

THE FEEDING AND ECOLOGY OF TWO NORTH PACIFIC
ABARENICOLA SPECIES (ARENICOLIDAE,
POLYCHAETA)^{1,2}

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Lugworms (*Arenicola* and *Abarenicola* spp.) often occur in dense populations on sandy or muddy beaches throughout the world. The two genera are separated on the basis of differences in the prostomium, mechanism of proboscis movement, number of oesophageal caeca, and length of the neuropodia (Wells, 1959). When Wells (1963) summarized the worldwide distribution of lugworms, he noted that, despite certain morphological differences, the mode of life seems to be basically the same for all lugworms. When two species live in the same geographical location, they occur in different habitats. Thus, the sympatric species are ecologically separated.

Most behavioral studies on lugworms have been concerned only with *Arenicola marina* Linné. Wells (1945) described the burrow of *A. marina* as consisting of a vertical tail shaft, a horizontal gallery, and a vertical head shaft. The head shaft is a column of sand loosened by an irrigation current set up by peristaltic waves of the lugworm's body. The sand is consumed at the base of the head shaft and deposited later as fecal castings on the sediment surface near the tail shaft. Wells (1949) recorded the irrigation of the burrow and found it to be cyclical, spontaneous, and predominantly headward. Krüger (1958) observed that *A. marina* could ingest particles suspended in the irrigation current by straining them off in the sediment of the head shaft.

The purpose of my research was to compare the ecology of the two genera of lugworms and of two sympatric species by studying the environment and feeding of two species of *Abarenicola* in False Bay, San Juan Island, Washington. These two species and *Arenicola marina* belong geographically to the same lugworm zone (see Wells, 1963).

The study area (Fig. 1) was centered around the Friday Harbor Laboratories, San Juan Island. Most field work was conducted in False Bay, a roughly circular tide flat (diameter at widest point is 1.2 km.), which consists at low tide of a series of bars and troughs extending from the head to the mouth of the bay. The populations of *Abarenicola pacifica* Healy and Wells and *A. claparedi vagabunda* Healy and Wells are patchy and are separated from each other by a lugworm-

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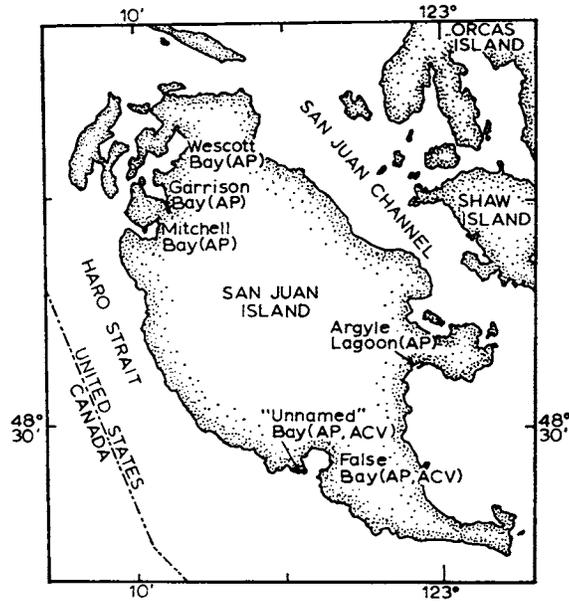


FIGURE 1. Bays sampled for sediment particle size (AP = *A. pacifica* present; ACV = *A. clapparedi vagabunda* present).

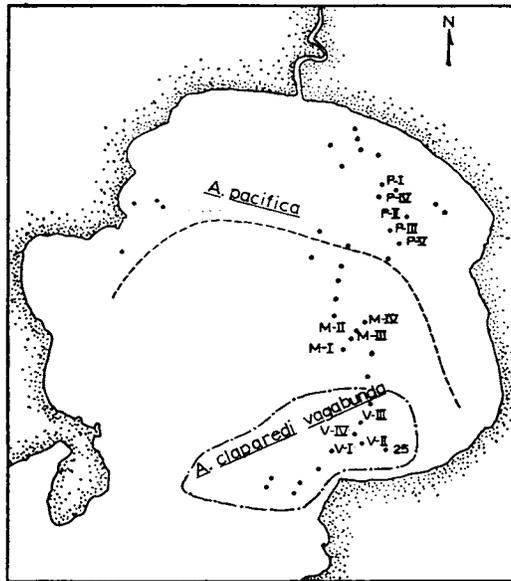


FIGURE 2. Approximate population boundaries in False Bay in summer, 1965. Dots represent sediment sampling locations, and those with Roman numerals represent transplant stations.

