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# INGESTION AND OXYGEN CONSUMPTION BY SLOPE ECHINOIDS

Very little information is available on the metabolic processes of benthic organisms that live on the slope just beyond the continental shelf. Understanding of the basic biology of indigenous organisms is necessary before effects of waste discharge can be understood. The proposal by the County Sanitation Districts of Orange County to discharge sludge at 350 m on the San Pedro Basin slopes provided us an opportunity to study two echinoids, *Allocentrotus fragilis* and *Brissopsis pacifica*, which constituted more than 90% of the trawl biomass collected in surveys of the proposed discharge area. These species were found to inhabit areas characterized by gradients of sediment grain-size, organic material, and dissolved oxygen concentrations--in areas that were comparatively uncontaminated. In studies of effects of discharge, it is important to use indigenous species to measure effects that can be related to in situ processes.

The purpose of our study was to measure and evaluate ingestion and oxygen consumption rates of the two dominant species in the proposed discharge area. These metabolic measures were selected because feeding is an organism's primary method of obtaining energy and probably contaminants; oxygen consumption rates provide information on the general metabolic condition of an organism and can be used as a measure of sublethal stress (Cantelmo et al. 1978; Brinkhurst et al. 1983). Together, these measurements are components of organismal growth.

Our study shows that both species are respiratory regulators and ingest small quantities of sediment and particulate organic material. Using size-specific oxygen consumption and ingestion rates, together with information from our surveys, we estimate that *B. pacifica* populations ingest 161.2 dry mg of sediment/sq m/hour and consume 794.7  $\mu\text{l O}_2$ /sq m/hour and *A. fragilis* populations ingest 1.9 dry mg of food/sq m/hour and consume 308.9  $\mu\text{l O}_2$ /sq m/hour. Both species

assimilated considerably more food calories than their oxygen consumption could utilize--especially *B. pacifica* which assimilated two orders of magnitude more food than could be oxidized.

## METHODS

Ingestion and oxygen consumption rate measurements were made in the laboratory under nearly ambient conditions. Warnings by Vernberg et al. (1977) and Pamatmat (1983) regarding the precision of respiration measurements made in the absence of sediment led us to develop nondisruptive methods for both ingestion and  $O_2$  consumption rate measurements.

The specimens and sediments used were collected from the upper slope sites off Newport in Orange County and Point Dume (see Figure 1 in Thompson et al., this volume). The urchins were kept cold and transported to the laboratory where they were placed in seawater-filled aquaria on 3- to 5-cm-deep screened (0.5 mm) sediment. The aquaria were maintained at 8-9°C, normal for upper slope bottom waters in the study area (SCCWRP, unpublished data). The seawater (salinity = 33 ppt) was obtained from Southern California Edison Company. Ingestion and  $O_2$  consumption rate measurements were made only after the test organisms had been acclimated to the aquarium for several days and were functioning (i.e., burrowing, etc.) with apparently normal activity. The organisms were not starved but were fed regularly using finely ground tetramin sprinkled on the mud.

To determine what kinds of foods urchins from the study area ingested naturally, gut contents were analyzed using preserved urchins collected from the trawl samples. The contents were divided into five categories (Table 1), and the percent of total gut volume was estimated visually and volumetrically. A subsample of the contents was used for particle-size analysis. The sample was ashed at 500°C to remove organic material, then placed on a microscope slide. Ten random fields of 10 particles (i.e., 100 particles) were measured at 1000x from each of three specimens.

Total organic carbon and nitrogen were also measured and bacterial counts made in sediment, foreguts, and hindguts of these species. C:H:N analysis were conducted by Dr. Bob Perry at The Institute of Marine Sciences, University of California at Santa Barbara, and bacterial counts were made by David Krempin at the Department of Biological Sciences, University of Southern California, using epifluorescence staining techniques.

Oxygen consumption was measured using small bell jars made from glass

Table 1. Gut contents of both echinoids showing average proportions (of total gut contents volume) in each food category. By volume, both ingested mostly detrital aggregates--i.e., aggregations of fine sediments, organic material, microbes, etc.

