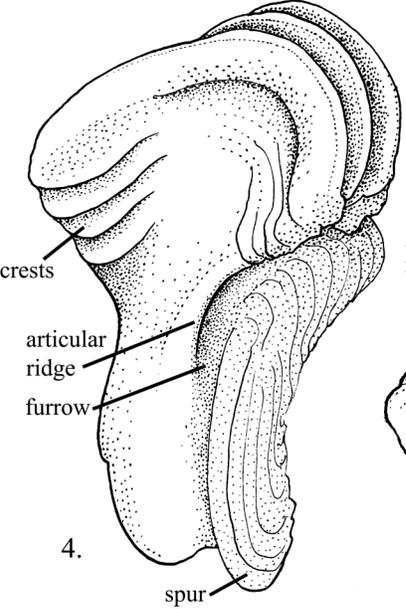
Aperture: The shell opening, from which the cirri emerge when feeding, is controlled by movement of the terga and scuta in conjunction with adductor and depressor muscles. When closed, plates produce a distinct and sinuous line at their junction in *B. glandula* (Kozloff 1993).

Cirri: Feathery, black and white and conspicuous. Each of the six pairs of legs (=cirri), bears 4–7 pairs of setae (Nishizaki and Carington 2014). The cirri of *B. glandula* were the first observed to exhibit ecophenotypic plasticity, where individuals adjusted response time (i.e. cirral withdrawal) to specific habitats. An adjustment from one habitat (e.g. wave-exposed) to the next (e.g. protected) occurred over a period of two molts (approximately 18 days) (Marchinko 2003).

Balanus glandula



B.



4. Tergum: deep depressor muscle crests; prominent articular ridge and furrow; short spur

5. Scutum: short adductor ridge with pit on each side; fine growth ridges, (exterior) prominent articular ridge

Possible Misidentifications

There are three groups (i.e. superorders) of cirripeds including the Rhizocephala (parasites among crustaceans), the Acrothoracica (shell-less burrowing forms), and the Thoracica. The Thoracica contains 1,000 species worldwide including the monophyletic taxa, Lepadomorpha, the stalked barnacles, and the Balanomorpha, or sessile barnacles (Perez-Losada et al. 2008; Chan et al. 2014). Among the sessile forms, there are four families represented locally. The family Chthamaloidea includes members of the genus *Chthamalus*. Juvenile *Balanus glandula* and *Chthamalus dalli*, often found together, are very alike. The genus *Chthamalus* has alae on its rostral plates, not radii (i.e. the rostral plate is overlapped, rather than underlapped, as in *B. glandula*, by the rostrolateral plates). *Chthamalus dalli* is found both with and at higher tide levels than *B. glandula*, and individuals are usually brown. The family Tetraclitoidea has one species locally (*Tetraclita rubescens*), and is characterized by a wall that is composed of four plates (rather than six in the Balanidae).

The remaining two families are the Balanidae and Archaeobalanidae. The Archaeobalanidae includes the genera *Armatobalanus*, *Conopea*, *Hesperibalanus* and *Semibalanus* (each with one local species). The latter genus includes a common local intertidal species *S. cariosus* (and former member of the genus *Balanus*). An isolated *S. cariosus*, is with splinter-like spines, nearly black cirri and is not likely to be confused with another barnacle. It has a thatched appearance, being irregularly ribbed and its walls have uneven, longitudinal tubes (Pilsbry 1916). However, where it is crowded or eroded, these spines may be worn off or not developed, and the barnacle would have to be distinguished from other common barnacles by its terga and scuta,

and by its unique and unusual membraneous base. *Semibalanus cariosus* have terga with a long pointed spur, quite different from either *B. crenatus* or *B. glandula*. *Semibalanus cariosus* commonly co-occurs with *B. crenatus*, *B. glandula*, as well as with *Chthamalus dalli*. Juvenile *S. cariosus* will show a typical heavy ribbing and starry basis outline, which would distinguish it from young *B. crenatus* or *B. glandula*. Generally, these latter two species are found higher in the intertidal than is *S. cariosus*, which occurs mostly subtidally.

Balanidae encompasses the genera *Megabalanus*, *Paraconcaucus*, and *Menesiniella* (each with one local species), *Amphibalanus* (three local species) and *Balanus* (four local species). *Balanus crenatus* is generally found in the intertidal at a lower level than the ubiquitous and morphologically similar *B. glandula*. *Balanus glandula* has no longitudinal wall tubes (except when young) and it differs in the structure of terga and scuta: the terga are very wide and have longer spurs and the scuta have no adductor ridges (compare Fig. 5 with *B. glandula* Figs. 4, 5, this guide). *Balanus crenatus*, on the other hand, has a shell wall with a single row of uniformly spaced tubes (Newman 2007). *Balanus crenatus* is a difficult barnacle to identify: "Not only does every external character vary greatly in this species, but the internal parts very often vary to a surprising degree, and to add to the difficulty, groups of specimens do not rarely vary in the same manner" (Charles Darwin in Cornwall 1951). *Balanus nubilus*, the giant acorn barnacle, is easily distinguished from *B. glandula* by its large size, reaching 100 mm in diameter, and a shell aperture that is relatively large and flaring (Newman 2007). *Balanus trigonus* is a lower intertidal species with a southern distribution (to Monterey Bay, California).