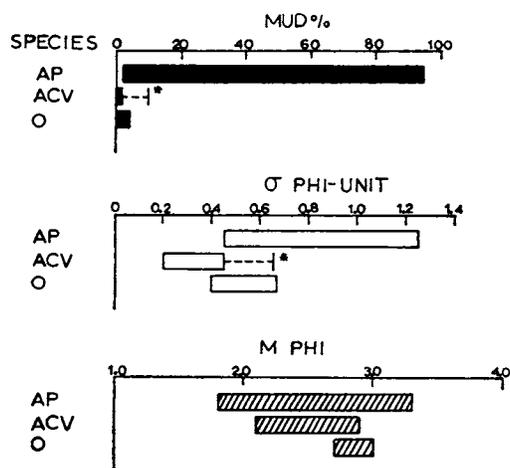


FIGURE 3. Ranges in mud content (Mud %), sorting (σ phi-unit), and mean particle size (M phi) of the sediment inhabited by *A. pacifica* (AP) and *A. claperedi vagabunda* (ACV) and of the sediment from the middle of False Bay (O). (* = a single exception to the ranges.)

free region in the middle of the bay. The population boundaries shown in Figure 2 vary both with season and year, as Healy and Wells (1959) have already noted.

According to Healy and Wells (1959), *A. pacifica* inhabits muddy sand around the margin of False Bay, and *A. claperedi vagabunda* inhabits loose, clean sand at a lower elevation near the mouth of the bay. Sediment rather than tidal exposure appears to govern their distribution. When the two species live in the same location, their relative elevations depend on whether the muddy sediment is higher or lower on the beach than the sandy sediment. Healy and Wells also noted that while the burrows of *A. pacifica* resemble those of *Arenicola marina*, those of *Abarenicola claperedi vagabunda* do not appear to have head shafts or funnel-shaped depressions in the sediment. This may be a result of sediment and water action, as I have observed that in the laboratory the latter species does form head shafts marked by funnel-shaped depressions.

THE ENVIRONMENT OF ABARENICOLA SPECIES

Sediment particle size

Fifty sediment samples were taken from the six locations in Figure 1. The samples were dried and separated into half-phi-unit size fractions and weighed. A phi-unit is the negative logarithm to the base two of the particle diameter in millimeters (Krumbein, 1936). Particle sizes smaller than 0.06 mm. (> 4 phi) were considered mud. Sorting (σ phi-unit) and mean particle size (m phi) were calculated using Inman's (1952) formulae.

Figure 3 shows the ranges from all six bays of the mud content, sorting, and mean particle size for each species and for stations in the middle of False Bay. *Abarenicola pacifica* inhabits a muddier (hence, less permeable) and more poorly sorted sediment than does *A. claperedi vagabunda*. Two small specimens of the

latter species were found at station 25 (mud % = 10.0) in False Bay and will be discussed later. The mean particle size is apparently of little importance in separating the habitats of the two species.

Organic content

Total organic matter of surface (0–0.5 cm.) and deep (6–10 cm.) samples from False Bay during spring and summer was measured as loss upon ignition (at 500° C. for 4 hrs.). The range in organic matter in 13 samples from the habitat of *A. pacifica* was 0.5–1.2% (mean = 0.8%; SD = 0.2%). The range in organic matter in 5 samples from the habitat of *A. claparedi vagabunda* was 0.5–0.7% (mean = 0.6%; SD = 0.2%). There was little if any difference between the surface and the deep sediments.

In summary, the environment inhabited by *A. pacifica* is a muddier and more poorly sorted sediment than that of *A. claparedi vagabunda*. Because it lives in a muddier sediment, *A. pacifica* tends to be found in sediment of higher organic content than does *A. claparedi vagabunda*, but it can also inhabit sediment of relatively low organic content.