	(n)	Gut Contents Categories				
		Detrital Aggregates	Single Mineral Particles	Particulate Organic Material	Animal Remains	Foraminifera
<i>Allocentrotus fragilis</i>						
Upper slope adults	69	0.53	0	0.17	0.28 <sup>a</sup>	0.03
Upper slope juveniles	10	0.44	0	+ <sup>b</sup>	+	0.56
<i>Brissopsis pacifica</i>						
Upper slope	43	0.88	0.07	0.04	0.02	+
Lower slope	89	0.86	0.07	0.04	0.03	+

<sup>a</sup>For *A. fragilis*, animal remains included gastropods, crustaceans, polychaetes, ophiuroids, fish, and invertebrate egg cases.

<sup>b</sup>Present in trace amounts.

BOD (300-ml) or reagent (2000-ml) jars with the bottoms removed so that they could be placed onto a small area of sediment containing the animal. A second identical jar was placed on adjacent bare sediment so that dissolved oxygen consumption by the sediment could be subtracted. An LG Nester Model 8000 oxygen meter and probe were used to measure dissolved oxygen concentrations in the bell jars. The meter and probe were initially calibrated using saturated sea water.

To determine the relationship between O<sub>2</sub> consumption and ambient dissolved oxygen concentrations, the organisms were allowed to deplete the O<sub>2</sub> under the bell jars, from saturation (10.3 ml/L) through 0 ml/L. Oxygen consumption rate measurements were run for 2-4 hours and

were conducted at 92-100% oxygen saturation, and additionally for *A. fragilis* at 38% saturation (4 ml/L).

Ingestion rates were measured differently for each species. Gut contents analysis showed that *A. fragilis* ingested a variety of food; therefore, we used several foods. Equal quantities (by weight) of algae (*Egrecia menziesii*), anchovy (*Engraulis mordax*), and tetramin tablets were spread over the sediment in an aquarium. *A. fragilis* was allowed to feed for 4 hours and then was removed and frozen. This species forms pellets as it feeds, each pellet usually of one food type. The foreguts were dissected out, the contents separated visually, and the volume and dry weight of each fraction measured.

For *B. pacifica*, ingestion rates were measured using spherical glass microbeads (53-74  $\mu\text{m}$ ) as sediment markers; we chose this size of microbead based on measurements of actual gut particle sizes. These were mixed into the sediment to a concentration of 0.259 g/cc of sediment. Test organisms were placed into shallow depressions made using the thumb and allowed to "settle in" for 15 min. After feeding in the sediment for 7 hours, they were removed and frozen. While the organisms were still frozen the guts were dissected out and sliced into thin sections. The contents of each section were subsampled and examined under the microscope (1000x) for the presence of glass beads. The gut contents with glass beads were separated, and the volume and dry weight of the material ingested were measured.

## RESULTS AND DISCUSSION

### Ingestion

**Gut Contents.** *Allocentrotus* is a motile surface feeder, primarily a predator-scavenger. It consumed a wide variety of foods. Most of its gut contents consisted of detrital aggregates, but a large proportion of the diet was particulate organic material (plant and animal) and remains of other animals (Table 1). Juveniles contained considerably more Foraminifera than the adults. *Allocentrotus* ingested fewer bacteria than were present in the sediment but selected carbon- and nitrogen-rich material--up to 45% organic carbon (Figure 1). These values vary because this material consisted mostly of large fragments of organic material, animal remains, etc. More bacteria were found in the hindgut of *A. fragilis* than in the foregut; Lasker and Giese (1954) discovered the hindgut of the intertidal urchin *Strongylocentrotus purpuratus* to harbor a symbiotic bacterial flora that produces cellulase to digest algae, and a similar situation may exist in *A. fragilis*.

*Brissopsis* is a burrowing deposit-feeder that ingests sediment composed mostly of detrital aggregates with only a small proportion of larger,

