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The relation between daily food intake and growth of the Pacific mangrove prawn Palaemon debilis Dana and its Atlantic relative Palaemon elegans Rathke, both from the Gulf of Elat

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Abstract

The behaviour and distribution of *Palaemon debilis* Dana was studied in mangrove lagoons along the east coast of Sinai. Food intake and growth of this prawn were measured in the laboratory and compared with the related Atlantic species *Palaemon elegans* Rathke, occuring in a saltwater fishpond at Elat. Daily food intake was similar in both species and correlated with their metabolic weight. By feeding groups of prawns different rations of prawnmeat during fourteen days the daily maintenance ration was estimated as approximately 14 percent of the metabolic dry weight while the net food conversion was estimated as 0.4. The role of *Palaemon debilis* in the mangrove foodweb is discussed.

Introduction

The most northern mangroves in the Red Sea area are found along the eastcoast of Sinai. Dwarfed mangrove trees, *Avicennia marina*, grow in patches along the shores of saltwater lagoons, separated from the sea by a shallow dead reef barrier and subjected to a tidal fluctuation in water height. The general situation, hydrography, flora and fauna of these mangroves or Shuras have been described by POR, DOR and AMIR (1977). Daily fluctuations in water temperature in the lagoons vary from 9° to 20°C in winter and from 28° to 36°C in summer, while salinity ranges from 40‰ S in winter to 47–48‰ S in summer.

The Indo-West Pacific mangrove prawn *Palaemon debilis* Dana (HOLTHUIS 1950) is abundant in the lagoons, particularly in the shallow area bordering the zone of *Avicennia* aerial roots or pneumatophores. During high tide the prawns search for food on the sandbottom and young ones enter the very shallow intertidal areas. With the receding tide they migrate to deeper and more sheltered resting places near the dense vegetation of *Avicennia* pneumatophores and often stick together in pelagic swarms or schools. This behaviour might be a mechanism to escape from predators such as the fishes *Aphanius dispar*, *Mugil* spp. and young *Therapon jerbua*, which are abundant in the lagoons.

A general picture of *Palaemon debilis* is shown in Figure 1, the size distribution of the prawns from samples collected in June (1979) is shown in Figure 2. Egg-carrying females (30–37 mm length) usually stay close by or on the aerial roots of the mangrove trees. They carry about 200 to 270 eggs, approximately 15–20 % of their wet weight with eggs, or 20–35 % of their dry weight without eggs. At 22° to 24°C the eggs hatch after 29 to 35 days. Fifteen females and four males kept in the laboratory showed monthly spawning from the end of December until the end of September next year.

The newly-hatched pelagic zoea larvae (Fig. 1) are 3.2–3.6 mm long and closely resemble those of *Palaemon elegans* Rathke (TSURNAMAL 1963, FINCHAM 1977). They are positively phototactic and rheotactic, swimming upside down and backwards against the current with an estimated speed of at least 2 cm per second. They catch zooplankton and also non-living food particles up to half their own size. At 26°C metamorphosis to the demersal postlarval stage takes place fourteen days after hatching at a length of 7–7.5 mm. The demersal young grow about 5–7 mm per month.

Considering its abundance, *Palaemon debilis* probably plays an important role in the mangrove food web. Therefore food intake and growth of this prawn were studied in

