respiratory activity to increase without generating locomotion, but progressively higher currents led to proportional increases in respiration and fictive locomotion.

One of the cats spontaneously developed recurring episodes of fictive locomotion, each lasting about 10 seconds. With each episode, respiratory (phrenic) activity and frequency rose in association with the locomotor activity; in most cases the phrenic activity had begun its increase before the onset of biceps femoris nerve activity. Phrenic activity fell promptly when locomotor activity disappeared.

Our experiments demonstrate that automatic locomotion and proportional increases in respiration and arterial pressure, changes that mimic those of natural exercise, can be consistently evoked from a very restricted subthalamic region. The development of similar responses during spontaneous locomotion, which does not occur in the absence of the hypothalamus (*10*), indicates that the evoked responses are due not to fortuitous stimulation of independent pathways but rather to activation of a single hypothalamic mechanism.

Our crucial experiments are those in which both the respiratory and cardiovascular responses occurred during fictive locomotion in the absence of muscular contraction, since they show that actual exercise is not required to produce the responses and thus rule out the causative role of feedback from mechanical receptors in working muscles.

Other workers have reported similar qualitative respiratory or cardiovascular responses during spontaneous locomotion in decorticate cats (*10, 11*) and during electrical stimulation of the hypothalamus in both decorticate animals (*12*) and those with intact brains (*13*). The cardiovascular responses persist after muscular paralysis (*13*) and therefore do not depend on muscular contraction and metabolic changes. Our experiments confirm that the cardiovascular events are independent of muscular contraction.

Our study provides experimental validation of the Krogh and Lindhard feedforward hypothesis (*2*), except that we have shown that the motor cortex is not an essential part of the mechanism. We propose that neural command signals emanating from the hypothalamic locomotor region are primarily responsible for the approximately proportional driving of locomotion and respiration, as well as the cardiovascular adjustments associated with exercise.

Feedback controls are not required for the operation of this mechanism. Nevertheless, the participation of secondary feedback mechanisms during exercise in the intact animal cannot be disregarded. It is likely that they are involved in the fine control of both respiratory magnitude and frequency, and may be responsible for the demonstrated close tracking of ventilation and metabolic events during exercise (*14*).

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Mutualism Among Sessile Invertebrates: A Mediator of Competition and Predation

Abstract. *Hydroids of the genus* Zanclea *are epizoic on encrusting bryozoans. The bryozoans protect these hydroids with skeletal material.* Zanclea *polyps on the bryozoan* Celleporaria brunnea *sting small predators and adjacent competitors, helping* Celleporaria *to survive and to grow over competing species. This mutualism enables the two species to cover a larger area than they could individually.*

Space is an important limiting resource for many organisms. In marine benthic communities this is most evident for sessile invertebrates and algae inhabiting rocky substrates. For these organisms the habitat exists as discrete patches of limited area. Individuals (or colonies) are restricted to the particular substrate onto which their larvae settle and attach. Population size, survival, and reproductive output are all influenced by the amount of space that is occupied. Competition is often intense and involves the shading, undercutting, or overgrowth of one individual by another (*1-4*). Single species can dominate and sometimes monopolize a patch of substrate. This competitive dominance by one or a few species can be reduced by predators and through the physical disturbance of patches of habitat (*2, 5*).

Competition, predation, and physical disturbance are not the only phenomena that can regulate a species' use of spatial resources. Mutualism, in which two species positively affect one another's abundances, may be equally important (*6, 7*). Mutualistic associations between benthic species have been demonstrated (*3, 7, 8*), but infrequently. In studying the succession of marine invertebrate communities living on experimental panels (*9*), we found an example of mutualism between the bryozoan *Celleporaria* and the hydroid *Zanclea*. The bryozoan protects the hydroid by depositing $CaCO_3$ and the hydroid reduces the impact of competitors and predators on the bryozoan. This association improves the survival of both species and increases the amount of space that they can cover and hold.

Zanclea grow as vinelike colonies in which polyps with capitate tentacles

Table 1. Ability of *Celleporaria brunnea* with or without attached *Zanclea* to overgrow competing species. Asterisks denote one (*) or two (**) interactions in which successful overgrowth by the competing species was arrested after *Celleporaria* was colonized by *Zanclea*.

Competing species	Frequency of overgrowth by *Celleporaria* (successes/contacts)			
	Zanclea present		*Zanclea* not present	
	Overgrowth at line of contact	Overgrowth of whole colony	Overgrowth at line of contact	Overgrowth of whole colony
Bryozoa				
Parasmittina sp.	7/7	3/3	7/32	1/34
Rhynchozoon rostratum	2/3	2/2*	5/24	1/15
Alcyonidium parasiticum				0/16
Smittoidea prolifica		7/7		
Costazia robertsoniae				2/2
Polychaeta				
Salmacina tribranchiata	1/1*	2/2**	0/3	0/18
Porifera				
Leucosolenia eleanor				1/2
Total	10/11	14/14	12/59	5/87

arise individually from a basal network of stolons. All known species are epizoic on other benthic species (*10*), usually on cheilostome bryozoans (*11*). These bryozoan colonies encrust the substrate as a calcareous sheet.