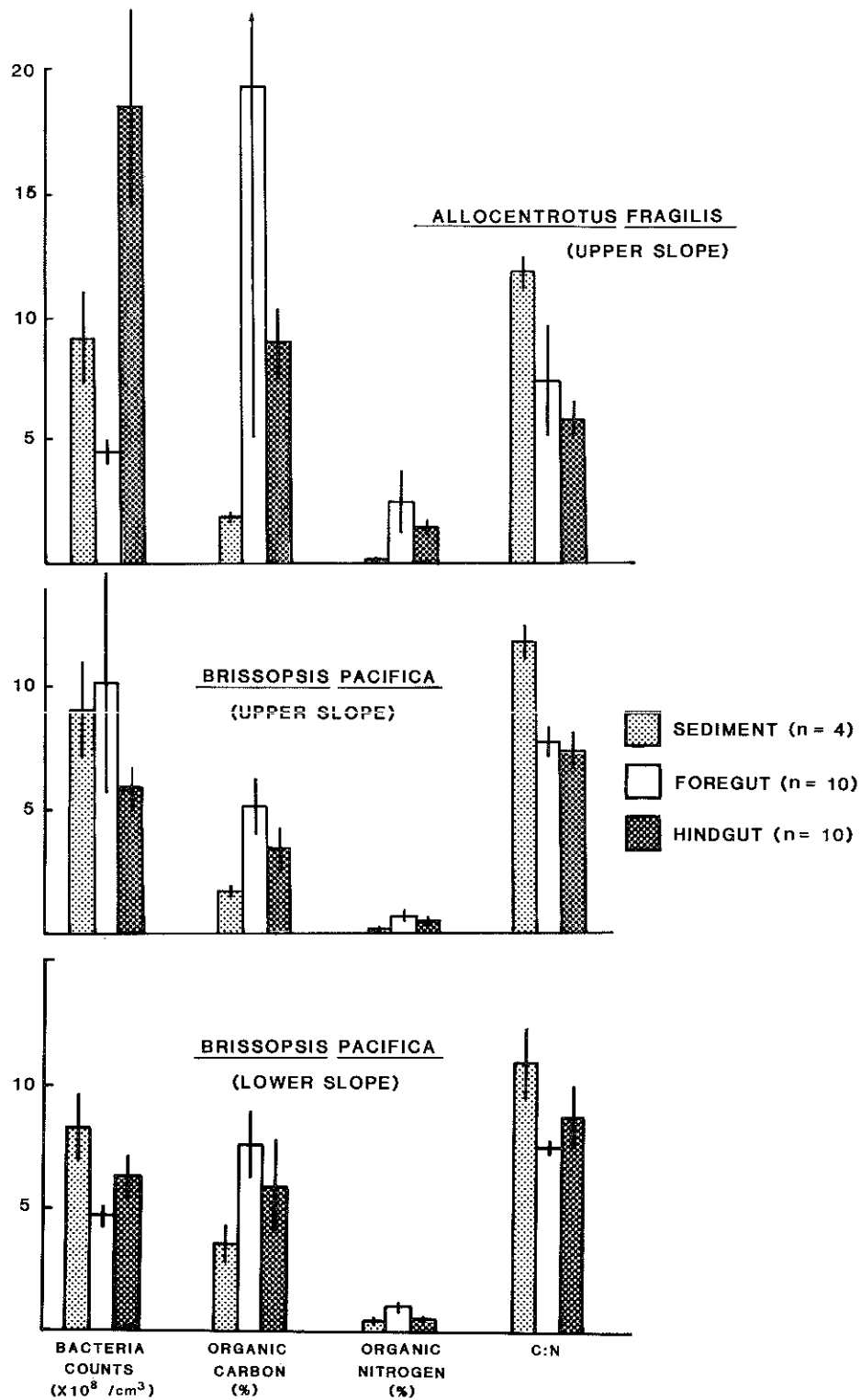


Figure 1. Comparison of bacterial density, percents organic carbon and nitrogen, and C:N ratio (mean  $\pm 1$  standard deviation) in surface sediments (0-2 cm) and foregut from the two echinoid species studied.

unaggregated mineral particles (Table 1). Although there was little difference in the sediment bacterial densities over depth (Thompson et al., this volume), *B. pacifica* ingested more bacteria on the upper slope than on the lower slope (Figure 1). Carbon- and nitrogen-rich sediments were selected by both upper and lower slope populations. The C:N ratio was lower in the foreguts than in the sediment, showing selection of more labile material.

The mineral particle sizes found in the guts are shown in Figure 2. Both species contained mostly silt-sized (4–62 μm) particles. *A. fragilis* contained 99.0% silt (median grain-size = 20 μm), and *B. pacifica* contained 77.8% silt (median grain-size = 30 μm)—reflecting the sediment at these sites, which is also mostly (78%) silt. Although the gut particle-size distributions are significantly different (Kolmogorov-Smirnov test:  $\alpha = 0.05$ ), they do exhibit moderate overlap (i.e., their Index of Proportional Similarity (Schoener 1970) = 0.499).