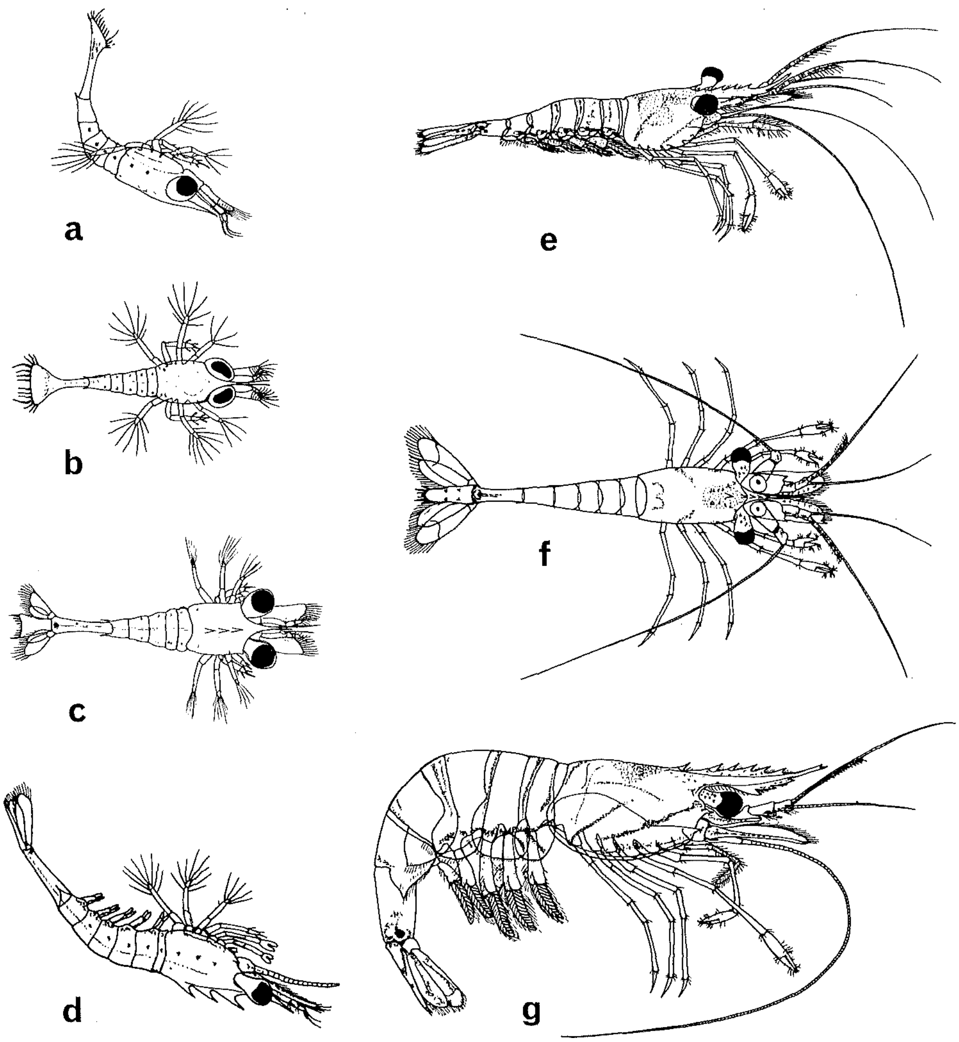

Figure 1

Palaemon debilis Dana. a and b: newly hatched zoea (3.2 mm), a shows the normal swimming position; c: older zoea stage (4 mm); d: final pelagic stage in normal swimming position (6.5–7 mm); e and f: demersal young prawns (14 mm); g: adult female (34 mm)

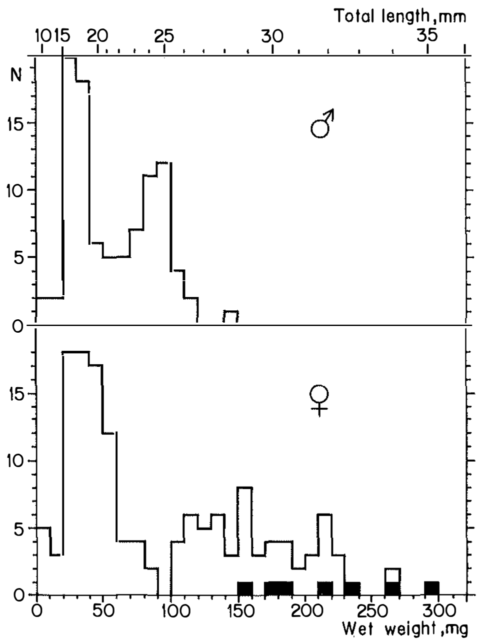

Figure 2

The lenght (L, mm) and wet weight (W, mg) distribution of male and female *Palaemon debilis* collected in the Shuras in June 1979 (hatched = females with eggs). The relation between length and wet weight can be described by $W = 0.0028\ L^{3.25}$ (W dry = $0.00059\ L^{3.31}$).

the Steinitz Marine Biology Laboratory (Elat), in comparison with the closely related Atlantic-Mediterranean species *Palaemon elegans* (HÖGLUND 1943, FORSTER 1951) which occurred in a saltwater fishpond near the laboratory, probably introduced with fish from the Mediterranean.

