

Significance of Near-bottom Copepod Aggregations as Food Resources for the Juvenile Red Sea Bream in Shijiki Bay

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The significance of copepod swarming near the bottom as food resources for juvenile red sea breams was investigated around the nursery ground of Shijiki Bay. Juveniles of 12.7 to 43.7 mm FL were found to predate upon a large number of pelagic copepods composed exclusively of *Acartia omorii* and *A. steueri*. The maximum number of copepods detected in a stomach increased markedly with juvenile length, reaching about 100 at 13 mm FL, 200 at 15 mm FL and exceeding 300 at 20 mm FL. However, few copepods were found in the stomachs of juveniles larger than 35 mm FL. The large quantities of ingested copepods observed were inferred to be caused by effective predation on highly aggregated copepods near the bottom.

The estimation for the daily ration of the red sea bream demonstrated that early juveniles can obtain enough energy for maintenance and growth solely through feeding on copepods. Within the bay, densities of copepods swarming near the bottom showed a landward increase. The density gradient induces the early juveniles to migrate into the innermost part of the bay, *i.e.* the nursery ground.

Together, these quantitative estimates and with qualitative evidence confirm that copepods swarming near the bottom are of great importance for the survival and growth of the early juveniles of the red sea bream, particularly as emergent food resources under deficient conditions of benthic prey organisms.

The previous article¹⁾ demonstrated how two pelagic copepod species, *Acartia omorii* and *A. steueri*, are commonly aggregated near the bottom around the nursery ground of the red sea bream, *Pagrus major* (Temminck et Schlegel), in Shijiki Bay. The juveniles have been reported to voraciously predate the aggregated copepods when they encounter them¹⁻³⁾ and were accordingly regarded as an efficient sampler for the near-bottom copepods in the previous article.¹⁾ In the present paper, however, we regard the juveniles as predators of copepods and consider the significance of such aggregations for inshore migration, growth and survival of early juveniles of the red sea bream.

Adaptive advantages of aggregation for copepods have been discussed from various viewpoints; reproduction, feeding, protection against predation, maintenance of position, *etc.*⁴⁻⁷⁾ How-

ever, the fact that aggregated copepods are voraciously predated by fishes has been rarely described,^{8,9)} and the role of such aggregations in the feeding of fishes has never been analyzed and discussed in detail.

For the early juveniles of demersal red sea bream, main food organisms are pelagic Copepoda and benthic Gammaridea.¹⁾ The latter is a more important food than the former in a quantitative sense.²⁾ However, since Copepoda is more commonly and densely distributed, it would play an important role for the juveniles when Gammaridea becomes deficient. The main purpose of this study is to describe the predation of aggregated copepods by juvenile red sea breams, and to discuss their role on the survival of the juveniles.

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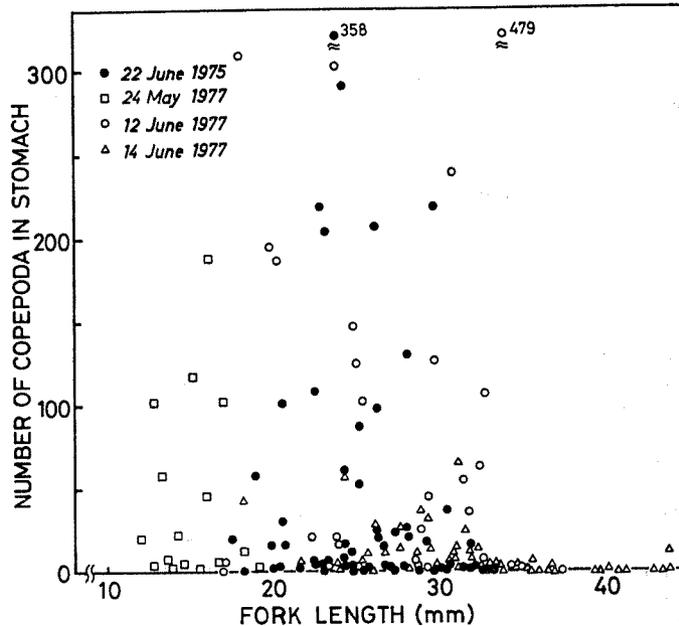


Fig. 1. Number of copepods found in a stomach of juvenile red sea bream. Juveniles were caught with Gochi-trawl and beam-trawl in May and June, 1975 and 1977.