**Measurements of Ingestion Rates.** Since the gut contents of *A. fragilis* collected from the upper slope showed that they had ingested several different foods, we measured their ingestion rates of several different foods. The size-specific ingestion rates for each food and a total rate

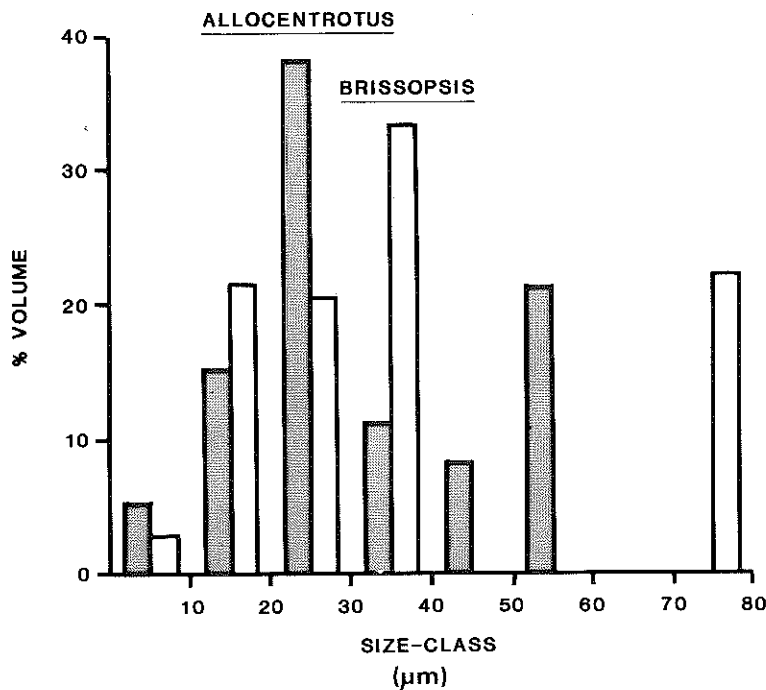


Figure 2. Mineral particle-size distributions (n = 300) from the guts of the two species of echinoids studied, collected from Station OCE16, summer 1982. These species ingest very similar particle sizes—mostly silts.