THE FEEDING BEHAVIOR OF ABARENICOLA SPECIES

Suspension feeding

I attempted to recover, in the castings, carmine particles that had been suspended in the overlying water (using the method of Krüger, 1958) to provide evidence of suspension feeding in *Abarenicola* species. When a red casting appeared, the inside was examined for carmine particles. Although both species could ingest particles suspended in the sea water, there were experimental runs in which no carmine particles appeared in the castings, even after 24 hours.

Sediment feeding

The feeding of individual worms was studied in 0.22-liter glass jars. The manner of feeding on the surface sediment was basically the same as that of *Arenicola marina*. Headward irrigation waves created an upward current of water and of the smaller sediment particles in the head shaft. As the worm crawled backward to defecate or ceased headward irrigation, the head shaft collapsed somewhat. The surface sediment, marked by orange or yellow chalk powder, moved down. The worm then crawled forward and appeared to consume sediment at the base of the head shaft and the cycle began again. Chalk powder appeared in the castings of both species 2 or more hours after its deposition on the surface. The head shaft of *Abarenicola pacifica* and *A. claparedi vagabunda*, like that of *Arenicola marina* (Wells, 1945), represents a subsiding column of surface sand consumed at the base by the worm and renewed at the surface by sedimentation.

The irrigation cycle

Wells (1953) showed that *A. marina* may integrate feeding and defecation into its irrigation cycle. I used Wells' (1953) method to study this behavior in

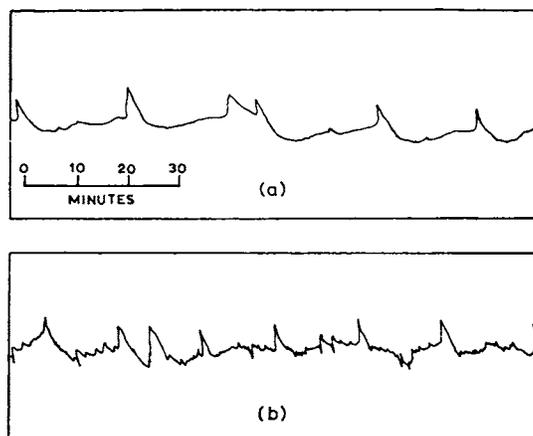


FIGURE 4. Typical irrigation patterns of (a) *A. pacifica* and (b) *A. claparedi vagabunda*.

Abarenicola species. The activities of a worm in a sediment-filled U-shaped tube (the "tail end" opens below the level of a constant level water bath) change the water level in the "head end" of the tube (which opens above the level of the water bath). A float in the "head end" of the tube is attached to a lever bearing a pen (a rise in water level is thus recorded as a downward stroke and usually indicates headward pumping). A narrow-bore capillary at this end just below the level of the water bath was necessary to prevent overflow due to the predominantly headward pumping of both species. Twenty-four individuals of *A. pacifica* and 13 of *A. claparedi vagabunda* (weighing 1–3 g.) were studied.

Figure 4 shows a typical irrigation pattern for each species, to be read from left to right. As the worm backs up the tail shaft, the pen moves upward. At the peak of the curve, the tip of the tail may appear at the surface, but defecation does not always occur. As the worm returns to its original position, the pen falls. The worm then resumes headward irrigation and, apparently, feeding. The average length of the cycles ranges from 10 to 30 minutes and varies considerably among individuals. The only consistent difference between the irrigation cycles of the two *Abarenicola* species is that *A. claparedi vagabunda* traced a more jagged cycle than *A. pacifica*. This difference persisted even when the two species were placed in each other's sediment.

Basically *Arenicola marina*, *Abarenicola pacifica*, and *A. claparedi vagabunda* have the same mode of feeding. All can feed on particles suspended in sea water, and all feed predominantly on surface rather than deep sediment. They irrigate their burrows in the same cyclical manner, integrating feeding and defecation into this cycle.

