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Energy Relations of the Crustacean Meiobenthos, *Tecticeps japonicus* and *Diastylopsis dawsoni* forma *calmani*

Akira FUJI* and Shigeru NAKAO*

Abstract

The population production of crustacean meiobenthos, *Tecticeps japonicus* and *Diastylopsis dawsoni* forma *calmani*, in Akkeshi Bay, Hokkaido, was analyzed from June 1969 to June 1970, using estimates of average weights and numbers of individuals in each size-group each month of the year. The recruits appear firstly in September for *Tecticeps* and in July for *Diastylopsis*. *Tecticeps* are densely distributed in the inner region of the bay throughout the year. *Diastylopsis* densely populate in the inner region of the bay during summer and autumn, while they distribute closely in the mouth area of the bay during the winter and spring months. From our laboratory results, the observation of the population size and knowledge of the monthly changes in environment temperature, the intake of the *Tecticeps* population and of the *Diastylopsis* population were calculated to be about 2050 cal m⁻² year⁻¹ and 630 cal m⁻² year⁻¹, and the estimate of annual production was given at about 670 cal m⁻² year⁻¹ and 150 m⁻² year⁻¹, respectively. Metabolic heat loss was estimated as 1310 cal m⁻² year⁻¹ for the *Tecticeps* population, and as 390 cal m⁻² year⁻¹ for the *Diastylopsis* population.

In our preliminary study¹⁾ on meiobenthos in Akkeshi Bay, it was pointed out that two crustacean populations, *Tecticeps japonicus* and *Diastylopsis dawsoni* forma *calmani*, were the dominant members among the meiobenthic fauna in this bay. Since secondary producers, such as meiobenthos, interact within the marine ecosystem as consumers, utilizing and recycling the products of net primary production²⁻⁶⁾, they could be expected to influence the energy and nutrient budgets of the marine ecosystem in this bay. Moreover, from the viewpoint of fishery science, they constitute an important fraction of the source of food supply for bottom fishes^{3,4),7-9)}, such as *Limanda schrencki*, *Liopsetta pinnifasciata* and *Platichthys stellatus*, which appear very commonly in this bay¹⁰⁾. Further information concerning the productivity and overall importance of the meiobenthos is necessary for a better understanding of the population dynamics of bottom fishes. For this approach, the specific objects of our study were pointed to clarify the population structure and to assess the annual population production of each species of the dominant meiobenthos.

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Study Area and Station

Akkeshi Bay is located on the easternmost part of Hokkaido, at latitude $43^{\circ}00'$ north and longitude $144^{\circ}50'$ east. As shown in Figure 1, the shape of the bay is roughly round measuring about 10 Km in diameter, and connecting with the Pacific Ocean at its southern part. Two small inlets lie in the mouth area of the bay. The position of routine stations for the present study are illustrated in Figure 1. The bottom sediments vary from coarse sand at the mouth area to very fine sand in the inner region of the bay. Although seasonal hydrographic data were not available for the central area of this bay, sea temperatures were measured from 1967 to 1969. These data indicated that the 5-meter deep sea temperature of Station 9 varies seasonally from 1.5°C to 18°C (Fig. 2).

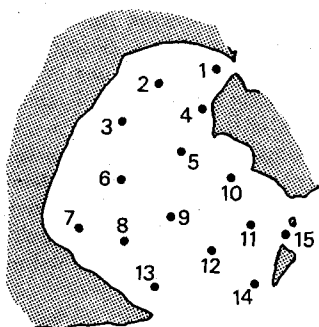


Fig. 1. Map of Akkeshi Bay, showing stations where sampling was performed.

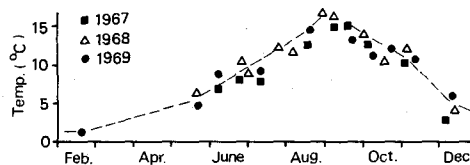


Fig. 2. Sea temperature (5 m in depth) at the central part of Akkeshi Bay.