Methods

The behaviour and distribution of *Palaemon debilis* in the mangrove lagoons was studied by snorkel diving. Samples of prawns were collected with handnets and males were separated from females on account of the sexual appendage on the second pleopod. Some prawns were kept in aquaria in the laboratory at 22-24 °C and larvae were reared in a round black polythene tank (65 cm diameter x 35 cm high) with *Brachionus*, "Tetramin" aquarium fishfood or finely chopped mussel as food (cf. KNOWLTON 1974, SCHULTE 1976, ROCHANABURANON and WILLIAMSON, 1976, SANDIFER and SMITH, 1979). The growth rate of pelagic larvae and early demersal stages were estimated for about 200 young prawns reared to a size of 12-16 mm at 26°C and 30 ‰ S.

Survival at extremely low or high temperatures and salinities was estimated with laboratory reared *Palaemon debilis*. Groups of 5 to 10 young prawns (about 15 mm) were transferred directly to different salinities, while for other groups temperature or salinity were gradually increased or decreased in steps of 2–5 degrees Celsius or promille salinity per week.

Measurements of food intake and growth were started with freshly caught *Palaemon debilis* and *P. elegans*, graded into different length classes. Groups of prawns were kept in the laboratory at room temperature (25–27 °C) in small transparent plastic tanks of 11 x 11 x 6 cm, in seawater (40 ‰ S) with an air supply. They were fed with a weighed excess amount of chopped prawn meat, daily prepared from freshly caught *Palaemon elegans*, and food left over was collected and weighed back the next day before changing the seawater in the tanks. One control tank was used to estimate the decrease in weight of the prawn meat in seawater and the estimated food consumption was corrected accordingly (cf. KLEIN BRETELER 1975).

Table 1

Dry weight as % of wet weight, fat content as % of dry weight, ash content as % of fatfree dry weight, and the calculated energy values in Joules per mg dry weight of the food and the prawns at the start (22 Oct.) and the end (5 Nov.) of the food intake measurements.

Palaemon debilis						*Palaemon elegans*					
Group code	Numbers of shrimp	Dry W %	Fat %	Ash %	Energy J/mg	Group code	Numbers of shrimp	Dry W %	Fat %	Ash %	Energy J/mg
Start:	24	25.1	2.9	24.5	17.9	Start:	26	25.3	3.6	22.0	18.6
End:						End:					
A 1–4	19	26.2	4.2	21.4	18.8	A 2–9	14	25.4	4.0	19.6	19.2
B 1–4	18	25.4	4.2	21.4	18.8	B 2–8	7	25.0	4.2	20.0	19.1
C 1–4	17	24.4	3.4	22.3	18.5	C 2–8	7	23.7	3.9	22.3	18.6
D 1–4	18	23.7	2.5	22.9	18.2	D 2–8	7	23.2	2.3	23.1	18.1
E 1	5	23.7	3.9	24.5	18.1	E 2	4	20.4	2.8	25.7	17.6
Food weighed in:						Food weighed out:					
shrimp meat:		19.0	3.4	13.8	20.4	shrimp meat:		15.6	1.6	16.2	19.5
algae:		21.6	0.8	70.0	6.2						

Different rations were given in four series of tanks by feeding every day (series A), once in two days (B), once in three days (C) and once in four days (D). In an extra tank (E) the prawns were fed daily with soft algae. The numbers and sizes of the prawns in the tanks are shown in Table 2.

At each feeding samples of food were dried at 80 °C. At the start of the experiment samples of prawns were rinsed shortly in freshwater to remove seawater and dried similarly, in order to estimate the dry weight of the animals in the tanks. All prawns were dried after the final measurements at the end of the experiment. The samples of food and prawns were stored during four weeks in chloroform and fat content was estimated by the decrease in dry weight (cf. BEUKEMA and de BRUIN 1979). Finally all samples were burned 1.5 hour at 600 °C to estimate ash content. Data on dry weight, fat- and ash content are summarized in Table 1. The energy value in Joules was approximated by multiplying fat with 36 J/mg (8.6 cal) and ashfree-fatfree dry weight with 23 J/mg (5.5 cal) for protein (1 calory = 4.186 Joules).