THE UTILIZATION OF ORGANIC CARBON

Although the three species have basically the same feeding behavior, there still may be quantitative differences in feeding. The percentage of the organic carbon

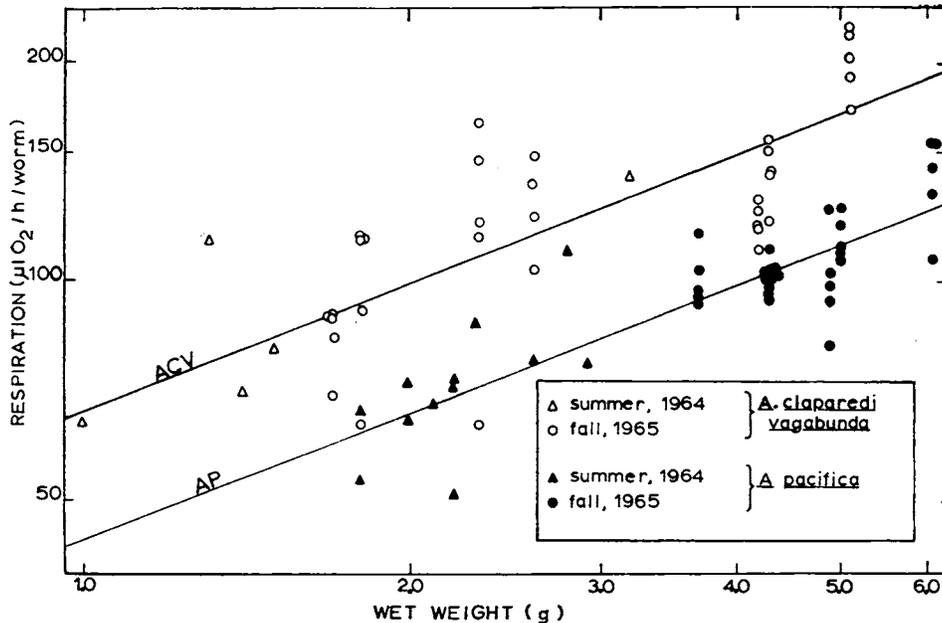


FIGURE 5. Respiration versus wet weight for *A. pacifica* (AP) and *A. clareredi vagabunda* (ACV). Values are on a logarithmic scale.

ingested that is needed for maintenance can be calculated for *Abarenicola pacifica* and *A. clareredi vagabunda* from their respiration rate, sediment turnover rate, and the average organic matter content of False Bay sediment.

Respiration rate

The respiration rates of both species were measured in summer, 1964, and fall, 1965, to determine the amount of carbon needed for maintenance. A modification of Conover's (1956) micro-Winkler technique was used. During experiments, each lugworm was placed in an opaque 275-ml. bottle filled with sea water that had been filtered through a glass-fiber filter and equilibrated with the atmosphere. Experimental and control bottles were kept at 12 to 14° C. for 3 hours. The oxygen content of a 25-ml. subsample was determined. Between experiments, the worms were kept in sand from their own habitat.

The results from unstarved worms that were acclimated to laboratory conditions for more than 12 hours are presented in Figure 5 (an open triangle representing 0.8, 73.5 could not be included on this figure). The logarithms of the values of respiration and wet weight were analyzed by covariance analysis. The two species have significantly different respiration rates ($P = < 0.01$, with 2 and 78 df). The slopes are not significantly different ($P = 0.10-0.25$, with 1 and 78 df). The slope of the regression lines ($b = 0.58$, with 95% confidence interval of 0.48-0.68) is determined from a narrow size range of experimental animals (0.8-6.1 g.) and therefore may not be accurate for the entire size range of the species.

The first few days of starvation do not affect the respiration rate. During summer, 1964, a respiration experiment was run on six *A. pacifica* after 3 days of starvation. There was no noticeable decrease in the respiration rate. Six individuals of *A. claparedi vagabunda* were starved for 3, 8, and 10 days. Only after 10 days of starvation was there a noticeable (about 30%) decrease in the respiration rate.

