

Physiological Ecology of Rocky Intertidal Organisms: A Synergy of Concepts¹

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SYNOPSIS. The rocky intertidal zone is among the most physically harsh environments on earth. Marine invertebrates and algae living in this habitat are alternatively pounded by waves and exposed to thermal extremes during low tide periods (Denny and Wethey, 2001). Additionally, they must deal with strong selective pressures related to predation and competition for space (Connell, 1961). As a result, the steep physical gradient and spatially condensed community has made the rocky intertidal zone an ideal “natural laboratory” to study the coupled role of physical and biological factors in determining the abundance and distribution of organisms in nature (Connell, 1961; Paine, 1966, 1994).

Early intertidal studies favored a major role of physiological adaptations to temperature and desiccation stress in determining patterns of vertical distribution (zonation) commonly found for intertidal organisms on rocky shores. It was shown that lethal limits of marine organisms correlated positively with the position of organisms along the physical gradient from the benign low-intertidal to the stressful high-intertidal zone, especially if differences in microhabitat and wave-exposure were taken into account (Gowanloch and Hayes, 1926; Orton, 1929; Broekhuysen, 1940; Evans, 1948). Zones characterized by indicator species appeared to correlate with shifts in the length of exposure to air, further supporting the potential role of physical factors in limiting distribution (Doty, 1946). The sharp distinction between some zones led Doty (1946) to conclude “Since the algae and their zones are sometimes, but rarely, intermixed and or arranged in these different orders, . . . , it seems unlikely that competition can be a factor in controlling vertical distribution.” However, it was also noticed that physical conditions in the field rarely exceed lethal physiological limits (Broekhuysen, 1940; Evans, 1948). These observations left unresolved the role of chronic sublethal stress or biological factors, *e.g.*, competition and predation, in setting distribution limits in the rocky intertidal zone (Wolcott, 1973).

Connell (1961) then demonstrated that interspecific competition between the two barnacles *Semibalanus* (previously *Balanus*) *balanoides* and *Chthamalus stellatus* was responsible for setting the lower limits of the vertical distribution range of the higher occurring *C. stellatus*. The influence of biological factors was further demonstrated by Paine, who showed that the lower limits of mussels beds of the species *Mytilus californianus* could be extended through the removal of the predatory seastar *Pisaster ochraceus* (Paine, 1974). Although these papers established the influence

of biological factors in setting distribution limits, Connell’s study also showed that *C. stellatus* was able to occupy a zone higher on the shore than *B. balanoides* due to its greater tolerance to heat and desiccation, which led him to conclude that: “The upper limits of most intertidal animals are probably determined by physical factors such as [heat and desiccation]. . . . However, evidence is accumulating that the lower limits of distribution of intertidal animals are determined mainly by biotic factors” (Connell, 1961).

Since these earlier studies, physiologists and ecologists have pursued somewhat different objectives: Physiologists were interested in testing the thermal limits of various physiological processes in intertidal organisms, *e.g.*, respiratory activity and oxygen uptake (Newell, 1979). Ecologists began to realize that the strength of species interactions, *e.g.*, predation and competition, in intertidal communities were often mediated by environmental stress (Connell, 1975; Menge and Sutherland, 1976, 1987). Physiologists summarized their progress, at least in part, during a symposium of the American Society of Zoologists (now the Society for Integrative and Comparative Biology) on the “Mechanisms of physiological compensation in intertidal animals” in 1988 (Ellington and McMahon, 1988).