In some samples of *Palaemon debilis* the amount of amylase and tryptic active enzyms, relative to total soluble body proteins, was estimated by the method of SAMAIN et al. (1977).

Respiration was measured for two groups of *Palaemon debilis* and *P. elegans* in two sealed conical flasks of 2 liter volume, with a seawater supply at the bottom and an outflow at the top. The oxygen content of the water was measured by Winkler titration

Table 2

Numbers of prawns at the start (N_1, 22 Oct.) and at the end of the experiment (N_2, 5 Nov.), numbers of skins (S), mean length (L), weight (W) and metabolic dry weight ($W^{0.8}$) of the prawns, mean food intake per meal in mg wet weight, mean daily food intake and daily growth in mg dry weight and as percentage of the metabolic dry weight of the prawns (%$W^{0.8}$)

Ration code Tank no.	Numbers N_1 N_2	S	Mean L mm	Mean wet W mg	Mean dry W mg	Mean $W^{0.8}$	Food intake (wet weight) mg per meal Mean ± S.D.	Daily food mg	Daily food % $W^{0.8}$	Daily growth mg	Daily growth % $W^{0.8}$
Palaemon debilis											
A 1	5–5	6	16	24	5.9	4.1	6.1– 1.9	0.9	22.0	0.13	3.13
2	5–5	5	19	46	11.8	7.2	6.6– 3.7	1.1	15.1	0.04	0.50
3	5–5	8	23	81	20.8	11.3	12.3– 5.7	1.7	15.0	0.06	0.57
4	4–4	4	30	172	45.3	21.1	23.2–10.6	3.1	14.7	0.24	1.15
								Mean:	16.7		1.34
B 1	5–5	3	17	28	7.2	4.8	10.7– 2.1	0.8	16.0	0.04	0.74
2	5–5	4	19	43	11.1	6.9	14.5– 3.0	1.0	15.1	0.01	0.21
3	5–4	5	23	79	19.8	10.9	20.1– 2.2	1.5	13.4	– 0.06	– 0.59
4	4–4	4	29	153	38.8	18.6	35.4– 5.1	2.6	13.8	0.04	0.19
								Mean:	14.6		0.14
C 1	5–5	4	18	39	9.8	6.2	17.5– 4.1	0.7	11.1	– 0.06	– 0.92
2	5–5	1	21	56	14.2	8.3	23.3– 5.7	0.9	11.1	– 0.02	– 0.26
3	5–3	0	25	98	24.9	13.1	28.5– 7.8	1.4	10.9	– 0.12	– 0.93
4	4–4	1	30	194	46.4	21.5	46.0– 6.3	2.3	10.6	– 0.16	– 0.73
								Mean:	10.9		– 0.71
D 1	5–5	4	19	38	9.1	5.8	15.4– 5.3	0.6	9.8	– 0.12	– 2.09
2	5–5	2	20	47	11.7	7.2	18.0– 4.6	0.7	9.4	– 0.04	– 0.60
3	5–5	0	24	97	21.0	11.4	33.7– 4.7	1.3	11.1	– 0.26	– 2.26
4	4–3	2	32	232	58.1	25.8	58.1–22.4	2.0	7.8	– 0.44	– 1.72
								Mean:	9.5		– 1.67
E 1	5–5	3	19	47	11.6	7.1	21.1– 8.7	3.2	45.5	– 0.16	– 2.31
Palaemon elegans											
A 5	5–4	6	21	81	20.3	11.1	10.9– 3.9	1.6	14.7	– 0.06	– 0.55
6	4–4	6	27	178	44.8	20.9	21.8– 7.2	3.0	14.3	– 0.03	– 0.15
7	3–3	3	30	245	62.5	27.3	28.4– 8.6	3.9	14.1	0.08	0.28
8	2–2	3	36	443	111.5	43.4	44.6–11.7	6.6	15.1	– 0.30	– 0.69
9	1–1	2	43	777	198.3	68.8	79.3–26.8	10.2	14.6	1.50	2.18
								Mean:	14.6		0.21
B 5	4–4	4	26	156	38.8	18.7	32.7– 6.4	2.5	13.1	– 0.35	– 1.89
6	3–1	2	30	236	59.1	26.1	46.2– 6.8	3.4	13.2	– 0.17	– 0.65
7	2–1	2	37	455	114.1	44.3	84.9–24.3	6.3	14.2	– 0.12	– 0.28
8	1–1	1	45	905	230.1	77.5	97.3–37.1	7.9	10.2	– 0.16	– 0.21
								Mean:	12.7		– 0.76
C 5	4–4	4	27	170	41.2	19.6	36.1– 1.8	1.8	9.4	– 0.45	– 2.28
6	3–1	2	35	390	98.2	–	– –	–	–	–	–
7	2–1	2	38	514	128.3	48.6	81.4–28.6	4.8	9.9	– 0.05	– 0.09
8	1–1	1	45	854	205.5	70.8	143.2–66.8	7.2	10.2	– 1.15	– 1.62
								Mean:	9.8		– 1.33
D 5	4–1	3	28	190	46.1	–	– –	–	–	–	–
6	3–2	1	34	362	85.4	35.1	65.6–11.1	2.6	7.4	– 1.45	– 4.12
7	2–2	0	38	500	121.0	46.4	89.5– 4.5	3.5	7.6	– 1.38	– 2.98
8	1–1	0	45	903	225.4	76.3	145.0–13.7	5.7	7.5	– 0.98	– 1.29
								Mean:	7.5		– 2.86
E 2	4–4	1	26	141	32.4	16.2	21.0–10.1	5.3	32.8	– 0.78	– 4.84

