Brachiopods versus Mussels: Competition, Predation, and Palatability

Abstract. *Unlike other shell-enclosed marine invertebrates, articulate brachiopods are repellent to predators. Fish, sea stars, snails, and crabs all prefer bivalve molluscs such as mussels to articulates. The mussels tested are mobile and outcompete immobile articulates when space is limited. In subtidal field experiments, mussels alone and predators alone each reduced the survivorship of articulates. However, adding mussels to articulates in the presence of ambient predation increased brachiopod survivorship by diverting predation from the brachiopods to the mussels. Competition from mussels (or mussel-like bivalves) is a plausible cause of the post-Paleozoic decline of articulates.*

Articulate brachiopods are the most abundant macroscopic fossil animals of the Paleozoic. In later deposits they are relatively rare and bivalved molluscs are usually the most abundant shelled benthos. The decline of the class Articulata has attracted much speculation. Both predation (*1, 2*) and competition with bivalved molluscs (*3, 4*) have been invoked, but no controlled experiments have tested the extent to which either factor determines the present status of articulates.

Articulate brachiopods and mussels are likely to compete with each other and be eaten by the same predators. Both are suspension feeders and often live on the surface of hard substrates. They occur together throughout the world (*5, 6*). Articulates dominate the macrobenthos in certain boreal (*7, 8*) and austral habitats (*9*). In Washington and British Columbia, I worked with four widespread genera representing two orders and three superfamilies (*10, 11*): *Hemithiris psittacea, Terebratalia transversa, Laqueus californianus*, and *Terebratulina unguicula*.

In laboratory experiments invertebrate and vertebrate predators showed a statistically significant preference for bivalves instead of articulates. Ten species of snails, seven starfish, three crabs, and eleven fishes were tested (*12*) because of their presence in brachiopod habitats, ability to consume shelled prey, abundance, and availability.

Ten individuals of each invertebrate predator were given a simultaneous choice of 12 mussel valves (6 *Mytilus edulis* and 6 *Modiolus rectus*) and 12 articulate valves (4 *Terebratalia*, 4 *Terebratulina*, and 4 *Laqueus*), all about the same size, with meat "on the half-shell." Individual fish (n = 44) were offered the shell-free meats of single bivalves (*M. edulis* and *M. rectus*) and articulates in alternating sequence (*13*). They often convulsed and regurgitated articulates.

Repellency aside, articulates yield a poor return for a predator's efforts. The ash-free dry weight of *Terebratalia* is only 3 percent of live weight, compared to 10 percent for *Modiolus demissus* (*14*). The claim that small size made articulates preferred prey (*1, 2, 15*) is inconsistent with the idea that predators maximize their rate of feeding (*16*). The argument that articulates are more vulnerable to predation than bivalves because of thinner shells (*1, 2*) becomes moot if the contents are repellent.

Competition, especially with mussels, is likely to limit the occurrence of articulates. Mussels are dominant competitors on rocky shores, but predation usually restricts their monopoly to the intertidal zone (*17, 18*). The mobility of mussels (*19, 20*) gives them a major advantage over the sessile articulates. For example, *M. edulis* climbs upward, avoiding predation and fouling by its own copious feces, and usually vacates the shady overhangs (*17*) favored by articulates (*21, 22*). *Mytilus edulis* engulfed a clump of *Terebratalia* suspended above them within hours; in this laboratory experiment, anaerobic mussel feces fouled the articulates and three of ten were dead after 3 days (*23*).

In subtidal cage experiments, the effects and the interaction of competition and predation were assessed. I transplanted articulates to trays, 79 to 86 brachiopods per tray. To evaluate predation, three different cage treatments were used: a complete cage excluded ambient predation, a cageless treatment admitted predators, and a partial cage (top only, no sides) allowed predator access while controlling for other effects of cages. To assess the interaction of predation and competition, each of the three cage (predator) treatments was conducted in three different forms: brachiopods only, a monolayer of *Mytilus edulis* covering brachiopods and tray, and likewise with *Modiolus rectus*. A single experiment thus used nine total treatments, one tray per treatment. The experiment was repeated twice so that a total of about 1480 individual brachiopods was used (*24*).