During the last decade ecologists have become increasingly interested in the potential for using newly developed molecular and biochemical indicators of physiological state to study the relationships between physiological performance and population and community ecology in nature. Concomitantly, physiologists have tried to better understand the ecological importance of physiological, biochemical and molecular processes in setting distribution limits in the rocky intertidal zone. Technology and theory have now advanced to a point where a true integration of detailed physiological measurements and mechanistic ecology can be achieved. We thus felt that it was time to organize a symposium on the ecophysiology of rocky intertidal organisms, first, to summarize the recent, unprecedented collaborations between ecologists and physiologists in the field, and, second, to foster dialogue between both groups in hopes of addressing

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questions that could intensify and expand these collaborations. Our target audience is the beginning graduate student, and our goals are to summarize the state of the field of intertidal physiological ecology, and to emphasize the diversity of open questions that await investigation.

Within the last two decades it has become obvious that the paradigm that assumes that lower and upper vertical distribution limits in the intertidal are solely set by biological and physical factors, respectively, represents a rather oversimplified dichotomy (as does the distinction between the “benign” low-intertidal and the “stressful” high-intertidal zone). It is now apparent that vertical zonation, and community dynamics in general, are largely driven by the interplay between environmental stress and species interactions (Menge and Sutherland, 1987; Bertness and Callaway, 1994; Menge *et al.*, this volume). Several studies have shown that biological factors, like competition, are at least in part influenced by the physiological tolerance to physical factors such as heat and desiccation. For example, Wethey (1983, 1984, this volume) has shown experimentally that the relative competitive abilities of the barnacles *Semibalanus balanoides* and *Chthamalus fragilis* depend on *S. balanoides*' tolerance of stressful physical conditions in the high-intertidal zone. In the low-intertidal habitats it has been shown that levels of predation by the seastar *Pisaster ochraceus* on the mussel *Mytilus californianus* depend on relatively small changes in sea water temperatures that are caused by near shore upwelling events (Sanford, 1999, this volume). Considering the role that has been attributed to the interaction between *P. ochraceus* and *M. californianus* in determining intertidal communities (Paine, 1974), temperature may thus have a major indirect effect on community structure.

On the other hand, by considering the ecology and in particular the thermal niche that an intertidal organism occupies, physiologists have illustrated how close physiological tolerance limits are to actual body temperatures experienced under field conditions. Upper limits of *in vivo* heart rates of the mid- to high-intertidal porcelain crab *Petrolisthes cinctipes* are within 1–2°C of maximum ambient temperatures, suggesting that this species' physiological limits are very close to body temperatures it may experience under natural conditions (Stillman and Somero, 1996; Stillman, this volume). The thermal limits of the heat-shock (or stress) response and protein synthesis in general in the mid-intertidal turban snails *Tegula funebris* and *T. rugosa* have also been shown to be within 1°C to 3°C of temperatures typically experienced during low tide periods (Tomanek and Somero, 1999). These studies illustrate how close body temperatures are to the thermal limits of important physiological processes, again emphasizing the role of physical factors. They further point towards the potential strength of combined ecological and physiological approaches to predicting the potential consequences of climate change on intertidal

communities (Barry *et al.*, 1995; Southward, 1991; Southward *et al.*, 1995; Sagarin *et al.*, 1999).

Temperature has played a dominant role in assessing the importance of physical factors in setting the limits of vertical zonation patterns in rocky intertidal communities. However, only recently have we begun to explore the environmental determinants of body temperature in the intertidal, and to measure spatial and temporal patterns in thermal stress under field conditions (Bell, 1995; Helmuth, 1998, 1999; Helmuth and Hofmann, 2001; Tomanek, this volume). These studies have shown that patterns in the temperatures of intertidal organisms are often highly complex, and that often variability over spatial scales of meters can exceed those observed over a latitudinal gradient (Helmuth, this volume). Importantly, because heat exchange between intertidal organisms and their environment can vary markedly with size, their behavior and morphological adaptations, two organisms exposed to identical climatic conditions can experience very different body temperatures (Helmuth, 1998). These studies emphasize the strength of biophysical approaches as a means of providing an environmental context for physiological studies, and for exploring how ecological interactions in turn drive patterns in thermal stress (Denny and Wethey, 2001; Helmuth and Hofmann, 2001).