and oxygen consumption of the prawns was estimated by the decrease in oxygen saturation in the flasks when the seawater flow was stopped for several hours, corrected for the B.O.D. of the water (Table 4).

Results

Palaemon debilis appears to be extremely eurytherm and euryhaline. Young animals survive in good health a direct transfer from 30‰ S to 6‰ S and to 60‰ S. With gradual acclimation lethal limits were reached at 80‰ S and at 0.3‰ S; they always died in freshwater. Lethal temperature limits were reached at 7–8 °C and at 39–40 °C.

All data on food intake and growth of the prawns are compiled in Table 2. Food intake in mg dry weight is plotted against the mean dry weight (W, mg) of the prawns in the different tanks on a double logarithmic scale in Figure 3, the calculated relations between daily food consumption and body weight are shown in Table 3.

Table 3

The exponential relation between daily food intake (dF) and body weight (W), both as mg dry weight, of the prawns at the four rations A to D. Values of p and q in the equation $dF = pW^q$ for *Palaemon debilis* (tanks 1 to 4) and *P. debilis* + *P. elegans* together (tanks 1 to 9)

Palaemon debilis					*Palaemon debilis* + *P. elegans*				
Ration groups and tanks	p	q	Correlation	n	Ration groups and tanks	p	q	Correlation	n
A 2–4	0.166	0.768	0.999	3	A 2–9	0.150	0.796	0.999	8
B 1–4	0.191	0.704	0.996	4	B 1–7	0.171	0.744	0.997	7
C 1–4	0.119	0.770	0.999	4	C 1–8	0.118	0.764	0.998	7
D 1–4	0.146	0.662	0.978	4	D 1–8	0.141	0.672	0.994	7

Table 4

Measurements of oxygen consumption in 2-liter flasks with *Palaemon debilis* (14→11 prawns, length 27 mm, mean wet weight 118.5 mg, dry 30.2 mg) and *P. elegans* (11→10 prawns, length 27–30 mm, mean wet weight 137 mg, dry 34.9 mg)

Date: Nov. 1979	Time of measurements: hours	Temp.: °C	*Palaemon debilis* mg O_2 24 hrs	*Palaemon debilis* mg O_2/day $W^{0.8}$	*Palaemon elegans* mg O_2 24 hrs	*Palaemon elegans* mg O_2/day $W^{0.8}$
8	11–14	24.5	2.22	0.145	1.86	0.108
8	15–17	24.8	2.01	0.132	2.01	0.117
9	11–13	26.0	1.62	0.106	2.01	0.117
10*	13–15	24.0	2.05	0.134	2.28	0.113
10**	17–19	25.0	2.34	0.153	2.43	0.141
11	9–12	24.0	2.35	0.154	1.86	0.108
14	12–15	25.5	1.13	0.074	2.18	0.127
* after feeding		Mean	1.96	0.128	2.09	0.121
** in the evening		S. D.	0.44	0.029	0.22	0.013