Materials and Methods

Collections of red sea bream were made in Shijiki Bay, located in the southwestern tip of Hirado Island. Juveniles used for stomach content analysis were caught with Gochi-trawl at 11 G-stations, and with beam-trawl at 15 MT-stations during late May to late June, 1977. These sampling stations and dates were described in the previous paper.¹¹ Specimens were fixed in about 10% sea-water formalin immediately after collection. After measuring fork length and wet body weight, their stomachs were removed and the contents were dissected to identify the species and developmental stage of ingested organisms.

A length-weight relationship was determined on another group of juveniles caught with Gochi-trawl in mid June, 1983 and 1986. Dry weight of juveniles was measured to 0.01 mg with an electromicrobalance after they had been left in an 60°C oven for 72 hours. Dry weights of pelagic copepods were calculated according to Uye.¹⁰ The daily ration of juveniles was estimated from the sum of the energy required for metabolism and daily growth.¹²⁻¹⁴ For calculation of the ration, the following data were used: oxygen consumption of the juveniles presented by Anraku and Azeta,¹⁵ daily growth of the juveniles by Azeta *et al.*,¹⁶ caloric values of fish tissues and oxy-caloric coefficient by Winberg¹² and Laurence.¹⁷

Results

Composition of Copepods in Stomachs

The stomach contents of 220 juveniles, ranging from 12.7 to 43.7 mm in fork length (FL), were mainly composed of Copepoda, Gammaridea and Mysidacea. Percentage numerical composition in 61 juveniles caught at MT-stations was 81.4% Copepoda, 14.5% Gammaridea, 3.6% Mysidacea, 0.3% Polychaeta, and 0.08% Ostracoda and Cumacea. Over 97% of the copepods were pelagic species. The number of copepods ingested varied greatly, even within the same size class of fish (Fig. 1). The maximum number increased markedly with an increase in juvenile length, reaching about 100 at 13 mm FL, 200 at 15 mm FL and over 300 at 20 mm FL. The maximum number was 479 copepods, found in a juvenile measuring 33.9 mm FL caught at MT-11 on June 14, 1977. However, usually few copepods were found in the stomachs of juveniles larger than 35 mm FL.

Species composition of copepods found in the stomachs of the juveniles collected at 11 G-stations is shown in Table 1. In the stomachs of 84 juveniles, a total of 1,768 copepods were counted. Benthic Harpacticoida occupied only about 4.3%. Seven pelagic copepod species were identified: *Acartia omorii*, *A. steueri*, *Paracalanus parvus*, *Pseudodiaptomus marinus*, *Corycaeus* sp., *Stiphos*

Table 1. Species composition of copepods found in stomachs of juvenile red sea breams caught at each G-station on June 14, 1977. Each value indicates the total number of copepods from all juveniles examined

Food items	Stations									Total
	G-1	G-2	G-3	G-4	G-5	G-6	G-7	G-8	G-9	
<i>Acartia steueri</i> adult	39	7			46	11		3	4	110
<i>Acartia omorii</i> adult	22	5		2	76	52		455	100	712
<i>Acartia</i> immature	61	2		1	105	41		516	99	825
<i>Paracalanus parvus</i>	2							4	3	9
<i>Pseudodiaptomus marinus</i>	16	1			5	1		4	2	29
<i>Corycaeus</i> sp.					1				1	2
<i>Stiphos</i> sp.						1		1		2
<i>Oithona</i> sp.								1		1
Unidentified Copepoda	1	1								2
Benthic Harpacticoida	22	14	3	4	6	1		15	11	76
Total	163	30	3	7	239	107	0	999	220	1768
Number of <i>P. major</i> examined	19	8	4	4	17	6	1	11	14	84
Copepoda per juvenile	8.6	3.8	0.8	1.8	14.1	17.8	0	90.8	15.7	21.0

Table 2. Species composition of copepods found in stomachs of juvenile red sea breams caught at each MT-station on June 12, 1977. Each value indicates the total number of copepods from all juveniles examined

