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ARTICULATE BRACHIOPOD FOOD

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Abstract—New evidence suggests that the mode of feeding of articulate brachiopods may be the same as that of ciliary suspension feeders, such as bivalve mollusks, but may vary according to the abundance of food or according to depth. Gut contents of four genera of articulate brachiopods and two genera of bivalve mollusks from both shallow (8–13 m) and deeper (100–120 m) areas were analyzed for relative proportions of inorganic versus organic particulate matter. Although the relative proportion of inorganic versus organic particulates varied between depths, it remained essentially identical for both the articulate brachiopods and bivalves at any given depth, indicating a similarity in their mode of feeding.

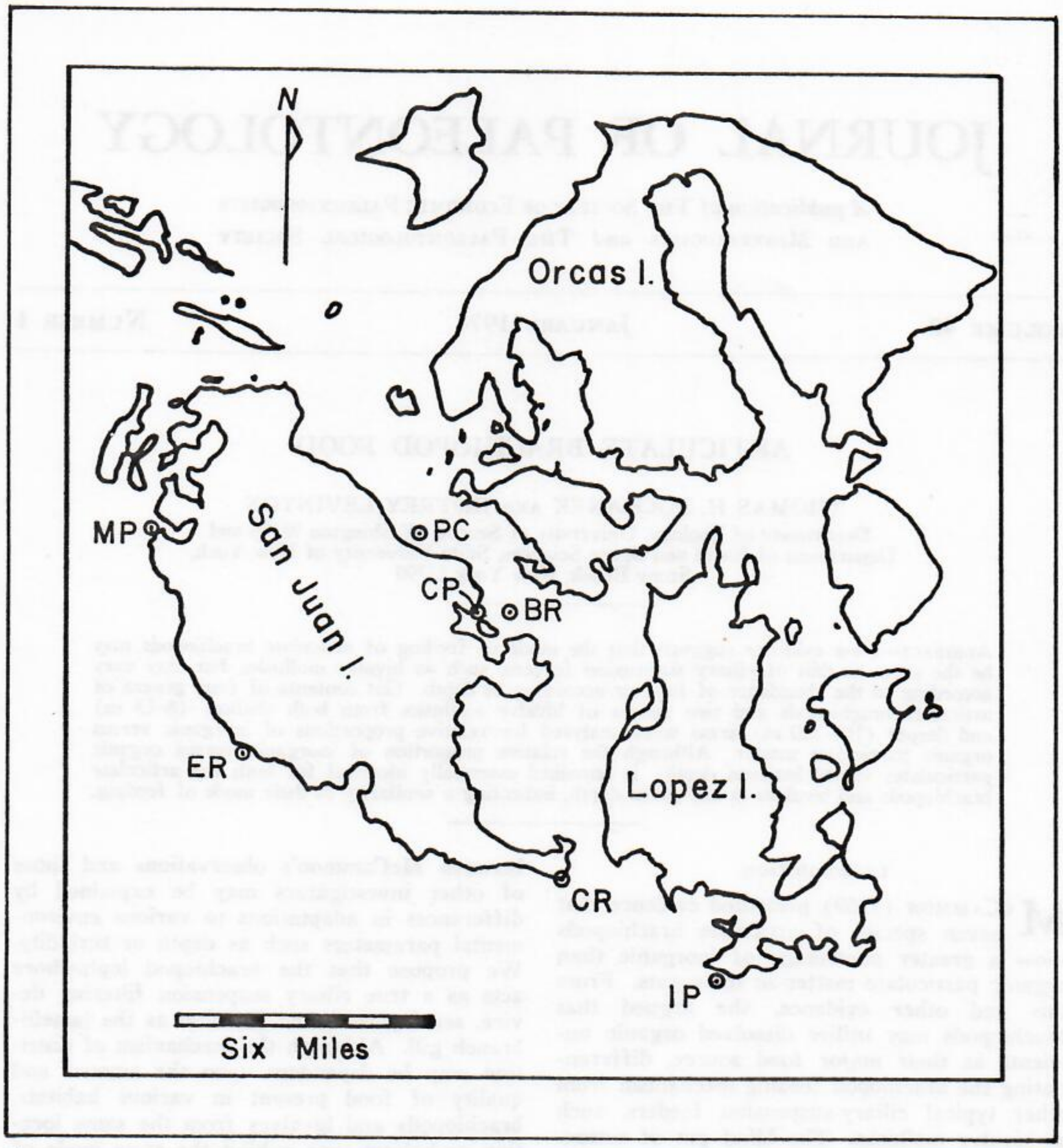
INTRODUCTION

McCammon (1969) presented evidence that seven species of articulate brachiopods show a greater percentage of inorganic than organic particulate matter in their guts. From this and other evidence, she argued that brachiopods may utilize dissolved organic nutrients as their major food source, differentiating the brachiopod feeding mechanism from other typical ciliary-suspension feeders, such as bivalve mollusks. The blind gut of articulates may be an adaptation for utilizing dissolved organics. Using autoradiographic techniques, *Terebratalia transversa* was shown to absorb dissolved ^{14}C-labeled glucose along surfaces of the mantle and lophophore, and can transport the products to muscles and other tissues (McCammon, 1972). With a nutrient drop in the world's ocean at the end of the Permian, the lowered fitness of the feeding mechanism of articulate brachiopods (differing from normal suspension feeders) may have contributed to the massive brachiopod extinction following that period.

Cowen (1971) has recently commented on this hypothesis, suggesting that the difference between McCammon's observations and those of other investigators may be explained by differences in adaptations to various environmental parameters such as depth or turbidity. We propose that the brachiopod lophophore acts as a true ciliary suspension filtering device, serving the same function as the lamellibranch gill. Although the mechanism of nutrition may be dependent upon the amount and quality of food present in various habitats, brachiopods and bivalves from the same location or habitat type exhibit the same mode of feeding and nutrition. The presumed loss of an anus remains enigmatic.

METHODS