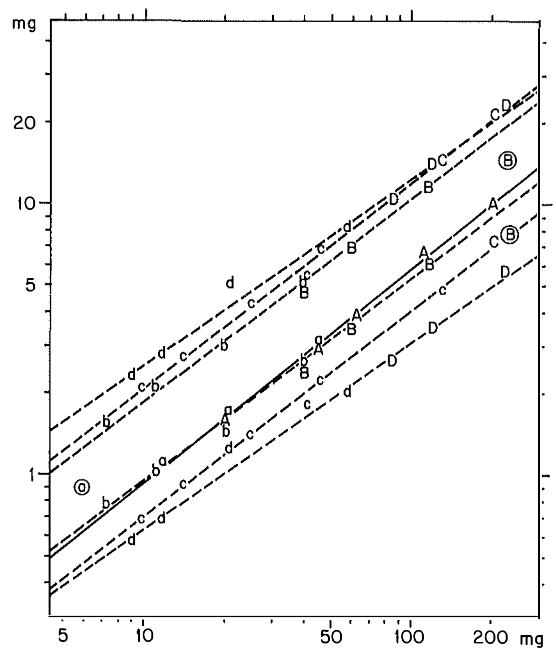

Figure 3

A double logarithmic plot of body weight (horizontal) against food intake (vertical), both in mg dry weight. The different rations are indicated as a, b, c, d for *Palaemon debilis* and as A, B, C, D for *P. elegans*. The drawn line indicates the daily fed groups (a, A), the upper hatched lines indicate food intake per meal at the different feeding frequencies, the lower hatched lines the calculated food intake per day (see Table 3).

Palaemon elegans is larger and heavier than *P. debilis*. However, the maximum daily food consumption in relation to body weight was similar for the two species and estimated as 15 % of $W^{0.8}$. In order to compare food intake of shrimps of different sizes at the different ration levels, both food intake and growth were expressed as a percentage of the metabolic dry weight (% $W^{0.8}$) and mean values were calculated for each ration level (Table 2). When mean daily food consumption (dF) is plotted against mean daily growth (dW) at the ration levels A to D (Fig. 4), a linear relationship is found for both prawn species:

$$dW = 0.4\ dF - 5.5 \text{ (corr. coeff. } r = 0.97,\ n = 8).$$

When growth is zero the daily maintenance ration can be calculated as 5.5/0.4 = 13.75 % of $W^{0.8}$, while the net food conversion of prawn meat into prawn is estimated as 0.4 or 40 %. When the energy values of food (20 J/mg) and prawns (18.6 J/mg), and the change in energy value of the prawns at the different rations (Table 1, see also ELLIOTT 1976a) are taken into account, the relation becomes:

dW (Joules) = 0.39 dF - 1.066, and maintenance becomes 0.137 $W^{0.8}$ x 20 J/day.

Daily oxygen consumption of the prawns varied in relation to feeding and activity (Table 4). When oxygen consumption is expressed as a percentage of the metabolic dry weight, the highest respiratory rates were 14.1 – 15.4 % of $W^{0.8}$ for active well-fed animals. Lower values of 10.7 % were measured for starving animals at rest, declining to 7.4 % after several days starvation. For comparison with food intake an oxycalorific