Materials and Methods

The Smith-McIntyre grab and the modified Tamura's grab were used for sampling the benthic animals. The covering area of a single sampling was 0.1 m^2 for both grabs, and three to five samples were taken at each station. Two species of crustacean meiobenthos, *Tecticeps japonicus* and *Diastylopsis dawsoni formacalmi*, were sorted out from sediments immediately after the sampling by a sieve with a 1-mm square mesh. The animals retained on the sieve were selected and kept in 10% formalin for counting the number of specimens in the laboratory. Besides the sampling for a census of the animals, several samples for clarifying the calorific contents were taken at each station. The animals obtained for this purpose were placed in a drying oven at 60°C , until constant weight was achieved. After drying, the weight of each specimen weighed less than 1 mg each.

Respiratory experiments were carried out in tightly sealed, glass-stoppered bottles of approximately 50 ml to 200 ml volumes, depending on the size of experimental animals. The bottles were placed in temperature-controlled water baths for 5 to 12 hours, the shortest time with large individuals at high temperatures, and the longest time with small animals at low temperatures. After a

given time, the water samples were removed and analyzed for oxygen by using the Winkler method. The differences between experimental and control bottles were used to calculate oxygen consumption. The oxycalorific factor of 4.8 cal per ml oxygen¹¹⁾ was employed to convert oxygen consumption to the calorific equivalent.

The calorific contents of the animals were determined with the Nenken YM-B type adiabatic oxygen bomb calorimeter after air drying at 60°C. The animals were combined to form pellets of similar-sized individuals prior to insertion in the bomb. In the calorific measurements, to some small samples were adopted the Karzinkin and Tarkovskaya modification¹²⁾ of the Wet combustion method.

Results

Population structure

The size structure was estimated on the basis of body weight distribution. The measurements of dry weight were divided into each group representing a range of 1 mg for *Tecticeps* and of 0.2 mg for *Diastylopsis*. Then the frequency of each group was represented into percentage. The bimodal frequency distribution obtained was graphically analyzed by making use of a probability graph paper derived from Harding¹³⁾. The frequency distribution of each group is represented in Figure 3, together with several fitted normal curves which were calculated by such a procedure. From this treatment, it is possible to determine the growth rate of the mean body weight of each of the size-group and to estimate the size-group structure in percentage occupancy. The results are illustrated in Table 1 and Figure 4, respectively. It can be seen from these results that the most rapid growth in the mean weight of each size-group of *Tecticeps* and *Diastylopsis* occurs in the autumn and winter months, and that it is the least rapid the other seasons. The recruiting members appear firstly in September for *Tecticeps*, in July for *Diastylopsis*, and they increase rapidly in number.

Figure 5 shows the results of the field work in terms of the number of animals per unit area (1 m²). As to the *Tecticeps* population, the high density of this animal tends to occur in the inner region of the bay throughout the year, although a level of density fluctuates markedly with successive months. In this annual pattern of distribution, it is noted that the marked high density in the months of early autumn (September and October) is found in the region of the inner part and the eastern coast of the bay. A numerical increase in density during the early autumn may be attributable to a recruitment of new members because of a domination of the small-sized animals as already shown in Figure 3. The annual distribution pattern of *Diastylopsis* differs slightly in extension from that of *Tecticeps*. *Diastylopsis* populate densely in the inner region of the bay in the months covering summer and autumn. From winter to spring, however, they populate highly in numerical density in the region covering from the mouth of the bay to the southwestern coast.

The population size for the entire area of the bay makes it possible to calculate on the basis of the average density at various habitats and the size-group structure