Species	Stations					
	MT-1	MT-2	MT-3	MT-6	MT-7	MT-8
<i>Acartia omorii</i> adult ♀	1		2	3		7
♂	2					1
<i>Acartia steueri</i> adult ♀	4		4		241	
♂					99	
<i>Acartia</i> immature	7		192		32	14
<i>Pseudodiaptomus marinus</i>	9	4			1	
<i>Stiphos</i> sp.						
Unknown Cyclopoida sp.						
Benthic Harpacticoida	4	3	3	2	11	2
Total	27	7	201	5	384	24
Number of <i>P. major</i> examined	5	8	5	5	10	5
Copepoda per juvenile	5.4	0.9	40.2	1.0	38.4	4.8

Table 2. (Continued)

Species	Stations					
	MT-9	MT-10	MT-11	MT-12	MT-13	Total
<i>Acartia omorii</i> adult ♀	22	29	40	31	22	288
♂	8	28	54	23	15	
<i>Acartia steueri</i> adult ♀	13		227	3	1	709
♂			115	2		
<i>Acartia</i> immature	35	90	768	661	86	1885
<i>Pseudodiaptomus marinus</i>						14
<i>Stiphos</i> sp.			1		2	3
Unknown Cyclopoida sp.				2		2
Benthic Harpacticoida	4	9	22		6	66
Total	82	156	1227	722	132	2967
Number of <i>P. major</i> examined	7	5	5	5	2	62
Copepoda per juvenile	11.7	31.2	245.4	144.4	66.0	47.9

Table 3. Estimated daily ration of juvenile red sea bream. Daily growth is calculated from an equation of length-weight relationship ($\log W=3.269 \log L-2.891$) and 5.0 cal/mg dry body weight of fish tissues. O_2 consumption is estimated from an equation of O_2 -weight relationship ($Q=0.009W^{0.714}$). An oxy-caloric coefficient of 4.77 is used. Corrected DR (daily ration) is obtained from dividing daily ration, sum of calories for growth and metabolism, by an assimilation coefficient of 0.8

Length (FL mm)	Weight (dry mg)	Daily growth (mg)	Daily growth (cal)	O_2 cons.* (ml/h)	Metabolism (cal)	Daily ration (cal)	Corrected DR (cal)
10	2.39	0.41	2.05	0.018	2.06	4.11	5.18
15	8.99	1.44	7.20	0.046	5.27	12.47	15.59
20	23.00	2.75	13.76	0.088	10.07	23.83	29.79
25	47.74	4.51	22.56	0.147	16.83	39.39	49.24
30	86.70	6.60	33.00	0.223	25.53	58.50	73.10
35	143.50	9.50	47.53	0.319	36.52	84.05	105.06
40	222.10	12.40	62.00	0.434	49.68	111.68	139.61
45	326.50	16.40	82.00	0.571	65.37	147.37	184.20

* Oxygen consumed by a juvenile (ml per hour).

sp., and *Oithona* sp. The two species of *Acartia* constituted 97.5% of total pelagic copepods and the latter five species were almost negligible in number. Adult and immature *Acartia* were present in almost equal proportions. The number of copepods per juvenile differed from 0 to 90.8 ($\bar{X}=21.0$), depending on sampling stations. The maximum number of 90.8 was found at G-8, which was located near a well vegetated *Sargassum* zone. Within the two *Acartia* species, *A. omorii* was over 6 times more abundant than *A. steueri*. This appeared to be caused by differences in distribution pattern; *A. omorii* was rather widely distributed, which *A. steueri* was restricted to a few stations near the shore like G-1 and 5.

Table 2 shows the specific composition of copepods found in the stomachs of juveniles collected at MT-stations. In 62 juvenile stomachs, 2,967 copepods, including only 2.2% of benthic Harpacticoida, were found. The average number of 47.9 per juvenile was more than twice that recorded from G-stations. Five species of pelagic copepods were found: *Acartia omorii*, *A. steueri*, *Pseudodiaptomus marinus*, *Stiphos* sp. and Cyclopoida sp. As seen at G-stations, the major portion of the copepods were occupied by *A. omorii* and *A. steueri*, and the other species were almost negligible in number. However, at MT-1 and 2, which were located near the shore of the innermost part of the bay, *P. marinus* was dominant.