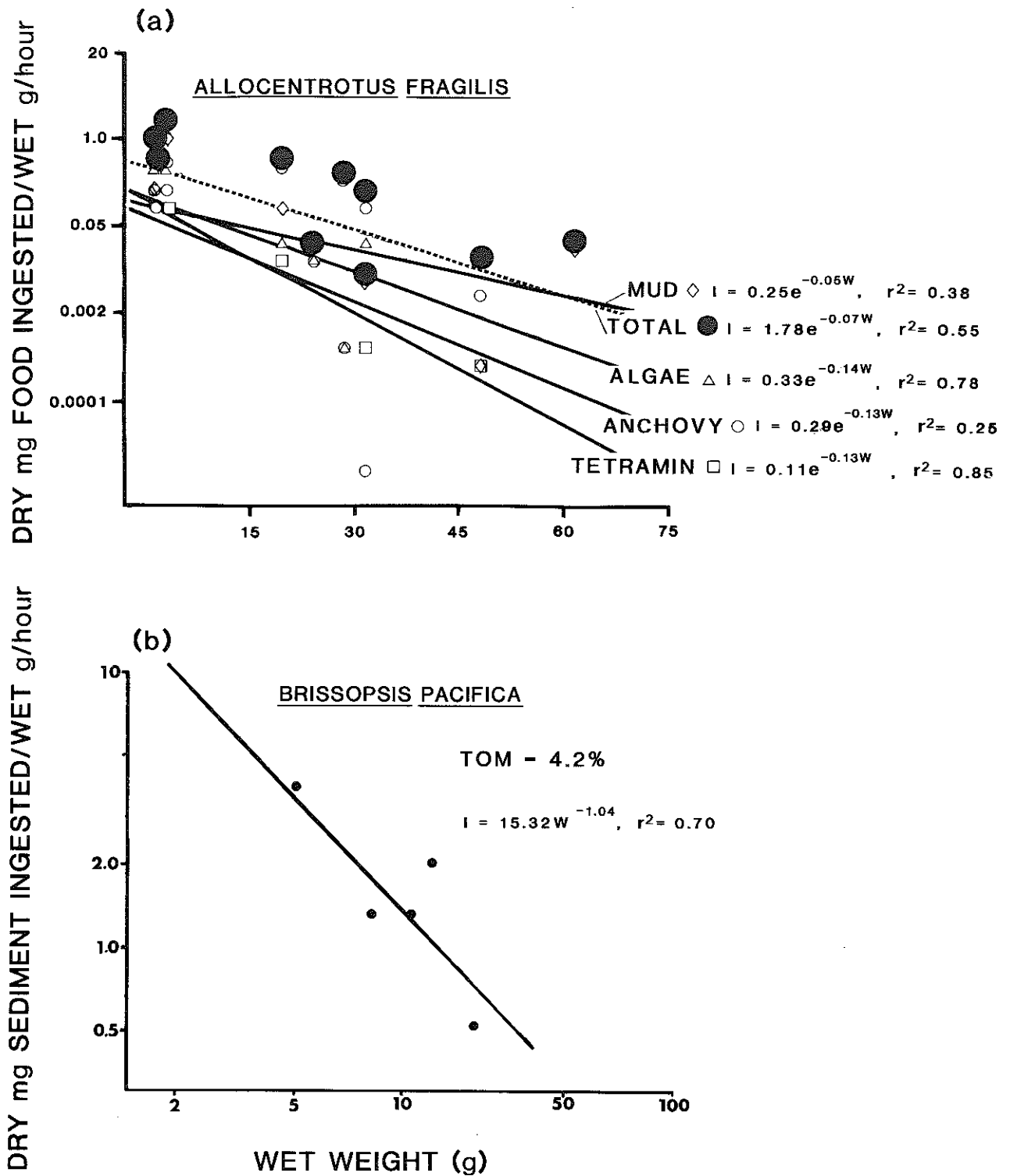


Figure 3. Size-specific echinoid ingestion rates at 85°C. *A. fragilis* (a) consumed a variety of foods; *B. pacifica* (b) ingested only sediment. Equations are "best fits" for each food type ( $I$  = ingestion rate,  $e$  = constant = 2.72,  $W$  = wet weight (g),  $r^2$  = coefficient of determination).

are presented in Figure 3a; the "best fits" of ingestion rate versus size for *A. fragilis* were calculated with exponential regressions. Smaller urchins ate more per unit weight, but the largest ones consumed the most total mass. Anchovy was consumed the most and tetramin the least, even less than sediment in the aquarium. There was more variation in the proportion of each food ingested by the larger urchins. An average *A. fragilis* (43.9 g wet weight) consumed a total of 1.59 dry mg/hour. *Brissopsis* ingested mostly whole sediment, thus there is only a single regression (Figure 3b); the best fit of ingestion rate versus size for *B. pacifica* was found with an allometric regression. An average-sized *Brissopsis* (11.8 g wet weight) consumed about 13.88 dry mg of sediment/hour.

Since we could find no ingestion rates for these species of urchin in the literature, it was difficult to evaluate the accuracy of our measurements. Our ingestion rate measurements were lower than those predicted by a generalized equation for deposit feeders (Cammen 1980): *A. fragilis* ingested only 1.3% and *B. pacifica* ingested 22.5% of the quantities predicted by Cammen's equations. However, Cammen's equations were for an ambient temperature of 15°C and our measurements were made at 8°C. Moreover, Cammen states that most of the species he used to derive his equations feed on organic-rich material and had ingestion rates lower than predicted. Both of the urchins we studied inhabited areas with organic-rich sediments which comprise the largest portion of their diets.