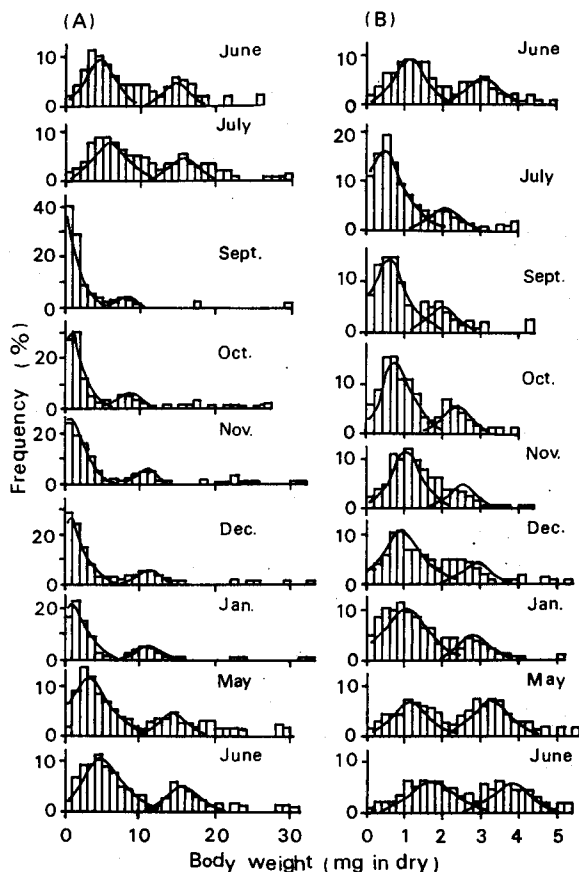


Fig. 3. Histogram showing the size frequency and several fitted normal curves calculated by the probability graph paper method. A: *Tecticeps* population, B: *Diastylopsis* population.

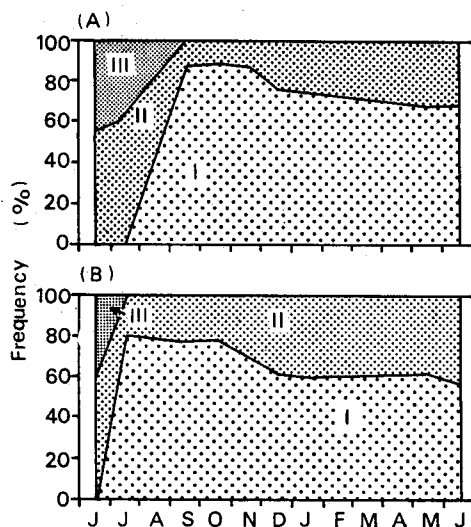
in percentage occupancy. This estimate is shown in Table 2. Here the weight of each size-group is estimated as the product of the number of individuals and the average weight. The sum of the weight of the separate size-groups gives the biomass (Table 3).

Production rate of natural population

The magnitude for population increment attributed to the individual growth is taken to be the difference between the initial and final body weight multiplied by the arithmetical mean of the initial and final population density. If it is positive, the difference between the initial and final population density multiplied by the arithmetical mean of the initial and final body weight corresponds to the

Table 1. Seasonal change in the average dry weight (mg) per individual. Each roman number indicates size-group.

Month	<i>Tecticeps japonicus</i>			<i>Diastylopsis dawsoni</i>		
	I	II	III	I	II	III
June	—	5.0	15.1	—	1.1	3.0
July	—	6.3	16.1	0.6	1.8	—
Sept.	0.3	7.0	—	0.6	1.8	—
Oct.	0.6	8.7	—	0.8	2.3	—
Nov.	1.3	10.3	—	1.0	2.5	—
Dec.	1.5	12.0	—	1.0	2.6	—
Jan.	1.5	12.3	—	1.0	2.8	—
May	4.0	15.2	—	1.3	3.3	—
June	5.2	15.6	—	1.7	3.8	—

Fig. 4. Size-group composition of the *Tecticeps* population (A) and the *Diastylopsis* population (B).

magnitude for immigrants. On the other hand, if it is negative, the above computation is taken to be the population loss attributed to mortality, emigration and predation. The annual production of the population is the sum of the growth increment for individuals, the addition of the newly born individuals and the immigrants.

The estimation on the population production of *Tecticeps* and *Diastylopsis* was made during a whole year, and the results in terms of the production structure were calculated as shown in Table 4. The net production per unit area per definite time varies from time to time and there are some differences in the seasonal pattern of