The relative proportions of the two species varied with stations; *A. steueri* overwhelmingly predominated over *A. omorii* at MT-7 and 11, but the opposite trend was seen at MT-6, 8, 10, 12 and

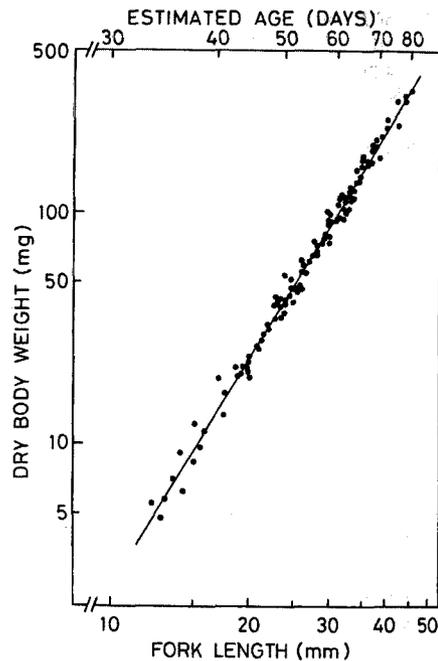


Fig. 2. Length-weight relationship obtained for the juvenile red sea bream caught in June, 1983 and 1986, representing an equation $\log W=3.269 \log L-2.891$ (W : dry body weight in mg, L : fork length in mm). Estimated age (days after hatching) was determined from Azeta *et al.*¹⁶⁾ with an average daily growth of 0.70 mm and daily growth increment examination of otolith (unpublished).

13, although the number of copepods per each station was not so large. These variations in the relative proportion were also reflected in the contents of stomachs examined at a given station.

At MT-11, for example, two juveniles exclusively predated upon *A. omorii* and the others exclusively upon *A. steueri*. Sex ratios differed between the two species, being nearly equal in *A. omorii*, whereas in *A. steueri*, females markedly outnumbered males.

Estimation of Daily Ration

The relationship between fork length and dry body weight of the red sea bream juveniles is shown in Fig. 2. Body weight increased exponentially with an increase in length from 8.99 mg at 15 mm FL to 222.1 mg at 40 mm FL. The relationship was expressed by an equation, $\log W = 3.269 \times \log L - 2.891$, where W and L are dry body weight in mg and fork length in mm, respectively.

Figure 2 also presents age (days after hatching) equivalent to size, estimated from an average daily growth rate of 0.70 mm in length for the juveniles¹⁵⁾ and 0.34 mm for the larvae determined by otolith daily growth increments (unpublished). A 15 mm FL juvenile grows from 8.99 mg to 10.43 mg in a day, resulting in a daily growth of 1.44 mg. This may be converted to 7.20 cal, assuming 1 mg dry weight of fish tissues = 5.003 cal.¹⁶⁾

From the relationship between O_2 consumption and body weight: $Q = 0.009W^{0.714}$, presented by Anraku and Azeta,¹⁴⁾ a 15 mm juvenile red sea bream requires 0.046 ml O_2 per hour. The juvenile consumes 1.104 ml O_2 during 24 hours, this being equivalent to 5.27 cal, assuming an oxy-caloric coefficient of 4.77.¹¹⁾ Thus, from the sum of 7.20 cal for growth and 5.27 cal for metabolism the energy that the juvenile gains from food during 24 hours is calculated as 12.47 cal. If the assimilation coefficient is assumed to be 0.8,^{11,12)} the daily ration may be estimated as being 15.59 cal. Similarly the daily ration of a 40 mm juvenile is calculated as being 139.61 cal. Table 3 shows the estimated daily ration in calories for each 5 mm size class.