Sediment turnover rate

The quantity of sediment passing through the gut per unit time was measured to assess the feeding rate of both species in False Bay during summer. Eight individuals of each species were used. Each worm was placed in a 0.22-liter jar (10 cm. high) in sediment from its own habitat. The castings were collected three or four times each day, dried, and weighed. In the first set of experiments, the jars were kept continuously under water (10–12.5° C.) to simulate continuous high tide. The same worms were used in the second set of experiments, but under simulated tidal conditions of False Bay. Both sets of experiments lasted for 9–11 days. To allow the worms to adjust to conditions, only the results from the last 5 days were used. Five hours of “low tide” was alternated with 7 hours of “high tide” for the experiments with *A. pacifica* to approximate the average exposure of the population. Low tide was simulated by draining the water bath and siphoning water from the jar and half the water from a vertical column in the sediment. The average exposure of the *A. claparedi vagabunda* population was estimated to be once a day for 2.5 hours and the jars were drained accordingly. Water was siphoned only from the sediment surface, simulating the loose watery sand near the mouth of False Bay. The rise in sediment temperature during “low tide” (13° C. average) roughly simulated that occurring in False Bay at about 10 cm. depth. At the end of the experiments, the sediments in six jars were sampled for organic matter.

Under continuous high-tide conditions, the average sediment turnover rate of *A. pacifica* was 3.8 g./day and that of *A. claparedi vagabunda* was 12.4 g./day. Under tidal conditions, the respective rates were 3.4 g./day and 9.4 g./day. Within the size range of worms used (1.0–3.5 g.) there was no relation of sediment turnover rate to size. Although I noticed that the castings left during “low tide” were smaller than at “high tide,” there was no significant difference in turnover rate between conditions of “tides” and “no tides” ($P = 0.10-0.25$, with 1 and 28 df). However, there was a significant difference between the turnover rates of the two species ($P = < 0.01$, with 1 and 28 df). There was no significant interaction between tidal conditions and species ($P = > 0.25$, with 1 and 28 df).

Because experimental conditions were meant to resemble the environmental conditions of the two species' habitats in False Bay, the organic content of the sediment could not be kept equal for both species during the experiment. As the organic content was lower in the *A. claparedi vagabunda* sediment (0.4%) than in the *A. pacifica* sediment (0.8%), one might expect a higher sediment turnover rate for the former species. However, the observed higher activity and the higher respiratory rate of *A. claparedi vagabunda* suggest that there is a real difference in sediment turnover rate between species.

TABLE I
Utilization of organic carbon by a 2-gram lugworm

Species	Respiration rate at 12°C. (μl. O ₂ /hr.)	Carbon needed* (mg. C/day)	Average carbon content of sediment** (mg. C/g.)	Average sediment turnover rate (g./day)	Carbon ingested (mg. C/day)	Carbon needed
						Carbon ingested (%)
<i>A. pacifica</i>	66	0.65	4.0	3.6	14	4.6
<i>A. claparedi vagabunda</i>	99	0.98	3.0	11	33	3.0

* An RQ of 0.8 is assumed.

** Organic carbon is assumed to be half the organic matter.

Utilization of organic carbon

The percentage of carbon utilized by the two species is calculated in Table I. *A. pacifica* needs 4.6% and *A. claparedi vagabunda* needs 3.0% of the carbon ingested (from sediment feeding only). It appears that the lugworms remove little of the organic carbon available from the sediment, and thus their food requirements are fairly low. One must consider, however, that not all of the carbon compounds passing through the gut could be broken down by the enzymes of the lugworm. George (1964) found that under optimal conditions the enzymes of the polychaete *Cirriformia tentaculata* (Montagu) digested only 14% of the ingestible organic matter. Even if the enzymes of the lugworm could digest only 10% of the organic carbon ingested, only 30–50% of this would be needed for maintenance. Because the time required for a dense population of 50 *A. pacifica*/m.² to turn over all sediment to 10 cm. depth is calculated to be about 800 days, it is unlikely that the lugworms would ever deplete the food supply in the sediment. In addition, suspension feeding would increase the amount of carbon ingested. It is probable, therefore, that *A. pacifica* inhabits a muddier sediment than *A. claparedi vagabunda* because of factors other than the high organic content of mud.

TRANSPLANTATION EXPERIMENTS

Both species were transplanted into their own habitat, each other's habitat, and the lugworm-free middle portion of False Bay in order to determine whether the difference in habitats influences the adult worms. The stations at these three locations are marked in Roman numerals in Figure 2.