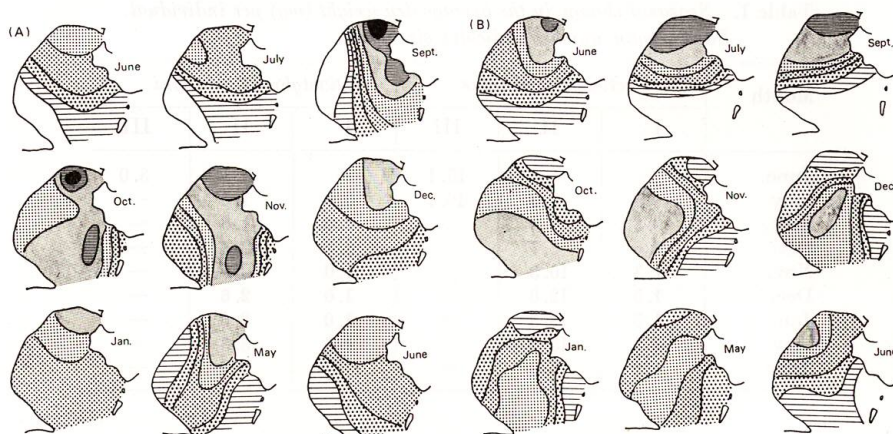


Fig. 5. Distribution of *Tecticeps japonicus* (A) and *Diastylopsis dawsoni* (B) in Akkeshi Bay. □: 0 ind./m², ▨: 0-5 ind./m², ▩: 5-10 ind./m², ▪: 10-30 ind./m², ▫: 30-50 ind./m², ▬: 50-100 ind./m², ▮: 100-500 ind./m², ■: more than 500 ind./m².

Table 2. Population sizes in numbers per square meter for *Tecticeps* and *Diastylopsis* living on the entire area of Akkeshi Bay. Roman numbers are the same as those shown in Table 1.

Month	<i>Tecticeps japonicus</i>			<i>Diastylopsis dawsoni</i>		
	I	II	III	I	II	III
June	—	8.26	6.06	—	16.48	10.50
July	—	8.48	4.37	46.64	10.10	—
Sept.	58.87	8.03	—	37.76	9.26	—
Oct.	70.31	7.69	—	31.85	9.09	—
Nov.	58.76	7.78	—	20.71	8.71	—
Dec.	24.86	7.14	—	14.91	9.61	—
Jan.	22.50	6.75	—	13.31	8.58	—
May	16.09	6.77	—	13.09	7.76	—
June	12.00	5.27	—	8.93	8.28	—

the net production of those two crustacean meiobenthos. The largest production of the *Tecticeps* population occurs between September and November, whereas the dominant production of the *Diastylopsis* population occurs from September to November and from May to July.

The annual balance sheet of biological production for those two crustacean populations is summarized in Table 5. The annual growth amounts to 222.6 mg per m² (or 667.8 cal per m²) for the *Tecticeps* population and 47.2 mg per m² (or 146.3 cal per m²) for the *Diastylopsis* population. The recruitment of 22.8 mg per m² and 28.0 mg per m² per year contributes considerably to the annual net produc-

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Table 3. Changes in the biomass (mg/m²) of two crustacean populations with the progressive months. Each roman number indicates size-group.

Month	<i>Tecticeps japonicus</i>			<i>Diastylopsis dawsoni</i>		
	I	II	III	I	II	III
June	—	41.30	91.51	—	18.13	31.50
July	—	53.42	70.36	27.98	18.18	—
Sept.	17.66	56.21	—	22.65	16.67	—
Oct.	42.19	66.90	—	25.48	20.91	—
Nov.	76.39	80.13	—	20.71	21.78	—
Dec.	37.29	85.68	—	14.91	24.99	—
Jan.	33.75	83.02	—	13.31	24.02	—
May	64.36	102.90	—	17.02	25.61	—
June	62.40	82.21	—	15.18	31.46	—

Table 4. Production structure for the meiobenthos. All data indicate dry weight (mg) per square meter.