Physiologists have recently begun to use a new promising tool in studying sublethal heat stress in a group of proteins, the heat-shock (or stress) proteins, that respond to protein damage that is caused by temperature and other stress (Feder and Hofmann, 1999; Hochachka and Somero, 2002). Protein damage and the enhanced and often preferential synthesis of heat-shock proteins (called the heat-shock or stress response) occur at the upper end of the physiological temperature range an organism will tolerate. The potential importance of heat-shock proteins as markers for interspecific variation in heat tolerance was first demonstrated by Sanders *et al.* (1991) for intertidal limpets of the genus *Collisella* (now *Lottia*) that occupy different tidal heights. Subsequently, it was shown that the endogenous levels of one of the major heat-shock proteins with a molecular mass of 70 kDa (hsp70) as well as the onset temperature of heat-shock protein synthesis are subject to seasonal changes in intertidal mussel species of the genus *Mytilus* (Hofmann and Somero, 1995; Roberts *et al.*, 1997; Chapple *et al.*, 1998). A comprehensive comparison of the interspecific and acclimation-induced variation in the heat-shock responses of several species of the genus *Tegula* showed that several traits of the response correlate closely with patterns of vertical zonation found for temperate congeners as well as with differences in biogeographical distribution patterns (Tomanek and Somero, 1999, 2000, 2002; Tomanek, this volume). These studies also showed, first, that low-intertidal *Tegula* congeners are not able to synthesize heat-shock proteins at the extreme temperatures that are frequently experienced by mid-intertidal congeners, and, second, that the mid-intertidal congeners are likely to activate

the stress response frequently under natural conditions. Thus, these studies strongly suggest that there are substantial physiological costs for a marine invertebrate to cope with the thermal stress experienced in the rocky intertidal zone (also see Dahlhoff *et al.*, 2001; Tomanek and Somero, 2002). Recent work has also emphasized that we still have much to learn about the heat-shock response, particularly in terms of the effects of thermal history and small-scale spatial variation. For example, acute temperature exposures, which are preceded by periods of chronically hot conditions, may elicit a different physiological response than extreme days that are preceded by periods of relatively cool weather (Helmuth and Hofmann, 2001; Halpin, this volume; Tomanek, this volume). This ecologically important variation may in turn depend on how organisms differ in regulating the synthesis of heat-shock proteins (Buckley *et al.*, 2001; Tomanek and Somero, 2002; Hofmann, this volume; Tomanek, this volume). Furthermore, recent work by Rossi and Snyder (2001) has shown that stress proteins can also be induced solely through biological stressors such as competition for space. Again, we are reminded of the importance of considering that abiotic and biotic stresses often work in concert with one another in driving the physiological ecology of intertidal communities.

Unlike thermal stress, energetic costs or physiological responses imposed by mechanical stress (Denny and Wethey, 2001), for example as increased strength in byssal threads due to seasonal changes in wave force, have not been elucidated but are likely to significantly constrain reproductive output (Carrington, this volume). The assumed gradient in multiple physical factors, (*e.g.*, temperature, aerial exposure, time for feeding, wave conditions, etc.) along the transition from the subtidal towards the high-intertidal may determine the energetic constraints of intertidal organisms and may therefore dictate life history parameters, like time of reproduction, and size (Sebens, this volume).

However, energetic constraints in rocky intertidal communities in the form of nutrients may depend highly on interactions with other environments. Strong links between the productivity of near-shore pelagic environments, community structure and physiological state of intertidal organisms suggest that the organismal response towards heat and desiccation stress, as well as the strength of predation and competition may depend at least in part on bottom-up effects (Menge, 1992; Dahlhoff and Menge, 1996; Menge *et al.*, 1997; Dahlhoff *et al.*, 2001; Menge and Branch, 2001; Dahlhoff *et al.*, this volume).