Ten worms of one species were placed on the sediment surface within the rim of cylinders of 1-mm. mesh plastic screen (height, 30 cm.; diameter, 30 cm.), which had been submerged to 27 cm. depth in the sediment. These cylinders allowed for natural drainage while preventing the escape of the lugworms. In each of the three locations, two cylinders were used for *A. pacifica* and two for *A. claparedi vagabunda*. Two series of these transplants were conducted on bars (above water level at low tide) and three series in troughs (below water at all times). Transplantation of *A. claparedi vagabunda* was discontinued after the first two series because even the control transplants did not survive well. At each sufficiently low

TABLE II
False Bay transplants

Habitat*	Sediment settled or unsettled**	Survival values*** (after 14 days)		Mean
		Bars	Troughs	
<i>A. pacifica</i>				
AP	S	9; 5;	2; 6	5.5
	U	9; 8;	7; 5; 2; 3	5.7
M	S	0; 0;	0; 0; 0; 0	0
	U	0; 0;	0; 0	0
ACV	S	0; 0;	0; 0; 0	0
	U	4; 1;	2; 3; 3	2.6
<i>A. claparedi vagabunda</i>				
AP	S	1; 0		0.5
	U	3; 0		1.5
M	S	5; 0;		1.6
		1; 1		
ACV	S	0; 0		0
	U	6; 3		4.5

* AP = in the habitat of *A. pacifica*; M = in the middle of False Bay; ACV = in the habitat of *A. claparedi vagabunda*.

** S = sediment has been allowed to settle for a day or more. U = sediment has not been allowed to settle.

*** Survival values represent the highest number of castings counted during the last spring tide period. For most "0" values, castings were never noticed after transplantation.

tide, the numbers of castings within each rim were counted, and the survival value for each cylinder was taken as the highest number counted during the week of spring tides. After about one to two weeks, the survival values leveled off, and statistical analyses were performed on the results obtained at the end of 14 days (except for the first series of transplants, which was not revisited until about a month later). In about half the experiments with *A. pacifica*, the worms were transplanted several days after the cylinders had been submerged, and thus planted in "settled" sediment rather than in freshly dug sediment. This was to determine the possible effect of physical factors.

The data of the transplantation experiments are summarized in Table II. The results obtained on bars and in troughs were not significantly different and are therefore combined. A *t*-test showed a significant ($P = < 0.01$) difference in survival of *A. pacifica* between settled and unsettled sand in the habitat of *A. claparedi vagabunda*. Settling apparently has no effect on *A. pacifica* in its own habitat or in the middle of False Bay. An analysis of variance showed that there is a significant ($P = < 0.01$) difference in survival among habitats in unsettled sediment.

The *A. claparedi vagabunda* transplants did not survive well even in their own habitat. There is no significant difference in survival among any of the habitats. However, even in settled sediment some worms were able to survive in the habitat of *A. pacifica* and some in the middle of False Bay. Therefore, it appears that the adults of *A. claparedi vagabunda* are able to survive in other habitats. The difference between survival of this species in settled and unsettled sand in its own habitat was not significant ($P = 0.05-0.10$), but these are the results of only two series of transplants.

In the laboratory, ten worms of a species were placed in a sediment-filled aquarium (20 by 30 by 15 cm.) under water for 1 to 6 weeks. Even after 6 weeks in sediment from the middle of False Bay, most individuals of *A. pacifica* were still alive. Both species could survive in the laboratory in sediment from any of the three locations in False Bay.

Some conclusions may be made from the contradictory results of the laboratory transplants. In the laboratory, conditions were the same as in the troughs of False Bay except for the absence of water action and of possible predation by birds and fish. Water action is the more likely explanation for the low survival in some field transplants. *Abarenicola pacifica* has been found only in sediment with more than 1.7% mud, and therefore is subject to less action by waves or currents than is *A. claparedi vagabunda*, which is usually found in a cleaner sediment. The inability of *A. pacifica* to survive in the habitat of *A. claparedi vagabunda* might then be due to the increased water action in this environment. The higher survival of *A. pacifica* in the habitat of *A. claparedi vagabunda*, when placed in unsettled sediment, may be related to the establishment of the burrow. The sediment becomes settled after a period of high tide, but before this time the *A. pacifica* have probably established their burrow. The mud content at two of the transplant stations (1.7%, 2.3%) in the middle of False Bay is within the range in which *A. pacifica* is found, so water action alone cannot account for the inability of *A. pacifica* to survive in this habitat.