Ecological Information

Range: Type range includes Alaska to Baja California (Darwin 1854), *B. glandula* was introduced to South America (Argentina) and Japan (Kado 2003; Newman 2007; Rashidul Alam et al. 2014).

Local Distribution: Ubiquitous in a wide variety of locations from the open rocky shores to the salty or brackish bays of the Oregon coast (Kozloff 1993), where populations show genetic heterogeneity over great distances (Barshis et al. 2011), except in central California where gene flow is more restricted between populations (Sotka et al. 2004).

Habitat: Very adaptable to a variety of habitats. Suitable substrates include rocks, pilings, wood, other crustaceans, molluscs, and barnacles. Often in conditions with extreme exposure to sun, wind, rain and can tolerate estuarine conditions quite well, including those of poor water circulation, low oxygen, and little wave action (Ricketts and Calvin 1971). Populations in polluted areas have been shown to exhibit lower genetic diversity, with more individuals of the same haplotype (southern California, Ma et al. 2000).

Salinity: Collected at salinities of 30, but can also survive at lower salinities (Ricketts and Calvin 1971). *Balanus glandula* resists desiccation better than other *Balanus* species (Newman and Abbott 1980).

Temperature: Survives a wide range of temperatures, but optimal temperatures for feeding range between 10° and 15° C (Nishizaki and Carrington 2014).

Tidal Level: One of the most important zonation indicators as very small barnacles often settle high in the dry uppermost intertidal zone, below *Littorina* (Ricketts and Calvin 1971). Individuals are most common in the high to mid-tide zone (Darwin 1854) and their upper limit appears to be set by substrate temperature as *S. cariosus* and *B.*

glandula individuals showed a negative correlation in abundance with substrate temperature in the mid-intertidal (Salish Sea, Washington, Harley 2011).

Associates: Forms dense clusters with *Chthamalus dalli*, *Nucella*, mussels and limpets (including *Lottia digitalis*) at high tide levels (Kozloff 1993; Newman 2007). Sometimes found on larger *Balanus cariosus* individuals.

Abundance: One of the most abundant animals on the coast with up to 70,000 individuals per square meter (Ricketts and Calvin 1971). Larval abundance can also be high in the plankton, where 10 cyprids per 200 liters were reported in central California (Gaines et al. 1985).

Life-History Information

Reproduction: Cirripeds usually brood their eggs and *B. glandula* produces 2–6 broods/year, in winter and spring (Oct–May in southern California), and through September on Vancouver Island and December in Friday Harbor (Høeg et al. 1987). Barnacles are one of the few sessile organisms with internal fertilization and plasticity in penis length has been observed, with shorter penises in high wave-energy environments (Neufeld and Palmer 2008). Individuals are hermaphroditic and self-fertilization is possible, but not common (MacGinitie and MacGinitie 1949; Yonge 1963). Spermcast spawning can occur (Barazandeh et al. 2014). Eggs and embryos are retained in ovisacs within the mantle cavity and are discharged as nauplii after four months (Yonge 1963; Høeg et al. 1987; Arnsberg 2001). Ascorbic acid in water stimulates copulation (R. Boomer personal communication). For detailed reproductive anatomy see Høeg et al. (1987).

Larva: Cirriped broods hatch as nauplius larvae and undergo 4–6 naupliar stages, each larger and more setose than the last (Høeg et al. 1987; Arnsberg 2001; Chan et al. 2014).