Ecologists and physiologists alike have often neglected the genetic basis of the populations they have studied. Spatial variability in physical factors in the intertidal and along coastlines has been shown to be a strong enough selective force to cause genetic polymorphisms for a wide range of enzymes. Among the enzymes that show strong selection are allelic forms of aminopeptidase-I in *Mytilus edulis* that differ in

their rates of changing concentrations of free amino acids with varying levels of salinity. The allelic composition was shown to vary along a gradient in salinity in the Long Island Sound (Hilbish, 1985; Hilbish and Koehn, 1985). Aspartate aminotransferase was shown to be under selection in the marine snail *Littorina saxatilis* on exposed rocky shores in Sweden (Johannesson *et al.*, 1995) and allozyme variation in several enzymes was greater in protected than in exposed sites in dogwhelks, *Nucella lapillus*, in southwestern England (Day, 1990). Mannose-6-phosphate isomerase (*Mpi*) was found to be under selection from temperature and/or desiccation in the northern acorn barnacle *Semibalanus balanoides* (Schmidt *et al.*, 2000; Schmidt and Rand, 2001; Rand *et al.*, this volume). These studies demonstrate how environmental heterogeneity in the rocky intertidal zone on a spatial and temporal scale (Wethey, 1983, 1984; Helmuth and Hofmann, 2001) can influence the genetic structure of populations (Rand *et al.*, this volume), and lead to different physiological characteristics in conspecifics from different habitats. It is clear that intertidal biologists have yet to fully consider the ecological consequences of such genetic variation for most species of intertidal organisms.

Clearly, as an historical perspective shows (Benson, this volume), the study of biological and physiological factors in setting distribution limits has progressed towards a more complex understanding than anyone could have imagined only two decades ago. The tasks ahead are many: Physiologists have to find additional markers for sublethal stress that is typically experienced under natural conditions, and need to address the limitations of indicators that are already being used (Somero, 1995, 1997; Hochachka and Somero, 2002; Somero, this volume). Ecologists have to elucidate the role that physiological processes may play in mediating biological factors that in turn greatly affect community structure (Menge and Sutherland, 1987; Sanford, 1999; Dahlhoff *et al.*, 2001; Menge and Branch, 2001). Both physiologists and ecologists must be more cognizant of how abiotic stresses in the intertidal zone change in space and time, and need to more actively consider the role of temporal change in these parameters. The roles of biological and physical factors in the rocky intertidal zone also need to be studied in the greater context of the near-shore pelagic environment, especially because many populations depend on larval dynamics and recruitment (Morgan, 2001). Recent years have shown that the synergy that develops when concepts and approaches from ecology, physiology and population genetics are applied together can lead to a much improved understanding of a question that is elusive to the perspective of one biological discipline alone. The common goal of these diverse disciplines is to elucidate the spatial and temporal heterogeneity in the varying role of biological and physical factors, and to map these onto physiological and genetic indices. It will then be necessary to experimentally test or compare the strength and importance of

the various interactions. The rocky intertidal zone thus will continue to serve as a useful tool and "natural laboratory" for elucidating the role of physical and biological factors in determining the abundance and distribution of organisms in nature.