I also measured predation in the absence of mussels by bolting "cages" over more than 1700 in situ brachiopods (mostly *Terebratulina*) on a rock wall. The same treatments were used: complete cage, none, and partial cage. Three replications produced a total of nine treatments (*25*).

The transplanted brachiopods (Table 1) showed significantly reduced survivorship in the presence of mussels, probably because mussels smothered them. There were no live articulates ($n > 100$) beneath mussels at the end of the experiment. Comparing this result with the

Table 1. Survivorship of articulates in field transplants. Values are for two replications at site 1 and site 2. Each value represents a single treatment (tray) with about 80 articulates. Blanks indicate lost treatments. Statistically significant effects are mussels present versus none at both sites and, at site 2, *Mytilus* versus *Modiolus* (reflecting greater mobility of *Mytilus*) and interaction of cage treatment with mussels (*37, 38*).

Cage	Survivorship (%)			Overall
	No mussels	*Mytilus*	*Modiolus*	
None	48, 36	31, 17	29, 64	36, 38
Partial	66	16, 14	42, 46	41, 29
Complete	56, 80	14	22, 32	29, 56
Overall	57, 58	19, 15	31, 47	35, 41

Table 2. In situ caging experiment showing articulate survivorship during 1 year. Values represent the mean ± 1 standard deviation (arcsine-transformed) for three replications. The same letter indicates values that are not significantly different (*38*).

Cage	Survivorship (%)	
	Terebratulina	*Laqueus*
	(n = 1615)	(n = 167)
None	57.9 ± 3.6 a	10.0 ± 9.1 c
Partial	55.2 ± 13.6 a	20.6 ± 17.7 c
Complete	93.6 ± 0.5 b	88.2 ± 3.2 d

lowest survivorship in any mussel-free treatment (36 percent) shows significantly increased mortality of articulates under mussels (*26*). Snails and starfish ate mussels, thereby increasing the survivorship of articulates (that is, significant interaction of cage and mussel treatments). Drilled mussels were observed beside live, undamaged articulates.

The in situ experiment lacked mussels to divert predation, and predators reduced survivorship of articulates (that is, the complete cage increased survivorship) (Table 2). Starfish were seen eating articulates. Brachiopods are apparently the only marine benthos with repellent shell-protected tissue (*27*). Other benthos are eaten despite shells (*28*) but have not evolved the added protection of repellency.

The ubiquity of Paleozoic articulates has been used as evidence both for and against their role as prey (*29*). Growing evidence (*30, 31*) of significant predation well in advance of the Mesozoic "revolution" (*32*) suggests that Paleozoic articulates may have evolved a repellent. Paleozoic articulates were abundant on unconsolidated bottoms, but accelerating biogenic disturbance of these sediments probably restricted them to hard substrata (*31, 33*), where they were outcompeted by epifaunal mussels that diversified during the late Paleozoic (*34*). If Paleozoic articulates were repellent, the evolution of numerous new predators in the Mesozoic may have aided the articulates in this competition and prevented some articulate extinctions.

The interactions reported here probably have a long history. *Modiolus* is known from the Devonian and *Mytilus* from the Jurassic (*11*). Although uniformitarianism must be cautiously applied, other ancient mussels were probably similar in their ability to detach, crawl with the foot, and reattach by a byssus. Articulates are immobile and cannot reattach if removed from the substrate (*7, 22*). Although mobility has surely varied within each group (*19, 35*), it seems likely that, on average, mussels (and ecologically similar bivalves) have always had a superior ability to relocate, and hence superiority in competition for space.

In the "stochastic" (*36*) view of Gould and Calloway (*3*), bivalves and brachiopods evolved like "ships that pass in the night." I suggest a more "deterministic" history: a long-term competitive interaction mediated by predators that found articulate brachiopods distasteful.