Fewer setae occur on the antennae rami and mandibles in *B. glandula* nauplii beyond stage I than is seen in congeners (Brown and Roughgarden 1985). For naupliar setal formulae and antenna morphology, see Branscomb and Vedder 1982. Larvae molt to the second naupliar stage shortly after hatching (Branscomb and Vedder 1982). The generalized cirriped nauplius has a triangular or shield-shaped carapace with frontolateral horns and a conspicuous naupliar eye (Fig. 1, Arnsberg 2001; Figs. 22.1–22.2, Chan et al. 2014). In *B. glandula*, the nauplius has curved frontal horns and a 3-lobed labrum (Brown and Roughgarden 1985; Figs. 4 and 7, Arnsberg 2001). The first naupliar stage lasts less than an hour and stages 4–6 are recognizable by a pair of well-developed dorsal carapace spines (Arnsberg 2001). The sizes of *B. glandula* nauplii begin at 271 μm (stage I) and end at 745 μm (stage VI) (Brown and Roughgarden 1985). The final larval stage in cirripeds is called a cyprid, a non-feeding stage that attaches to a substrate by its antennae, secretes a cement and builds the adult calcareous shell (Ricketts and Calvin 1971). Cyprids are oblong and composed of a bivalve shell, six thoracic appendages, a pair of compound eyes and a conspicuous lipid reserve anteriorly (Fig. 3, Arnsberg 2001; Figs. 22.2–22.3, Chan et al. 2014). Cyprids prefer rough surfaces for settlement (Yonge 1963). Cyprid larvae in *B. glandula* are golden in color and have a distinct carapace shape and surface that is dull and decorated with papillae and four pigment patches, they are 640–780 μm in length and can be observed in the plankton year round except in winter months (Fig. 8, Arnsberg 2001). The pelagic larval duration in *B. glandula* is estimated at 3–4 weeks (Brown and Roughgarden 1985). Larval settlement is effected by degree of coastal upwelling, where more settlement is observed in years when upwel-

ling is weak and larvae stay closer to shore (Connolly and Roughgarden 1998; Barshis et al. 2011). Most larval settlement occurs in spring and autumn in Friday Harbor, Washington (Høeg et al. 1987), but may vary with sea temperature (e.g. January–June, Santa Barbara, California, Connell 1970). Where cyprids were abundant in the water column, settlement occurred at a rate of 2 cyprids per square centimeter of available space (Gaines et al. 1985). Like other marine invertebrate larvae, the cyprid larvae of *S. cariosus* and *B. glandula* become concentrated in convergence zones over internal waves, which provides a mechanism for shoreward transport of larvae prior to settlement (Shanks and Wright 1987).

Juvenile: Newly metamorphosed juveniles can be found settled in the intertidal from -0.6 meters to -0.3 meters and have six pairs of setae situated near and around the opercular opening (Høeg et al. 1987). The shell wall in juveniles consists of empty vertical tubes, which only become filled and irregular in the adult. Individuals from the upper tidal levels reach sexual maturity and spawn during their second year, while those from lower areas do so in their first year (Yonge 1963).

Longevity: 8–10 years (Newman and Abbott 1980).

Growth Rate: Cirriped body growth occurs in conjunction with molting (Kuris et al. 2007). Shell growth proceeds as follows (basal diameters): 7–12 mm in first year, 10–16 mm by the second year and 14–17 mm by three years (Newman and Abbott 1980). Adults under high densities form “hummocks” where individual barnacles grow tall and form tightly-packed columns (Bertness et al. 1998). Shell size (e.g. terga and scuta) may correlate with temperature (Barnes and Healy 1969). Those *B. glandula* that settle at lowest tidal heights grow fastest in the first year, but after that, those higher in the intertidal exhibit the fastest growth (Yonge 1963).

Food: Filter or suspension feeders (Nishizaki and Carrington 2014), barnacles eat plankton and some detritus, that is strained from incoming currents by several pairs of hydrostatically-extended thoracic appendages called cirri (Fig. 1) (MacGinitie and MacGinitie 1949).

Predators: Snail *Nucella* at low tide levels, as well as sea stars, worms (particularly on juveniles), birds and occasionally humans (e.g. Northwest Native Americas). Three snail species, *Thais emarginata*, *Thais canaliculata* and *Thais lamellose*, are also common predators of *B. glandula* and *S. cariosus* (Washington, Connell 1970). Furthermore, it has been suggested that predation by this genus of drilling gastropods has driven the evolution of balanomorph barnacle plate morphology (Palmer 1982). Predators on *B. glandula* larvae include many plankton feeders (e.g. fish, MacGinitie and MacGinitie 1949).

Behavior: Adults exhibit anti-predatory hiding behavior (i.e. withdrawal of cirral fan) in response to shadow (Dill and Gillet 1991). Cyprid larvae can actively search out settling area by “walking” on antennules, and adult distribution is at least in part determined by these pre-settlement behaviors and zonation in the plankton (Grosberg 1982; Gaines et al. 1985).