Discussion

Together, the present study and with the previous one¹⁾ have clearly demonstrated that red sea bream juveniles predate upon large quantities of copepods swarming near the bottom. One may question whether juveniles can satisfy their energy requirements with only copepods. To answer this question we have to undertake a quantitative analysis. The maximum number in

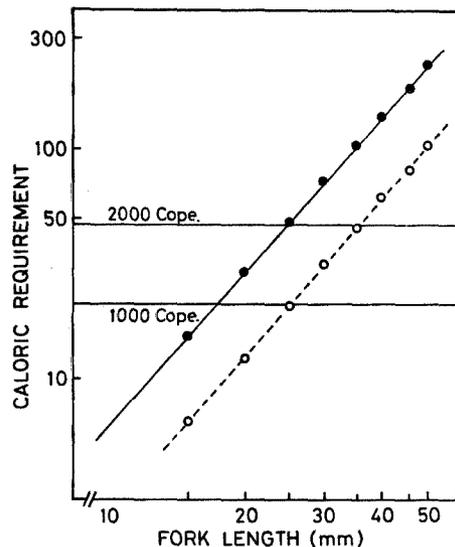


Fig. 3. Daily caloric requirement for red sea bream juveniles. Solid circles show daily ration in calories, and open circles caloric requirement for metabolism only. 1,000 and 2,000 Cope. lines indicate the daily calories obtained by juveniles predated that number.

the stomach of a 15 mm FL juvenile was about 200 copepods (Fig. 1) and the daily turnover rate of stomach contents may be reasonably assumed to be five times, judging the excretion time¹⁷⁾ and hours available for feeding in a day. Therefore, a 15 mm juvenile could ingest some 1,000 copepods in a day. One thousand individuals of *Acartia* with 0.8 mm in body length are equivalent to 5.8 mg dry weight, using the length-weight relationship of copepods: $\log W = 3.061 \log L - 8.120$ (W : μg , L : mm) presented by Uye.¹⁰⁾ Furthermore, on the basis of their caloric contents¹⁸⁾ 5.8 mg of pelagic copepods can be converted into 29.0 cal. Assuming 0.8 digestibility, the juvenile red sea bream could obtain 23.2 cal from 1,000 copepods of 0.8 mm in length. This value exceeds the daily ration of 15.59 cal (Table 3) and we can, therefore, conclude that a juvenile can obtain enough energy only from swarming copepods, at least during its early days.

The importance of copepods decreases in larger juveniles in a quantitative sense. For example, a 30 mm FL juvenile obtains 58.0 cal from copepods under a maximum ingestion of 400 copepods and a turnover rate of 5. The value of 46.4 cal corrected by digestibility is less than the daily ration of 73.1 cal (Table 3 and Fig. 3). However, it is higher than the energy required for

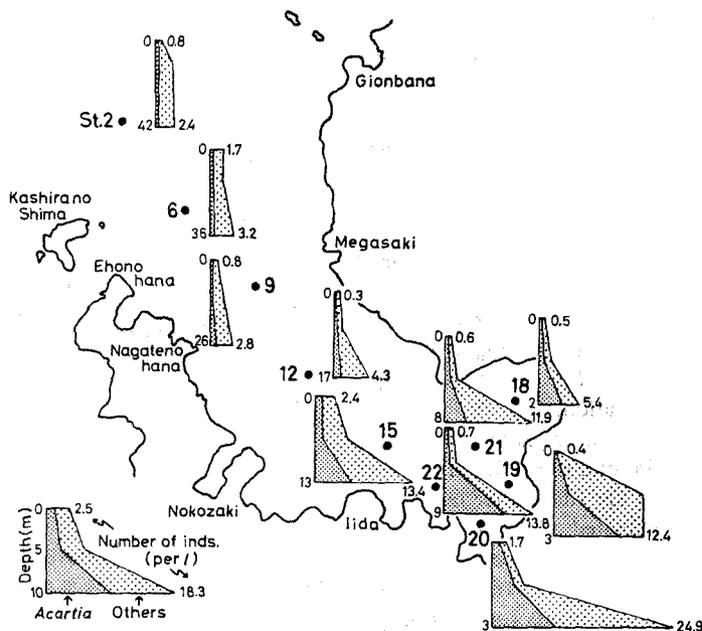


Fig. 4. Horizontal changes in the vertical profile of copepods in Shijiki Bay. Sampling was carried out by horizontal tows of plankton nets at 3 layers on June 22, 1977 (profiles are adapted from Table 1 of previous paper¹). Numerals on the left of the profiles show towing depths and those on the right, copepod densities per liter.

metabolism 25.5 cal. Figure 3 demonstrates that juveniles smaller than 35 mm can obtain enough energy for body maintenance from 2,000 copepods, and those smaller than 25 mm, from 1,000 copepods. All estimates in the present calculation are made assuming maximum ingestion. Although a major proportion of juvenile do not always predate upon the copepods near the maximum ingestion level, these estimates appear to verify the quantitative importance of copepods.