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12. $P < 0.005$ except *$P < 0.05$ and **$P < 0.0125$; χ^2, 2 by 2 contingency table of eaten versus not eaten by bivalves versus brachiopods. Numbers in parentheses represent number of bivalves and brachiopods eaten, respectively; †tested with *Hemithiris*, ten of each invertebrate predator, one of each fish; ‡single fish; otherwise two to ten fish. Gastropods: *Amphissa columbiana* (12, 0.5), *Boreotrophon* spp. (9.5, 0), *Ceratostoma foliatum* (8, 0), *Fusitriton oregonensis* (12, 0), *Neptunia lirata* (12, 0), *Ocenebra lurida* (12, 0), *Searlesia dira* (12, 0), *Thais canaliculata* (7, 0), *T. emarginata* (9, 0), and *T. lamellosa* (7, 0). Asteroids: *Dermasterias imbricata* (12, 6), *Evasterias troschelii* (12, 6), *Leptasterias hexactis* (12, 2), **Orthasterias koehleri† (7.5, 2.5), *Pisaster ochraceus* (12, 2), *Pycnopodia helianthoides* (12, 5), and *Solaster stimpsoni* (ate 12 *Cucumaria*, its normal prey, 0 bivalves, and 0 brachiopods). Crabs: *Cancer magister* (12, 3), *C. oregonensis* (12, 2.5), and *C. productus*† (12, 1). Fish: *Citharichthys sordidus*† (4, 0), *Hemilepidotus hemilepidotus*† (9, 0), *Hexagrammos decagrammus*† (36, 6), **H. stelleri† (2, 0), *Hippoglossoides elassodon* (17, 5.5), *Isopsetta isolepis*† (5, 0), *Lepidopsetta bilineata* (6, 1), *Leptocottus armatus* (13, 1), *Parophyrys vetulus‡ (4, 1), *Platichthys stellatus*† (36, 11.5), and *Sebastes caurinus*† (38, 20).
13. Sequence included infaunal (hence unfamiliar) bivalves (*Humilaria kennerlyi* and *Protothaca staminea*), which were eaten, thus controlling for unfamiliarity of brachiopod prey. The rejection of *Hemithiris*, which lacks an internal skeletal loop, and acceptance of bivalves with shell fragments controlled for the presence of the loop in terebratulids. Rejections of brachiopods were counted only if acceptance of a bivalve followed.
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23. Normal lab mortality was less than 1 percent ($n > 100$).
24. Brachiopods were glued to trays by still-attached natural substrata. Each tray contained all four species in the same proportion, spaced regularly and not in contact. I set transplants in San Juan Channel, Wash., at sites with indigenous *Terebratalia* at depths of 10 to 17 m and censused them in the laboratory in September 1976 and July 1977. Trays were horizontal, brachiopods up. Cages used moats so that upwardly mobile mussels would not climb the walls and terminate the interaction.
25. Saanich Inlet, B.C., at depths of 17 to 21 m., some *Laqueus* and a few *Terebratalia* included. Photocensused in August 1977 and August 1978. Each partial cage had a top and two sides only. These and transplant cages were cleaned about monthly to reduce shading, current baffling, and sedimentation. ANOVA showed no statistically significant cage treatment effects, and survivorship of articulates increased in cages without mussels (sediment and reduced current should inhibit sessile suspension-feeders).
26. Analysis in 2 by 2 contingency table with mussels versus no mussels by number surviving versus number dying (χ^2, $P < 0.005$).
27. I exclude food-derived, reproductive, and predatory toxins. *Anomia* may be an exception [M. P. Carriker, *Malacologia* **20**, 403 (1981)] but the repellent tentacles of *Lima* cannot be housed in the shell [T. H. J. Gilmour, *J. Mar. Biol. Assoc. U.K.* **47**, 209 (1967)], and limpets [J. M. Watanabe, *J. Exp. Mar. Biol. Ecol.* **71**, 257 (1983)] are not totally enclosed. *Crania* (Inarticulata) from British Columbia is repellent (M. LaBarbera, personal communication).
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37. ANOVA for preplanned comparison of arcsine-transformed data ($P < 0.05$). The mussel-cage interaction was assumed to be the same for both species of mussel in order to reserve some degrees of freedom for error. The effect of a partial cage is not significantly different from that of no cage [$F(2, 4) = 0.322$, $P > 0.5$], so to gain degrees of freedom, this sum of squares is pooled with the residual, and the residual sum of squares for the two sites is pooled.
38. Differences between replications probably reflect chance discovery by predators and other heterogeneities of the natural environment.

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