Four genera of brachiopods (*Terebratalia, Terebratulina, Laqueus,* and *Hemithiris*) and two genera of bivalves (*Chlamys* and *Mytilus*) were collected from the waters around San Juan Archipelago, Washington (Text-fig. 1). Deeper water samples from Point Caution, Iceberg Point and Brown Island were collected by the use of a six foot beam dredge at depths ranging from 100–120m. Shallow water sites at Edward's Reef and Cantalever



TEXT-FIG. *1*—Map of the San Juan Islands, Washington, showing brachiopod localities. MP: Mitchell Point, ER: Edwards Reef, CR: Cattle Point, CP: Cantalever Pier, BR: Brown Island, PC: Point Caution, IP: Iceberg Point. Localities are described in Table 1.

Pier ranged from 8–13m in depth and were hand-sampled by means of SCUBA. Specimens were fixed in formalin either immediately, or two hours after collection. Gut contents of all individuals were analyzed for relative proportions of inorganic versus organic particulate matter by performing random counts of fields on a modified haemocytometer. We assume that gut contents are an indication of usable food sources.

RESULTS

As shown in Table 1, gut contents from deep water bivalves were essentially identical to deep water brachiopods, consisting of predominantly inorganic particulate matter (approx. 6 μ diameter) with few phytoplankton present. Inorganic particles constituted 70–90% of the gut contents and only four genera of phytoplankton in low abundance were found

TABLE 1.—Gut contents of articulate brachiopods and bivalve mollusks. Reported data is based on 2 specimens per sample, though other examined individuals showed similar results.

	Location	Depth	Size(1)	Gut Contents (volume)	Characteristic associated substrate	Characteristic associated fauna
BRACHIOPODS						
Terebratalia transversa	Point Caution	120m	22mm	Either empty or 90% coarse inorganic	Mud	*Modiolus modiolus*
Terebratulina spp.	Point Caution	120m	17mm	80–90% inorganic (5–6μ)	Mud	*Modiolus modiolus*
Laqueus spp.	Iceberg Point	110m	30mm	70% inorganic	Coarse gravel	*Gorgonocephalus*
Hemithiris psittacea	Brown Island	100m	19mm	70% inorganic	Coarse gravel	
Terebratalia transversa	Edward's Reef	13m	30mm	50–60% phytoplankton [minor const.-inorganic (5–6μ)]	Gravel and hard rock	Sponge-tunicate-hydroid community
Terebratalia transversa	Cantalever Pier	8m	20mm	50–70% organic part. large phytoplankton	Gravel and hard rock	Anemone-sponge-tunicate community
BIVALVES						
Chlamys hericius	Point Caution	120m	50mm	85% inorganic (less than 5μ)	Mud	*Modiolus modiolus*
Chlamys hericius	Cantalever Pier	8m	50mm	More than 90% organic particulates (dinoflagellates and diatoms)	Gravel and hard rock	Anemone-sponge-tunicate community
Mytilus californianus	Cattle Point	Intertidal	150mm	More than 90% organic part. (dinoflagellates and diatoms)	Gravel and hard rock	Barnacles, mussels, limpets

in these specimens. The substratum at these deeper water localities ranged from coarse gravel to mud and included a variety of characteristic associated fauna.