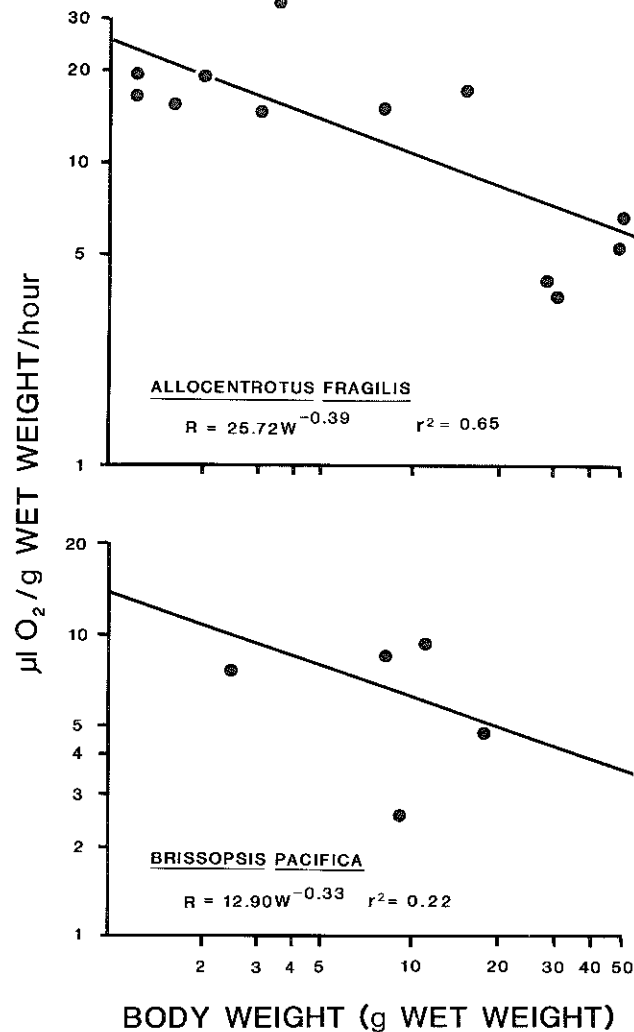
### Oxygen Consumption

The primary respiratory organs in echinoids are their contractile tube feet which exchange oxygen by diffusion. Other tube feet may have specialized chemosensory functions for feeding. *B. pacifica*, a burrower, has specialized tube feet that construct and maintain an ephemeral respiratory funnel to the sediment surface through which water is circulated into the burrow, such as is described for other heart urchins (e.g., Cheshier 1963; Buchanan 1966).

**Effects of Dissolved Oxygen Concentrations.** Both *A. fragilis* and *B. pacifica* consumed oxygen at a constant rate over a range of  $O_2$  concentrations from saturation to anoxia. Regression analysis showed highly significant fits to a linear equation (for *A. fragilis*,  $r^2 = 0.997$ ; for *B. pacifica*,  $r^2 = 0.87$  to  $0.94$ ), indicating that they are respiratory regulators.

Echinoderms have generally been considered to be respiratory conformers (Farmanfarmian 1966). Similar measurements from the Baltic Sea by Dries et al. (1975) showed that many invertebrates can regulate  $O_2$  consumption down to about 10% of saturation. We observed *A. fragilis*, when held below 2 ml  $O_2/L$ , to extend their tube feet to such





**Figure 4.** Size-specific oxygen consumption rates at 8.5°C for the two echinoids studied; smaller individuals consumed more oxygen per unit weight. (Equations given are for oxygen consumption rate as a function of body weight  $W$  (g wet weight)).

an extent that the urchins appeared "fuzzy." This effective increase in respiratory surface area may allow them to regulate  $\text{O}_2$  consumption.

**Measurements of Oxygen Consumption Rates.** Size-specific oxygen consumption rates for each urchin species are shown in Figure 4. Allometric solutions to the regressions were used. The smaller specimens had higher rates per unit weight, but the larger ones consumed larger total volumes of  $\text{O}_2$ . Based on our regressions, an average-sized *B. pacifica* (11.8 g wet weight) consumed about 67.5  $\mu\text{l O}_2/\text{hour}$  and an average-sized *A. fragilis* (43.9 g wet weight) consumed about 258.3  $\mu\text{l O}_2/\text{hour}$ . The fit for *B. pacifica* is not very good and may be due either to the burrowing activities of this species (no

burrowing occurred in the control), or to metabolic factors as discussed below. Oxygen consumption rate measurements gave values that are near to those measured for other echinoderms (Dries 1975; Smith 1983). *A. fragilis* had higher respiration rates than *B. pacifica*, possibly because it inhabits shallower, more oxygenated areas than *B. pacifica*, which exists in highest densities where dissolved oxygen is below 1 ml/L.

**Sediment Oxygen Consumption.** During the course of these experiments, sediment  $O_2$  consumption rates (as controls) were measured 18 times. This measurement reflects chemical oxidation, bacterial and protozoan respiration, etc. The average for 18 measurements was equivalent to 5.32 ml  $O_2$ /sq m/hour, with high variability (coefficient of variation = 61.2%). The variation may be due to differences in organic content, small-scale (cm) differences in microfaunal distributions, or feeding activities of the urchins. Deposit feeding has been shown to stimulate microbial activity (Juniper 1981; Hargrave 1970).