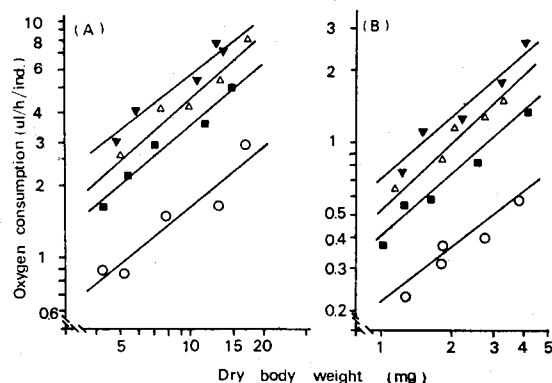
Species	Duration	Growth (mg)	Recruit (mg)	Immigration (mg)	Predation, Mortality and Emigration (mg)
<i>Tecticeps japonicus</i>	June- July	16.1	—	1.2	26.4
	July- Sept.	5.8	17.7	—	—
	Sept.- Oct.	32.8	5.1	—	2.7
	Oct.- Nov.	57.6	—	0.9	11.0
	Nov.- Dec.	21.1	—	—	54.6
	Dec.- Jan.	2.1	—	—	8.2
	Jan.- May	67.9	—	0.3	17.6
	May- June	19.2	—	—	41.9
<i>Diastylopsis dawsoni</i>	June- July	9.3	28.0	—	40.8
	July- Sept.	—	—	—	6.8
	Sept.- Oct.	11.6	—	—	4.4
	Oct.- Nov.	7.1	—	—	10.6
	Nov.- Dec.	0.9	—	1.1	5.8
	Dec.- Jan.	1.8	—	—	3.2
	Jan.- May	8.1	—	—	2.8
	May- June	8.4	—	1.9	6.2

tion of 247.8 and 78.2 mg per m² per year. The loss of population, which is attributed to natural mortality, predation and emigration, in this study, is not known separately. So the loss of population is lumped together, and 235.8 and 80.6 mg per m² per year corresponds to the above loss from the *Tecticeps* population and from the *Diastylopsis* population, respectively.

It is generally agreed that the logarithm of oxygen consumption, R , is linearly related to the logarithm of an individual dry weight, W . The exponential equa-

Table 5. Annual balance sheet for the meiobenthic populations living on the entire area of Akkeshi Bay, from June 1969 to June 1970.

Items	<i>Tecticeps japonicus</i>		<i>Diastylopsis dawsoni</i>	
	mg/m ²	cal/m ²	mg/m ²	cal/m ²
CREDIT SIDE				
Initial biomass	132.8	398.4	49.6	153.8
Growth	222.6	667.8	47.2	146.3
Recruitment	22.8	68.4	28.0	86.8
Immigration	2.4	7.2	3.0	9.3
DEBIT SIDE				
Predation, Mortality and Emigration	235.8	707.4	80.6	249.9
Final biomass	144.6	433.8	46.6	144.5

Fig. 6. Logarithmic plot of oxygen consumption against body weight of *Tecticeps* (A) and *Diastylopsis* (B). ○: 6.0°C, ■: 13.0°C, △: 18.0°C, ▼: 23.5°C.

tion is $R=aW^b$ where a is a constant, and b is a regression coefficient. Figure 6 shows the oxygen consumption per unit hour per animal plotted against dry weight on logarithmic scales for a range of temperature. The linear relationship is found throughout the size ranges investigated at each temperature. No significant difference is recognized among the b (regression coefficient) of the regression lines when tested by the analysis of variance ($F_{(0.05)}=27.05 > F_0=15.00$ in *Tecticeps*, and $F_{(0.05)}=27.05 > F_0=2.47$ in *Diastylopsis*). Then, the regression formulae calculated from the pooled data are estimated as follows:

$$\textit{Tecticeps} \quad R = aW^{0.8100} \quad (1)$$

$$\textit{Diastylopsis} \quad R = aW^{0.8253} \quad (2)$$

When the constant a in the oxygen consumption - dry weight regression equation was plotted against temperatures of 6°C to 23.5°C, they fell closely about a

straight line (Fig. 7). The equations are described as follows:

$$\textit{Tecticeps} \quad a = 0.0389 t + 0.0330 \quad (3)$$

$$\textit{Diastylopsis} \quad a = 0.0307 t + 0.0021 \quad (4)$$

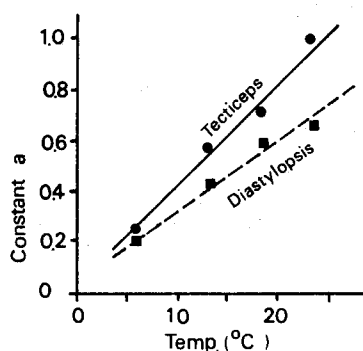


Fig. 7. Values of the constant a , denoting the intercept with the ordinate, belonging to the regressions of \log_{10} oxygen consumption on \log_{10} dry body weight at several temperature.