In communities of sessile invertebrates the competitive dominants usually include species of bryozoans. These dominant bryozoans are seldom overgrown by other species. They also prevent metamorphosing larvae from attaching to their exposed frontal surfaces. These surfaces thus represent abundant "secondary" substrate that remains relatively free of sediments, debris, and other species. *Zanclea*, however, can penetrate the bryozoan's antifouling defenses and colonize this, competitor-free substrate.

We found two species of *Zanclea* that are obligate epizoites on bryozoans. In Vineyard Sound, Massachusetts, *Z. gemmosa* (*12*) was found exclusively on the bryozoan *Schizoporella errata* (*13*). On experimental panels, *Z. gemmosa* larvae attached themselves only to *Schizoporella* colonies. The hydroid did not appear to interfere with the normal activities of its host. Its basal stolons grew over the bryozoan's surface, never extending beyond the colony's edge unless another *Schizoporella* colony adjoined. The stolons usually followed the shallow grooves between zooids of the bryozoan colony and never grew over the zooidal apertures from which the lophophores (tentacular feeding organs) protrude. *Zanclea* feeds on microcrustaceans (*14*) and bryozoans feed on phytoplankton (*15*), so these species do not compete for food.

Schizoporella responds to the presence of *Zanclea* by depositing $CaCO_3$ underneath and around the basal stolons of the hydroid (Fig. 1), ultimately forming a tube from which the *Zanclea* polyps protrude. This pattern of calcification was observed only in the presence of *Zanclea* (*16*); stolons of other hydroids that occasionally grew on the *Schizoporella* colonies never caused the reaction. Although we do not know what specific stimulus is responsible for this pattern of $CaCO_3$ deposition, it clearly isolates the hydroid tissues from the bryozoan, protects the hydroid against physical damage and predation, and incurs some energy cost to the bryozoan. The fact that *Schizoporella* deposits additional $CaCO_3$ only in the presence of *Zanclea* suggests that the association is not merely fortuitous.

Along the coast of southern California (*17*) we found a second, unidentified species of *Zanclea* that is an obligate epizoite on the bryozoan *Celleporaria brunnea*. The relationship between these species is similar to that described for *Z. gemmosa* and *Schizoporella*. However, there are three differences. The surface of *Celleporaria* is more rugose than that of *Schizoporella*. This is because *Celleporaria*, upon maturity, undergoes a secondary calcification that obscures the regular arrangement of zooids and gives it a nodular appearance; the basal stolons of colonizing *Zanclea* are covered by this secondary calcification. Second, *Celleporaria* is not an absolute dominant; it is commonly overgrown by a variety of other species. Third, *Celleporaria* has a specific predator, *Hoploplana californica*, a cryptically colored flatworm (*18*). We examined the effects of *Zanclea*'s presence on the ability of *Celleporaria* to compete with other sessile invertebrates and to escape predation by *Hoploplana*.

Competition was measured as the frequency with which *Celleporaria* was able to overgrow other species on experimental panels (Table 1). Instantaneous measurements of overgrowth were taken at the line of contact between two colonies: the colony whose edge was covering zooids of the other colony was counted as having competed successfully. Long-term observations were also made by photographing the panels about every 6 weeks; the interaction between specific colonies was followed through time until one colony completely covered the other. Overgrowth of a large

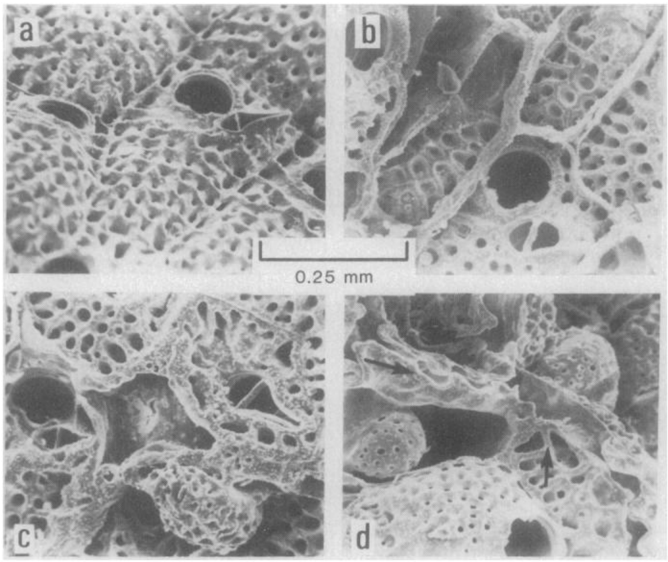

Fig. 1. Scanning electron micrographs of the $CaCO_3$ skeleton of *Schizoporella errata* with or without *Zanclea gemmosa*. Specimens were prepared with a 10 percent solution of chlorine bleach to remove all organic material. (a) Normal calcification of *Schizoporella* without *Zanclea*. (b) Portion of a *Schizoporella* colony with *Zanclea*, showing the added calcification around the basal stolons of *Zanclea*. Note that the stolons generally occur between zooids and do not pass over the zooidal apertures. (c) Opening in the calcification around the basal stolons through which a *Zanclea* polyp protruded. (d) Area of a colony with only partial calcification around the stolons. The arrow on the left indicates the forming suture between skeletal material deposited by two adjacent *Schizoporella* zooids. The arrow on the right indicates a raised area where additional deposition of $CaCO_3$ underneath the hydroid stolon is evident.