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REFERENCES

- Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267:672–675.
- Bell, E. C. 1995. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kützinger. *J. Exp. Mar. Biol. Ecol.* 191:29–55.
- Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9:191–193.
- Broekhuysen, G. J. 1940. A preliminary investigation of the importance of desiccation, temperature, and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. *Trans. R. Soc. South Afr.* 28:255–292.
- Buckley, B. A., M.-E. Owen, and G. E. Hofmann. 2001. Adjusting the thermostat: The threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. *J. Exp. Biol.* 204:2816–2829.
- Chapple, J. P., G. R. Smerdon, R. J. Berry, and A. J. S. Hawkins. 1998. Seasonal changes in stress-70 protein levels reflect thermal tolerance in the marine bivalve *Mytilus edulis*. *L. J. Exp. Mar. Biol. Ecol.* 229:53–68.
- Connell, J. H. 1961. The influence of intra-specific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In M. L. Cody and J. M. Diamond (eds.), *Ecology and evolution of communities*, pp. 460–490. Belknap Press, Cambridge.
- Dahlhoff, E. P., B. B. Buckley, and B. A. Menge. 2001. Physiology of the rocky intertidal predator *Nucella ostrina* along an environmental stress gradient. *Ecology* 82:2816–2829.
- Dahlhoff, E. P. and B. A. Menge. 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Mar. Ecol. Progr. Ser.* 144:97–107.
- Day, A. J. 1990. Microgeographic variation in allozyme frequencies in relation to the degree of exposure to wave action in the dogwhelk *Nucella lapillus* (L.) (Prosobranchia: Muricacea). *Biol. J. Linn. Soc.* 40:245–261.
- Denny, M. and D. Wetthey. 2001. Physical processes that generate patterns in marine communities. In M. D. Bertness, S. D. Gaines, and M. E. Hay (eds.), *Marine community ecology*, pp. 3–37. Sinauer Associates, Sunderland.
- Doty, M. S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. *Ecology* 27:315–328.
- Ellington, W. R. and B. R. McMahon. 1988. Introduction to the symposium: Mechanisms of physiological compensation in intertidal animals. *Amer. Zool.* 28:37–38.
- Evans, R. G. 1948. The lethal temperatures of some common British littoral molluscs. *J. Anim. Ecol.* 17:165–173.
- Feder, M. E. and G. E. Hofmann. 1999. Heat shock proteins, molecular chaperones, and the stress response: Evolutionary and ecological physiology. *Annu. Rev. Physiol.* 61:243–282.
- Gowanloch, J. N. and F. R. Hayes. 1926. Contributions of the study of marine gastropods 1. The physical factors, behavior, and intertidal life of *Littorina*. *Contr. Can. Biol. Fish.* 3:133–166.
- Helmuth, B. 1998. Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 68:51–74.
- Helmuth, B. 1999. Thermal biology of rocky intertidal mussels: Quantifying body temperatures using climatological data. *Ecology* 80:15–34.
- Helmuth, B. and G. E. Hofmann. 2001. Thermal heterogeneity and physiological gradients of stress in the rocky intertidal zone. *Biol. Bull.* 201:374–384.
- Hilbish, T. J. 1985. Demographic and temporal structure of an allele frequency cline in the mussel *Mytilus edulis*. *Mar. Biol.* 86:163–171.
- Hilbish, T. J. and R. K. Koehn. 1985. The physiological basis of natural selection at the LAP locus. *Evolution* 39:1302–1317.
- Hochachka, P. W. and G. N. Somero. 2002. *Biochemical adaptation: Mechanism and process in physiological evolution*. Oxford University Press, Oxford.
- 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*. *J. Exp. Biol.* 198:1509–1518.
- Johannesson, K., B. Johannesson, and U. Lundgren. 1995. Strong natural selection causes microscale allozyme variation in a marine snail. *Proc. Natl. Acad. Sci. U.S.A.* 92:2602–2606.
- Menge, B. A. 1992. Community regulation: Under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755–765.
- Menge, B. A. and G. M. Branch. 2001. Rocky Intertidal Communities. In M. D. Bertness, S. D. Gaines, and M. E. Hay (eds.), *Marine community ecology*, pp. 221–251. Sinauer Associates, Sunderland.
- Menge, B. A., B. A. Daley, P. A. Wheeler, E. P. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proc. Natl. Acad. Sci. U.S.A.* 94:14530–14535.
- Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *Amer. Nat.* 110:351–369.
- Menge, B. A. and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, and predation in relation to environmental stress and recruitment. *Amer. Zool.* 130:730–757.
- Morgan, S. G. 2001. The larval ecology of marine communities. In M. D. Bertness, S. D. Gaines, and M. E. Hay (eds.), *Marine community Ecology*, pp. 159–181. Saunders Associates, Sunderland.
- Newell, R. C. 1979. *Biology of intertidal animals*. Marine Ecological Surveys, Faversham, Kent.
- Orton, J. H. 1929. Observations on *Patella vulgata* Part III Habitat and habits. *J. Mar. Biol. Ass. UK* 16:277–288.
- Paine, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.* 100:368–378.
- Paine, R. T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120.
- Paine, R. T. 1994. Marine rocky shores and community ecology: An experimentalist's perspective. Ecology Institute, Oldendorf/Luhe, Germany.
- Roberts, D. A., G. E. Hofmann, and G. N. Somero. 1997. Heat-shock protein expression in *Mytilus californianus*: Acclimatization (seasonal and tidal-height comparisons) and acclimation effects. *Biol. Bull.* 192:309–320.
- Rossi, S. and M. J. Snyder. 2001. Competition for space among sessile marine invertebrates: Changes in HSP70 expression in two Pacific cnidarians. *Biol. Bull.* 201:385–393.
- Sagarin, R. D., J. P. Barry, S. E. Gilman, and C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* 69:465–490.