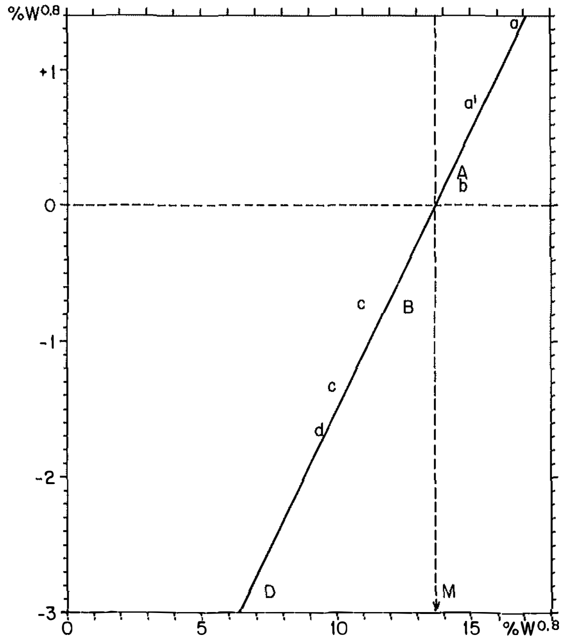

Figure 4

The linear relation between mean daily food intake (horizontal) and mean daily growth (vertical), both expressed as a percentage of the metabolic dry weight of the prawns. Values for the different rations are indicated by a, b, c, d for *Palaemon debilis* and by A, B, C, D for *P. elegans* (a' is the value of a when tank A1 is omitted, M indicates the maintenance ration).

coefficient of 13.4 J per mg oxygen has to be used for ammonioteles (BRAFIELD and SALOMON, 1972; ELLIOTT and DAVISON, 1975). Maintenance food intake and oxygen uptake of fed prawns can be compared as

$$\text{Maint.} = 0.137\ W^{0.8} \times 20\ J = 2.74\ W^{0.8}$$
$$\text{Respir.} = 0.153\ W^{0.8} \times 13.4\ J = 2.05\ W^{0.8}$$

This suggests that about 25 % of the food is lost, possibly in waste products (ELLIOTT 1976b). In the tanks where prawnmeat was used as food little or no faecal pellets were found.

The prawns in tanks E (Table 2) consumed large amounts of algae and produced a lot of faecal pellets. However, they showed a decrease in weight. If the energy value of algae is taken into account (PAINE and VADAS 1969) their daily energy consumption was comparable to ration level C, at which the prawns also decreased in weight. Analysis of digestive enzymes in adult and (reared) young *Palaemon debilis* showed that they contain remarkably high levels of amylase (0.7–0.9 Units per mg soluble body protein) as compared to enzymes with tryptic activity (0.01–0.03 Units per mg body protein). This proves that the prawns can digest carbohydrates from algae (see also van WORMHOUDT et al., 1980).

Discussion

Palaemon debilis is very well adapted to the physical environment of the Shura. In metahaline pools (POR 1972) this species might be found at salinities up to 60–70 ‰ S and temperatures up to 38°C. More important for the establishment of dense populations are probably food supply and predation. The limitation of the distribution of the prawns to the vicinity of the protecting canopy of mangrove aerial roots, and the pelagic schooling behaviour, could be mechanisms to avoid predators in the lagoons: mullets and perchlike young Therapons hunt at night on prawns by swimming rapidly over the sandbottom, and the schooling shrimps usually face the open lagoon.

The estimates of maintenance ration and net food conversion can be used to calculate food consumption of a population if biomass (standing stock), size distribution and growth (production) are known. Food consumption can then be calculated as:

(standing stock x maintenance) + (production x net food conversion).

Palaemon debilis in the lagoons behaves as an agressive scavenger that grabs any crustacean steak or fish fillet coming near its claws. When feeding on the sandbottom the prawns rapidly search the surface with their chelae, which suggests that they hunt for meiobenthos chops like polychaets, harpacticoids, etc. According to POR (pers. comm.) they also feed on detritus, while it is evident that they eat algae. According to FORSTER (1951) *Palaemon elegans* also eats algae, which is confirmed by our observations. Detritus in the Shuras originates from litter of the mangrove trees and also from decaying algae washed over the reef barrier into the lagoons. According to WELSH (1975) the grass shrimp *Palaemonetes pugio* breaks down large amounts of detritus in the tidal marsh ecosystem of Bissel Cove. *Palaemon debilis* might play a similar role in the Shuras of Sinai. However, in our experiments the prawns did not grow on a diet of algae, and they produced a lot of faecal pellets which indicates that the algal food was poorly utilized. The animals probably need proteins for proper growth while carbohydrates are mainly used for metabolism (see also NEW, 1976, van WORMHOUDT et al. 1980). It is also possible that by eating algae the prawns produce faecal pellets as food for meiobenthos, which may be the cattle they eat. It is therefore of interest to continue the study of food intake and growth of this "clever" *Palaemon debilis*, with particular reference to its omnivorous habits and its role in the food web.

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