colony took up to 19 months; for interactions that were still incomplete at the end of the study, the colony on top was judged successful if it was continuing to advance over the other colony.

As shown in Table 1, when *Zanclea* was present on *Celleporaria* the bryozoan was clearly successful in growing over its competitors. When *Zanclea* was absent, *Celleporaria* was quickly overgrown. In several cases in which *Celleporaria* (without *Zanclea*) was being overgrown, subsequent colonization of the bryozoan by *Zanclea* resulted in the arrest or reversal of overgrowth.

On *Celleporaria* colonies without attached *Zanclea* the predatory flatworm *Hoploplana* was present at a density of 0.53 ± 0.06 per square centimeter (mean ± standard error; $N = 151$); the corresponding value for colonies with *Zanclea* is 0.18 ± 0.05 ($N = 20$). This difference is significant at $P < .05$ [$t(169) = 2.09$].

Zanclea probably uses the same mechanism both to aid *Celleporaria* in achieving dominance and to reduce the density of predators like *Hoploplana*. As a coelenterate, the hydroid possesses nematocysts (stinging cells) in its tentacles. Polyps of *Zanclea* have no supporting perisarc, rendering them flexible and contractile (they may be held erect or laid across the surface of the bryozoan colony). Thus it is possible for them to contact and repel or kill predators of *Celleporaria*. Furthermore, the polyps are often extended beyond the edge of the colony, allowing them to contact adjacent areas—that is, competitors. We took a series of measurements along the border between a *Celleporaria* colony with attached *Zanclea* and a colony of *Parasmittina* (a competing bryozoan) where a zone of discolored (moribund or dead) *Parasmittina* zooids was observed. The mean width of this zone (2.07 ± 0.15 mm; $N = 12$) was not significantly different from the mean length of the extended *Zanclea* polyps (2.32 ± 0.15 mm; $N = 12$) along the border. Finally, we observed the predatory nudibranch *Hermissenda crassicornis* being repelled repeatedly by *Zanclea*; upon contacting the tentacles of *Zanclea*, the nudibranch contracted and reversed its direction of movement. (*Hoploplana* also contracts when contacting *Zanclea* but, as we have seen, is not necessarily repelled.)

We conclude that the interaction between *Celleporaria* and *Zanclea* is mutualistic. In the presence of *Zanclea*, *Celleporaria* becomes a competitive dominant, and together the two species cover and hold a larger area than they could individually. The effects of this mutualism on competition and predation influence the distribution and survival of *Celleporaria*. Although *Celleporaria* colonized experimental panels at all localities, it was most abundant at those stations (3 of 20) where *Zanclea* was also present. At these three stations, the final mean abundance of *Celleporaria* on panels with *Zanclea* (30 ± 10 cm^2 per panel; $N = 5$) was significantly higher [$t(16) = 4.3$; $P < .001$] than its abundance on panels without *Zanclea* (2.5 ± 1.9 cm^2 per panel; $N = 13$). Similarly, the mean survival time of *Celleporaria* colonies with *Zanclea* (17 ± 4 months; $N = 9$) was significantly different [$t(98) = 7.7$, $P < .001$] than that of colonies without *Zanclea* (8 ± 3 months, $N = 91$). The evidence seems overwhelming that the ability of these species to utilize space is strongly affected, if not determined, by mutualism.

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12. The taxonomy of *Zanclea* is confused. Since the *Zanclea* on *Schizoporella* never developed a perisarc on the hydrocaulus, we call it *Z. gemmosa* rather than *Z. costata* or *Z. implexa*.
13. Observations were made on experimental panels (*4*), granite cobbles, bivalve shells, and *Schizoporella* nodules collected from depths of 0.5 to 15 m.
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17. Experimental panels were placed at 26 locations along the California coast between San Clemente and Oceanside (a distance of 30 km) at depths of 8 to 15 m. Replicate panels were initially exposed in June, September, and December 1978 and March 1979.
18. *Hoploplana* is usually much smaller than a *Celleporaria* colony and preys on only a few zooids at a time.
19. We thank C. Mann, J. Deacon, R. Day, and T. Dean for field assistance and helpful comments. This work was supported by grants from the Marine Review Committee of the California Coastal Commission. Scanning electron microscope facilities and support were supplied to R.W.O. by the Geology Department at Northern Illinois University.

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