- Sanders, B. M., C. Hope, V. M. Pascoe, and L. S. Martin. 1991. Characterization of stress protein response in two species of *Collisella* limpets with different temperature tolerances. *Physiol. Zool.* 64:1471–1489.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–2097.
- Schmidt, P. S., M. D. Bertness, and D. M. Rand. 2000. Environmental heterogeneity and balancing selection in the acorn barnacle *Semibalanus balanoides*. *Proc. R. Soc. London B* 267: 379–384.
- Schmidt, P. S. and D. M. Rand. 2001. Adaptive maintenance of genetic polymorphism in an intertidal barnacle: Habitat- and life-stage-specific survivorship of *Mpi* genotypes. *Evolution* 55: 1336–1344.
- Somero, G. N. 1995. Proteins and temperature. *Annu. Rev. Physiol.* 57:43–68.
- Somero, G. N. 1997. Temperature relationships: From molecules to biogeography. In E. Danzler (ed.), *Handbook of physiology*, Section 13: *Comparative physiology*, Vol. II, pp. 1391–1444. Cambridge University Press, Cambridge.
- Southward, A. J. 1991. Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *J. Mar. Biol. Assoc. UK* 71:495–513.
- Southward, A. J., S. J. Hawkins, and M. T. Burrows. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J. Thermal Biol.* 20:127–155.
- Stillman, J. H. and G. N. Somero. 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): Correlation of physiology, biochemistry and morphology with vertical distribution. *J. Exp. Biol.* 199:1845–1855.
- Tomanek, L. and G. N. Somero. 1999. Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: Implications for limits of thermotolerance and biogeography. *J. Exp. Biol.* 202:2925–2936.
- Tomanek, L. and G. N. Somero. 2000. Time course and magnitude of synthesis of heat-shock proteins in congeneric marine snails (genus *Tegula*) from different tidal heights. *Physiol. Biochem. Zool.* 73:249–256.
- Tomanek, L. and G. N. Somero. 2002. Interspecific and acclimation-induced variation in levels of heat-shock proteins 70 (hsp70) and 90 (hsp90) and heat-shock transcription factor-1 (HSF1) in congeneric marine snails (genus *Tegula*): Implications for regulation of *hsp* gene expression. *J. Exp. Biol.* 205:677–685.
- Wetthey, D. S. 1983. Intrapopulation variation in growth of sessile organisms: Natural populations of the intertidal barnacle *Balanus balanoides*. *Oikos* 40:14–23.
- Wetthey, D. S. 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: A field experiment. *Biol. Bull.* 167:176–185.
- Wolcott, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): A critical look at "limiting factors." *Biol. Bull.* 145:389–422.