The average value for sediment  $O_2$  consumption is within the range of in situ measurements reported in the literature which range from less than 1 ml  $O_2$ /sq m/hour in the deep north Atlantic (Smith et al. 1978) to 67.8 ml  $O_2$ /sq m/hour near a sewage outfall in Buzzards Bay, Massachusetts (Smith et al. 1973). Values of 2.31 ml  $O_2$ /sq m/hour were reported from the floor of the San Diego Trough (Smith et al. 1974).

### Estimates for Urchins Populations

Size-specific ingestion and  $O_2$  consumption rate measurements can be extrapolated to rate estimates for the populations of each urchin.

There are many problems with extending laboratory data to an in situ context. Metabolic rates are known to be affected by many environmental factors. Temperature, dissolved oxygen tensions, salinity, pH, pressure, and organism size and reproductive condition will all affect metabolic rates (Crisp 1971; Prosser and Brown 1961). For our purposes here, we assume that our measurements are reasonably equitable to in situ rates. From our survey data we know the average densities (for *A. fragilis*, 1.2/sq m; for *B. pacifica*, 11.6/sq m) of each species on the upper slope off Newport. Additionally, we measured size-frequency distributions of samples from each urchin population. We can therefore calculate rates for each size (weight) class in the population and estimate the total population rate by summing the values in all of the size-classes.

The estimates for population ingestion and  $O_2$  consumption rates are shown in Table 2. Upper slope *A. fragilis* populations can consume

Table 2. Estimates of population ingestion and oxygen consumption rates for the two echinoids studied on the upper slope off Newport. These estimates are based on laboratory rate measurements and survey data on densities and population size-frequencies.

Species	Mean Density (No./m <sup>2</sup> )	Ingestion Rate (dry mg/m <sup>2</sup> /hour)	O <sub>2</sub> Consumption Rate (μl O <sub>2</sub> /m <sup>2</sup> /hour)
<i>A. fragilis</i>	1.2	1.9	308.9
<i>B. pacifica</i>	11.6	161.2	794.7

308.9 μl O<sub>2</sub>/sq m/hour, and *B. pacifica* populations can consume 794.7 μl O<sub>2</sub>/sq m/hour, for a total urchin O<sub>2</sub> consumption rate of 1103.6 μl O<sub>2</sub>/sq m/hour. For comparison, Smith (1983) measured in situ oxygen consumption of 1130.7 μl O<sub>2</sub>/sq m/hour by the two dominant echinoderms (ophiuroid and holothuroid) at 1300 m in the Santa Catalina Basin.

*A. fragilis* populations ingest a total of 1.9 dry mg/sq m/hour, and *B. pacifica* populations ingest 161.2 dry mg sediment/sq m/hour, which is equivalent to about 0.05% of the sediment in a square meter per day. *B. pacifica* populations have much higher ingestion rates than *A. fragilis* populations, although *A. fragilis* probably ingests food of higher nutritive value.

### Energetic Considerations

Oxygen is required for aerobic metabolism of food assimilated. In theory, approximately 4.8 cal of food can be oxidized for each milliliter of oxygen consumed (Crisp 1971). Therefore we calculated and compared the calories available from food assimilated and the calories that could be oxidized from oxygen consumed. Such a comparison facilitates evaluation of the metabolism condition of the urchin.

Assimilation efficiencies were estimated from mean C:N concentrations in foregut and hindgut samples from urchins collected in the trawls. These values were used to correct the ingestion rates from our laboratory studies presented above. The proximate nutritional composition of food assimilated was calculated as protein = 6.25 x organic nitrogen (Crisp 1971). Fats in sediment usually compose about 1% (Emery 1960); but for *A. fragilis*, which ingests plant and animal tissue, a value of 10% fat was used. Carbohydrates were estimated by subtraction. Calorific factors of 9.45, 5.65, and 4.1 cal/mg for fat,

protein, and carbohydrate, respectively, were used (Crisp 1971).