Bibliography

1. ARNSBERG, A. J. 2001. Arthropoda, Cirripedia: the barnacles. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press.
2. BARAZANDEH, M., C. S. DAVIS, and A. R. PALMER. 2014. Where even a long penis can't help: evidence of long-distance spermcast mating in two acorn barnacles. *Journal of Experimental Marine Biology and Ecology*. 454:49-54.
3. BARNES, H., and M. J. R. HEALY. 1969. Biometrical studies on some common cirripedes. II. Discriminate analysis of measurements on the scuta and terga of *Balanus balanus*, *Balanus crenatus*, *Balanus improvisus*, *Balanus glandula* and *Balanus amphitrite stuttsburi*, *Balanus pallidus stuttsburi*. *Journal of Experimental Marine Biology and Ecology*. 4:51-70.
4. BARSHIS, D. J., E. E. SOTKA, R. P. KELLY, A. SIVASUNDAR, B. A. MENGE, J. A. BARTH, and S. R. PALUMBI. 2011. Coastal upwelling is linked to temporal genetic variability in the acorn barnacle *Balanus glandula*. *Marine Ecology Progress Series*. 439:139-150.
5. BERTNESS, M. D., S. D. GAINES, and S. M. YEH. 1998. Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology*. 79:1382-1394.
6. BRANSCOMB, E. S., and K. VEDDER. 1982. A description of the naupliar stages of the barnacles *Balanus glandula* (Darwin), *Balanus cariosus* (Pallas), and *Balanus crenatus* (Bruguiere) (Cirripedia, Thoracica). *Crustaceana*. 42:83-95.
7. BROWN, S. K., and J. ROUGHGARDEN. 1985. Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia, Thoracica). *Journal of Crustacean Biology*. 5:574-590.
8. CHAN, B. K. K., J. T. HØEG, and R. KADDO. 2014. Thoracica, p. 116-124. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
9. CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs*. 40:49-78.
10. CONNOLLY, S. R., and J. ROUGHGARDEN. 1998. A latitudinal gradient in north-east Pacific intertidal community structure: Evidence for an oceanographically based

- synthesis of marine community theory. *American Naturalist*. 151:311-326.
11. DARWIN, C. 1854. A Monograph of the subclass Cirripedia (Part II Balandiae). Royal Society, London.
 12. DILL, L. M., and J. F. GILLETT. 1991. The economic logic of barnacle *Balanus glandula* (Darwin) hiding behavior. *Journal of Experimental Marine Biology and Ecology*. 153:115-127.
 13. GAINES, S., S. BROWN, and J. ROUGHGARDEN. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia*. 67:267-272.
 14. GROSBERG, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology*. 63:894-899.
 15. HARLEY, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science*. 334:1124-1127.
 16. HØEG, J. T., P. L. LIIG, R. R. STRATHMANN, and D. S. WETHEY. 1987. Phylum Crustacea, class Maxillopoda, subclass Cirripedia, p. 370-392. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 17. KADO, R. 2003. Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. *Marine Ecology Progress Series*. 249:199-206.
 18. 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.
 19. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 20. MA, X. L., D. L. COWLES, and R. L. CARTER. 2000. Effect of pollution on genetic diversity in the bay mussel *Mytilus galloprovincialis* and the acorn barnacle *Balanus glandula*. *Marine Environmental Research*. 50:559-563.
 21. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 22. MARCHINKO, K. B. 2003. Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* (Darwin)): magnitude, age dependence, and speed of response. *Evolution*. 57:1281-1290.
 23. NEUFELD, C. J., and A. R. PALMER. 2008. Precisely proportioned: intertidal barnacles alter penis form to suit coastal wave action. *Proceedings of the Royal Society B-Biological Sciences*. 275:1081-1087.
 24. NEWMAN, W. A. 2007. Cirripedia, p. 475-484. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
 25. NEWMAN, W. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Cirripedia: the barnacles. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, California.
 26. NISHIZAKI, M. T., and E. CARRINGTON. 2014. Temperature and water flow influence feeding behavior and success in the barnacle *Balanus glandula*. *Marine Ecology Progress Series*. 507:207-218.
 27. PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in Balanomorph barnacles. *Paleobiology*. 8:31-44.
 28. PEREZ-LOSADA, M., M. HARP, J. T. HOEG, Y. ACHITUV, D. JONES, H. WATANABE, and K. A. CRANDALL. 2008.

The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution*. 46:328-346.

29. PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. U.S. National Museum Bulletin. 93:1-366.
30. RASHIDUL ALAM, A. K. M., T. HAGINO, K. FUKAYA, T. OKUDA, M. NAKAOKA, and T. NODA. 2014. Early phase of the invasion of *Balanus glandula* along the coast of Eastern Hokkaido: changes in abundance, distribution, and recruitment. *Biological Invasions*. 16:1699-1708.
31. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
32. SHANKS, A. L., and W. G. WRIGHT. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *Journal of Experimental Marine Biology and Ecology*. 114:1-13.
33. SOTKA, E. E., J. P. WARES, J. A. BARTH, R. K. GROSBERG, and S. R. PALUMBI. 2004. Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology*. 13:2143-2156.
34. YONGE, C. M. 1963. The Sea shore. Atheneum, New York.

Updated 2015

T.C. Hiebert and M. Jarvis