The observed distribution of *A. claparedi vagabunda* in sandy sediment is probably a result of larval ecology. The finding of two specimens (station 25) in 10.0% mud and the survival of some worms both in the middle of False Bay and in the habitat of *A. pacifica* suggest that adults of *A. claparedi vagabunda* are capable of living in these locations.

DISCUSSION AND CONCLUSIONS

The feeding behavior of two North Pacific *Abarenicola* species is basically the same as that of *Arenicola marina*. The representatives of both genera feed predominantly on surface rather than deep sediment, are capable of feeding on particles suspended in the sea water, and integrate feeding, defecation, and irrigation into their activity cycle.

There is a definite quantitative difference in feeding between the two *Abarenicola* species. The higher activity of the irrigation cycles, the higher respiratory rate, and the higher sediment turnover rate demonstrate that *A. claparedi vagabunda* is generally more active than *A. pacifica*. The utilization of organic carbon is nearly the same for the two species and they need little (3-5%) of the organic carbon ingested. Although the lugworms cannot digest all of the organic carbon

ingested, calculations show that even in dense lugworm populations the food supply in the sediment probably would not be depleted. Of what value, then, is the suspension feeding? Krüger (1964) believes that suspension feeding may contribute a high percentage of the food requirements of *Arenicola marina*. Because the carbon requirements of the species studied here are low, either sediment or suspension feeding probably could supply much of the needed organic carbon. We must first determine what percentage of the organic carbon in the sediment can be assimilated by lugworms before assessing the value of suspension feeding. If the organic content of the sediment becomes very low or is chiefly in a form unavailable to the enzymes of the lugworms, particles suspended in the sea water would be an important supplement to the lugworms' diet.

If these two species of *Abarenicola* are not limited by food, their distribution should be a result of larval ecology, physical factors, and/or predation and parasites. The transplant experiments suggest that physical factors, probably the action of waves and currents on the sediment, render the sediment of sandier habitats unsuitable for *A. pacifica*. Thus, this species is found in a muddy habitat, where water movement is comparatively lower. On the other hand, the transplant experiments suggest that larval settlement and survival may be responsible for the usual occurrence of *A. claparedi vagabunda* in clean sand. Because, for the reasons proposed above, *A. pacifica* and *A. claparedi vagabunda* live in sediments of differing mud content, they should never compete with each other—even when sympatric as in False Bay.

Why should three species of two genera have the same type of feeding behavior? The amount of food available from sediment and suspension feeding is large compared to the amount needed. At low tide aerial respiration and defecation may be fitted to the activity cycle, and at high tide suspension and sediment feeding, defecation, and burrow irrigation are integrated. This appears to be a feeding mechanism that should be successful throughout the range of lugworm habitats. There should be no selection pressure to change a successful way of feeding. Competition for food should not have caused a divergence in feeding mechanisms because, even if the two species had occurred at the same point in the past, food probably was not limiting. It is probable, therefore, that this feeding behavior has been retained throughout lugworm evolution.

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SUMMARY

1. A comparison of the habitats of two sympatric lugworms shows that *Abarenicola pacifica* lives in a muddier and more poorly sorted sediment than does *A. claparedi vagabunda*.
2. Both species, like *Arenicola marina*, are capable of suspension feeding, feed

predominantly on surface rather than deep sediment, and integrate feeding and defecation into their irrigation cycle.

3. Respiration and sediment turnover rates indicate that *Abarenicola claparedi vagabunda* is more active than *A. pacifica*. Both species seem to need little (3–5%) of the organic carbon ingested.

4. Transplantation experiments suggest that physical factors rather than availability of food may limit *A. pacifica* to muddier sediment and that the distribution of *A. claparedi vagabunda* may be a result of larval settlement and survival.

5. It is proposed that this mode of feeding has been retained throughout lugworm evolution because the observed feeding behavior should have been successful throughout the range of lugworm habitats, and because of the probable lack of interspecific competition for food.

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