For an average-sized *A. fragilis*, the amount of oxygen consumed could metabolize about 29% of the assimilated food (4.23 cal/hour). For an average-sized *B. pacifica*, oxygen consumed could metabolize only about 1.7% of the assimilated calories (18.8 cal/hour). Estimated assimilation efficiencies for these species were probably underestimated but within the normal range of values for deposit feeders (32% for *B. pacifica*; 50% for *A. fragilis*), making interpretation of such low calorific efficiency difficult. Errors in these caloric values exist due to imprecise estimates of assimilation and the estimated proximate composition of food.

Excess calories assimilated (above metabolic requirements) may be used for growth, reproduction, or storage products. Organismal growth rates,  $G$  (dry g/day), were calculated for average-sized urchins as:

$$G = A - R$$

where  $A$  is the assimilation rate and  $R$  is the oxygen consumption rate. Calories were converted to dry grams using a factor of 5.03 cal/mg (Thayer et al. (1973) for the urchin *Arbacia*). The above formula is similar to that used in "scope for growth" measurements made by Widdows et al. (1980) and Martin et al. (1984), except that they also included an ammonia loss term. Recent in situ measurements of ammonia excretion by echinoderms showed that only 0.25% of total metabolic energy losses was from ammonia excretion (Smith 1983); therefore, we ignored this loss in our calculations. It does represent, however, an important loss term and is useful for evaluating differential rates of catabolism of fats, proteins, and carbohydrates under stress (Widdows et al. 1980).

We calculated that, for an average-sized *A. fragilis*,  $G = 14.32$  dry mg/day, and for *B. pacifica*,  $G = 88.05$  dry mg/day. It is difficult to evaluate the accuracy of these estimates. No growth rate estimates for these species were found in the literature, and some form of verification, either from size-frequency analyses of trawl samples or direct measurements of biomass increments in the laboratory, is necessary.

There are numerous other factors that may affect  $G$ . Another energy source is soluble nutrients absorbed by the urchins' epidermal tissue; Stephens et al. (1978) showed that most of the oxidative requirements of the sand dollar, *Dendraster excentricus*, could be absorbed. Other important energy loss terms that should be included are fecal loss, exudia (slime, etc.), and reproductive losses (Winberg 1960; Crisp 1971).

Assuming that  $A$  and  $R$  are the largest of these energy influx and

loss terms, an alternate explanation for such differences in the calories assimilated and oxidized by respiration, for *B. pacifica* at least, is the use of anaerobic metabolic pathways in which the electron acceptors are organic substrates, such as fumarate, rather than oxygen (Hochachka and Mustafa 1972).

## SUMMARY AND CONCLUSIONS

The urchins *A. fragilis* and *B. pacifica* are the most conspicuous organisms of the nearshore basin slope benthos. Existing gradients of decreasing sediment grain-size, increasing organic material, and decreasing dissolved oxygen concentrations over depth are reflected in the distributions, diets, and metabolism of these species.

*A. fragilis* inhabits the upper slopes of the region where sediment organic material (3-6%) and dissolved oxygen (1-5 ml/L) concentrations are moderate. This species was found to assimilate about 3.5 times more food than oxygen consumption could balance. *B. pacifica* inhabits the lower slopes, where organic material is present in high concentrations (6-13%), but where the dissolved oxygen concentrations are very low--below 1 ml/L. This species consumed only enough oxygen to utilize less than 2% of the food assimilated. Although both species can regulate oxygen consumption rates, these results suggest the use of anaerobic metabolism, especially by *B. pacifica*. Oxygen consumption in *A. fragilis* was more equitable to assimilation than in *B. pacifica*, reflecting the higher dissolved oxygen levels on the upper slope compared with the lower slope.

The discharge of sludge on the slopes will probably change the existing organic material and dissolved oxygen concentrations on the sea floor. Sludge is composed of up to 75% organic material and may be ingested as food. Changes in ingestion rate due to this increased food supply, and/or the bioaccumulation and detoxification of contaminants associated with sludge, may result in changes in oxygen consumption rates.

The next steps should be to 1) measure ingestion and oxygen consumption rates using sludge, or its separate components, added to the sediment and 2) compare those rates with the rates presented in this paper. Concurrent measurements of changes in bioaccumulation and detoxification activities within the organism would add an important dimension to our understanding of the effects on organisms of sludge disposal. Most importantly, ingestion and oxygen consumption rates are components of organismal growth and can be used to link changes in organisms to changes in populations, thus providing a fully integrated approach to determining the effects of waste discharge on these indigenous populations.

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