Qualitative evidence for the importance of aggregated copepods for red sea bream juveniles has been given¹⁹; during years of high population density, early juveniles appeared to depend upon copepods even when over 50 mm FL. This phenomenon suggests that, under overpopulated conditions in which Gammaridea, their preferred food, are relatively scarce even larger juveniles compensate this energy by ingesting pelagic copepods. These quantitative analyses and qualitative evidence demonstrate the copepod swarms near the bottom around the nursery ground are of very great importance for growth and survival of the juvenile red sea bream; particularly as emergent food resources under deficient conditions of benthic prey animals.

Another significance of aggregated copepods

seems to be a role contributing to the inshore migration of the earliest juveniles. The pelagic juveniles, which have already metamorphosed but not yet transferred to demersal life, immigrate from the mouth area to the central area of the bay. There, they encounter *Acartia* aggregations and synchronization of the diel vertical movement of the predator and prey, dusk-upward and dawn-downward, enhances the chance of encounter. Copepod densities near the bottom increase landward as shown in Fig. 4. This gradient contributes to the juveniles newly recruited in the central area moving spontaneously landward, resulting in a high concentration on the bottom of the bay. Gammaridea, the favorite food organism of demersal juveniles, has been reported to occur most abundantly in the innermost area of the bay¹⁰ and thus, juvenile red sea breams can smoothly transfer their food habit from pelagic organisms to demersal ones in synchronization with their habitat shift into the nursery ground.

Average population densities of the red sea bream in Shijiki Bay can vary annually as nearly twenty times of the ratio between the lowest and the highest year-class densities. This is mainly attributable to the abundance of recruiting pelagic larvae.²⁰ However, annual population densities

are also affected to some extent by the annual variations in abundance of swarming copepods. The variation in development of aggregations seems to occur on daily, seasonal and annual time scales; it is more evident on fine days, and develops from spring to early summer, terminating in mid-summer. These variations may influence the survival and growth of the early juveniles, resulting in annual fluctuations in abundance and production. It is necessary to investigate the influence of the variable aspects of copepod aggregations as regulating mechanism for juvenile red sea bream populations in greater detail.

The adaptive significance of copepod swarming has been discussed from various viewpoints.⁴⁻⁷⁾ In their observations on copepod swarms on coral reefs, Hamner and Carleton⁴⁾ suggested swarming to be an adaptation evolved by resident plankton species to survive within the reef ecosystem. They also noted that protection from predators is probably the most common adaptive explanation. In the present study, however, swarming was confirmed to be undoubtedly beneficial for effective predation by juvenile red sea bream and this situation is not restricted solely to this species. In Shijiki Bay, evidence for predation on swarming copepods has been provided by stomach content analyses of some juvenile fishes; crimson sea bream* in winter, gobioid fishes²¹⁾ in spring, and Japanese grunt²²⁾ in summer. Furthermore, the predation on *Acartia* by sand eel⁹⁾ suggests this to be a rather widespread phenomenon in coastal waters.

In the nursery ground of Shijiki Bay, the maximum population density of juvenile red sea bream was estimated by scuba divers using a line transect method,²³⁾ as being 0.34 fishes per m². If we assume a daily consumption of 1000 copepods per fish, 340 copepods per m² are ingested by a juvenile each day. At the same time, the modest estimation of a swarm density of 100 copepods per l, is equivalent to 30,000 per m² at the swarm thickness of 30 cm.¹⁾ Even without new recruitment, numbers of swarming copepods are adequate to supply foraging juveniles for about 90 days. During the first month of the juvenile stage red sea breams are temporal plankton feeders and thereafter change their food habits from plankton to benthic animals. Furthermore, swarms are daily renewed by the upward nighttime dispersion.²⁴⁾ On the basis of this qualitative and

quantitative evidence, we can consider that over-predation on swarms by juvenile fishes might never occur, although it may well influence swarming copepod populations.

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