They are used to compute a value for various temperatures. The value of expressing metabolism (R) as a function of temperature (t) and body weight (W) is of especial interest, particularly in studies pertaining to the bio-economics of ecological system. Such relationships are obtained in the present study by combining equations (1), (2) and (3), (4), and are shown thus

$$\textit{Tecticeps} \quad R = (0.0389 t + 0.0330) W^{0.8100}$$

$$\textit{Diastylopsis} \quad R = (0.0307 t + 0.0021) W^{0.8253}$$

The above equations were used to correct the respiration metabolism of the populations as a function of temperature (Fig. 2), dry body weight (Table 1) and population size (Table 2). The energy lost by metabolic activities is easily estimated from the indirect method of converting respiration rate into heat output by the application of an oxycalorific coefficient. There are 1310 cal per m^2 per year in the *Tecticeps* population and 390 cal per m^2 per year in the *Diastylopsis* population. An energy assimilated from food is equal to the sum of energy used for the formation of new tissues (growth increment) and energy used for muscular work and maintenance which are lost to the surroundings as heat. The food assimilated is amounted to 1980 cal per m^2 per year for the *Tecticeps* population and 540 cal per m^2 per year for the *Diastylopsis* population.

Discussion

It should be emphasized that many assumptions have been made in order to estimate the productivity of the crustacean population. Our data, as shown in Table 5, were based on the following assumptions; (1) they are composed of two groups, which are based on the analysis of their successive growth pattern,

(2) the growth includes an increment of the body weight owing to carrying the eggs, (3) the loss by ecdysis is out of consideration. Corey¹⁴) drew together all known data on the occurrence of mature males and gravid females of several species of cumacea, and he inferred that most subtidal species probably breed twice whereas most deep water species breed once per annum. Of the above assumptions, although nothing is known about the time of year when mature males and gravid females occur for *Diastylopsis* and *Tecticeps*, belonging to the cold-water species¹⁰⁾¹⁵⁾, it is assumed that they breed once annually during the summer months because of the one appearance of the small-sized member throughout the year.

A flow sheet diagram facilitates the description of the flow and use of energy through a population. Figure 8 indicates schematically the rate of energy flow through the crustacean population. The energy entering the population is the sum of the energy assimilated as food, the rate of immigrants, and the recruitment members. As for the *Tecticeps* population, these values are 1978 cal per m², 68 cal per m² and 7 cal per m², respectively, and 2053 cal per m² gives an input rate of energy. On the other hand, the whole amount of energy converted by the population during a whole year is 2685 cal per m². However, since the energy remained as the growth increment into the population corresponds to 668 cal per m², it can be seen that the true value for the energy lost from the population amounts to 2017 cal per m². For this reason, the value of 36 cal per m² is equal to

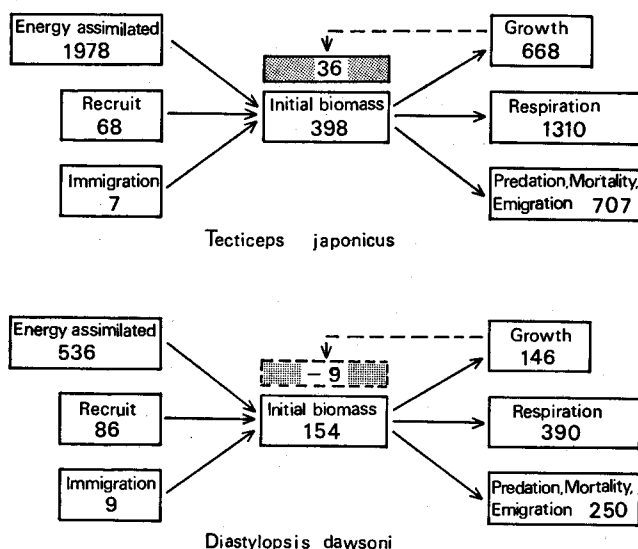


Fig. 8. Scheme showing the annual energy flow for two crustacean populations. The arrow indicates the direction of energy conversion. Rates are cal per m² per year. Shadow area shows a difference between initial and final biomass. Values for the initial biomass are cal per m².

the actual amount of energy which was added into the population during a whole year. Regarding the *Diastylopsis* population, it is computed the same manner, as mentioned above, that its co-ordinate value is -9 cal per m² per year.