From shallow water localities, the gut contents were again similar for bivalves and brachiopods, and were packed with diatoms and dinoflagellates, with approximately nine dominant genera comprising the majority of phytoplanktonic forms found. Gut contents consisted of 50–70% organic particles. The substratum of these shallow water sites consisted of gravel and hard rock; a sponge-tunicate-hydroid community predominating the associated fauna.

DISCUSSION

In considering the evidence for absorbing dissolved nutrients, McCammon accepts the ability of other groups to absorb this resource, but questions their ability to subsist wholly on dissolved nutrients. She states that brachiopods were kept alive in artificial sea-water for two years by simple addition of nutrients. McCammon notes that nutrients may have been utilized by primary producers which could subsequently be filtered out by the brachiopods. We have maintained bivalves (*Mytilus californianus*) for over 12 months in an aquarium without addition of any substances and have observed no adverse effects to date (experiment still in progress at the time of writing). These observations are evidence that marine bivalves and most likely brachiopods can subsist for long periods without direct nutrient input.

The argument that a blind gut has been an adaptation for the utilization of dissolved organic matter is discussed by Cowen (1971) who cites various other ciliary suspension feeders such as *Echinaster* (Ferguson, 1967; 1969) and *Henricia* (from Anderson, 1960;

Rasmussen, 1965) which are also capable of utilizing dissolved nutrients. These echinoderms have blind guts and utilize a wide variety of organic material from particulate matter (such as phytoplankton) to macroinvertebrate sources (such as bivalves and echinoids). Rudwick (1962, 1965) shows that articulates are quite efficient at rejecting fecal pellets from the mouth by antiperistalsis, presenting no major interferences with the feeding mechanism.

Although *Terebratalia* assimilates dissolved glucose (McCammon, 1972), at least four genera of bivalves (*Mercenaria, Aequipecten, Mytilus,* and *Yoldia*) can absorb amino acids from solution (Stephens and Schinske, 1961). To provide evidence that the articulate brachiopod is, in fact, different from the classically presumed ciliary-suspension feeder, we suggest that bivalves and brachiopods from the same location be analyzed for their ability to assimilate dissolved organics. At the same time, careful determinations should be made of the actual concentration of phytoplankton (and all other organic particulates) present in the surrounding water mass to determine the relative efficiency of each species as a suspension feeder.

Further, many other marine invertebrate groups of widely varying life habits assimilate dissolved organic nutrients. A wide variety of genera from 11 out of 12 phyla studied so far have shown significant uptake of dissolved organic matter (Stephens, 1960; 1962a,b; 1963; 1968; Stephens and Schinske, 1957; 1961; Johannes, et al., 1969) so the observation that one more phylum exhibits this ability is not surprising.

Our data for deep water brachiopods show close agreement to McCannon's observations (1969) demonstrating a predominance of inorganic particulate matter. However, an inherent problem arises in attempting to generalize, from a limited sample, for brachiopods living in all types of habitats. McCammon's specimens were all obtained from 25–3600 meters depth, probably well below the compensation depth in these regions. However, our data demonstrate significantly different gut contents for both bivalves and brachiopods when comparing shallow zones from 8–13 m depth (above the compensation depth) with deeper stations from 100–120 m depth (below the compensation depth). In shallow waters, bivalves and brachiopods filter out primarily diatoms and dinoflagellates whereas in deeper zones, where phytoplankton are more scarce, the mode of nutrition may be altered (possibly from suspension feeding to absorption of dissolved nutrients) for both groups. The use of gut content analyses is limited and must be supplemented in the future with the above mentioned feeding experiments.

It is not necessary to assume a special mode of feeding and a nutrient drop at the end of the Paleozoic to explain the Permo-Triassic brachiopod extinction. During this time interval, the offshore articulate brachiopod fauna was replaced by the rapidly radiating bivalve fauna (Bretsky, 1969; Stanley, 1969; 1972) and as Stanley suggests, this may just as well have been either a result of competitive exclusion for a hard substratum space resource, or simple replacement by a more eurytopic bivalve fauna after some geologically sudden event such as a change in salinity or temperature caused the extinction of the offshore brachiopods. With regard to the former possibility, studies by Harger (1972) of competition between the eurytopic mussel, *Mytilus edulis,* and the relatively stenotopic *Mytilus californianus* come to mind as a potential model system for the study of space utilization. Furthermore, sympatric brachiopod and byssate bivalve species may be readily studied within the San Juan Islands region, particularly at Point Caution where several brachiopods are found to live on *Modiolus modiolus.* Because so little is understood about this problem, further studies are needed on space utilization and trophic adaptations of sympatric bivalve and brachiopod species.

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