McNeill & Lawton¹⁶⁾ found that the common logarithm of metabolism (R) and the common logarithm of production (P) in short-lived poikilotherms, in which category isopoda and cumacea lie, fell closely about a regression line given by the following equation:

$$\log_{10} R = 0.1352 + 1.1740 \log_{10} P$$

Values for the *Diastylopsis* population ($R=390$ cal per m² per year, $P=146$ cal per m² per year) and for the *Tecticeps* population ($R=1310$ cal per m² per year, $P=668$ cal per m² per year) were found to fit the line quite well. This relationship may be useful as a short-cut method in predicting the total energy flow through a population of which either metabolism or production is known.

The study of bio-economics enable one to make prediction in general terms about production processes in a variety of food relationships into the animal community. One sort of such prediction is the ecological efficiency rates. The average percentages of assimilated energy lost in respiration (respiration efficiency), 66% in *Tecticeps* and 72% in *Diastylopsis*, are slightly lower than the value of 75% derived from Teal¹⁷⁾ for nematodes and polychaetes. But these values are within the range found for other marine invertebrates, and these published data on respiration efficiency add support to the present findings. Growth efficiency (production \times 100 / assimilation) for the *Diastylopsis* population and *Tecticeps* population is 33% and 27%, respectively. These values bear a close resemblance to 25% for nematodes¹⁷⁾ and 33% for *Orchelimum fidicinium*¹⁸⁾, both of which are partial detritus feeders in a salt marsh community. Slobodkin¹⁹⁾ pointed out that growth efficiencies of 20-28% may be considered almost universal. Working with meiobenthos, Sanders²⁰⁾ calculated a production of the above twice biomass for species living more than one year and estimated a factor of five for short-lived species, with two generations per annum. Richards & Riley²¹⁾ found that the turnover rate (net production/average biomass) of the *Neomysis* population was about 3.66. Cooper²²⁾ discussed the turnover of a freshwater amphipoda population, the *Hyalella azteca*, and he estimated it at about 3.2. On the other hand, in one marine amphipoda population, the co-ordinate rate of 1.1 was reported by Yamamoto *et al.*²³⁾ Chironomid biomass was replaced 8-9 times each year in the shallows and 2-3 times in the deep colder waters²⁴⁾. Such information would allow one to estimate an approximate production of meiobenthos population based on the average biomass. In our study, the average biomass was estimated 116.3 mg per m² for the *Tecticeps* population and 43.4 mg per m² for the *Diastylopsis* population (Table 3). If a turnover rate of 2.0 is admissible for the benthic members investigated in the present study, the annual net production is computed about 230 mg per m² and about 86 mg per m² for each respective population. These computations bear a close resemblance to 248 mg per m² and 78 mg per m² of their annual net production.

The ecological efficiency of the population is possible to calculate from the

equation: $E \times 100/C$, where E is the energy passing to the next higher trophic level and C is the food ingested. The next higher trophic level, in this context, means predators, i.e. bottom fishes or other lower predacious benthic members. Since the loss from the population, which is attributed to natural mortality, predation and emigration, in our study, is not known separately, we have no information on the ratio of apportionment among them. As far as the feeding habits of the meiobenthos are concerned, most representatives of the same are epistrate feeders and/or deposit feeders^{25,26}) and the assimilation efficiencies of 36–86%, with about 60% in most species, have reported on several deposit-feeding macro- and meio-benthos^{18),27–29}). Assuming for the moment that the one third of loss of population is taken up by predators, and that the assimilation efficiency is 60%, the value of 7% for the *Tecticeps* population and 9% for the *Diastylopsis* population corresponds to the ecological efficiency. Slobodkin³⁰) suggested that ecological efficiencies fall in the range of 6–15%.

The contribution of the meiobenthos, in terms of productivity and energy provided for predators, is difficult at present to assess because of the scarcity of the knowledge about food supply for bottom fishes or other predacious benthic animals in Akkeshi Bay. It is important to gain as much information as possible on the ecological energetics of the multiple relations between these meiobenthos and their predators in a given natural environment. Further study along this direction may provide a better understanding of the functional role of the meiobenthic fauna within the food web in shallow waters.

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