

Characteristics of the Copepod Assemblage in the Southwestern Japan Sea and its Implication for Anchovy Population Dynamics

Kazumasa HIRAKAWA¹⁾ and Yoshihiko OGAWA¹⁾

Abstract

This paper describes the seasonal variations in the copepod assemblage as food resources for larval anchovy (*Engraulis japonicus*) in relation to both the biotic and abiotic environments. The data used was taken from field observations at a station in the southwestern Japan Sea from 1992 to 1994. The results demonstrate that the food composition of anchovy larvae clearly reflects the seasonal succession of copepod assemblage. The spring larvae depend on the higher peak abundance of a copepod assemblage which consisted of only a few temperate species supported by the large spring phytoplankton bloom in the low temperature and high salinity water mass. The autumn larvae, however, depend on a more highly diversified copepod assemblage with a lower peak abundance of temperate-subtropical species in association with the small autumn phytoplankton bloom under high temperature and low salinity water conditions. The results also imply a possible key mechanism in the regulation of anchovy population levels through interannual fluctuations in abundance and species composition of the copepod assemblage.

Key words: anchovy larvae, copepod assemblage, gut contents, seasonal succession, Tsushima Current

Introduction

Copepods are the most dominant mesozooplanktonic group in the seas and are the main food item for most marine fish larvae in the form of eggs, nauplii and copepodids (LAST 1980; TURNER 1984; IKEWAKI and SAWADA 1991). POULET and WILLIAMS (1991) theorized that the abundance of fish recruited is related to the community structure of copepods, and to the occurrence of new generations of nauplii, as well as to the number of generations produced during the first feeding stage of the fish. They argue that it is essential to understand the functional role of the copepod assemblage as a food resource in determining the recruitment abundance of pelagic fish populations (anchovies, sardines and herrings, etc.).

In the Japan Sea, anchovy (*Engraulis japonicus*) is mainly distributed in the Tsushima Current waters (FISHERIES AGENCY 1979) and an important target of many coastal fishing industries. Copepods, on the other hand, are the most dominant constituent of the zooplankton in the Tsushima Current waters (FURUHASHI 1953; YAMAZI 1953; MORIOKA 1985; SHIM

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¹⁾ Japan Sea National Fisheries Research Institute, Suido-cho, Niigata 951, Japan.

(〒951 新潟市水道町1丁目 5939-22 日本海区水産研究所)

and LEE 1986; HIRAKAWA *et al.* 1995, etc.) and are a major food item for anchovy (YAMANAKA and ITO 1957; YAMASHITA 1957; MATANO 1984). OGAWA and NAKAHARA (1979) reported a significant positive correlation between the number of copepod nauplii and CPUE (Catch per unit effort) of anchovy in coastal waters of the southwestern Japan Sea. However, there have been few studies which provide detailed information about the relationship between seasonal changes in the abundance and structure of copepod assemblage and anchovy catches in the seas around Japan.

In order to evaluate the effects of the copepod assemblage as a food resource for anchovy populations, it is necessary to detail any changes in the abundance and species composition of the copepod assemblage, which vary seasonally with both biotic and abiotic environments. The present paper describes the characteristic features of the copepod assemblage as a food source for postlarval Japanese anchovy in the southwestern Japan Sea. For this purpose, we examined the relationship between the seasonal variations of the copepod assemblage, the gut contents of anchovy larvae and the occurrence of anchovy larvae. In addition, the relationship between these factors and the seasonal changes in hydrographic structure and phytoplankton biomass of the Tsushima Current water was examined. We show that the seasonal variation in the copepod assemblage implies a possible key mechanism in the regulation of anchovy population levels.

Materials and Methods

1 Plankton sampling and hydrographic survey

Field observations were carried out monthly at an offshore station close to the Tsushima Straits (34°38'N, 130°41'E, Fig. 1), using the R/V "Kuroshio-Maru" of the Yamaguchi Prefectural Open Sea Fisheries Experimental Station. The sampling station is located in the Tsushima Current waters.

Zooplankton samples were taken during the first 10 days of each month from January through to December 1992 (for practical reasons December's sampling was carried out on the 30th November). The samples were collected by vertical tows of twin-type NORPAC nets (45cm mouth diameter, 0.33mm and 0.10mm mesh apertures) from a near bottom depth (ca. 126m) to the surface. Each net was equipped with a Rigosha flow-meter on the mouth ring to register the water volume passing through the net. After collection, the samples were preserved in a 10% buffered formalin-seawater solution. At each sampling time, temperature and salinity profiles from the near bottom depth (ca. 126m) to the surface were recorded with a STD system (AST 1000, Alec Electronics Co. Ltd.).

In the laboratory of the Institute, the 0.33mm mesh net-samples were split into 1/2 or 1/4 aliquots to sort copepods using a Folsom plankton splitter. After sorting under a dissecting microscope, species identification was made for the copepodids and adults. The 0.10mm mesh net-samples were split into 1/2 aliquots using a Folsom plankton splitter; one sample for investigating the copepod naupliar abundance, and the other for the phytoplankton biomass (as a total cell count). Data on phytoplankton are based on the results of the

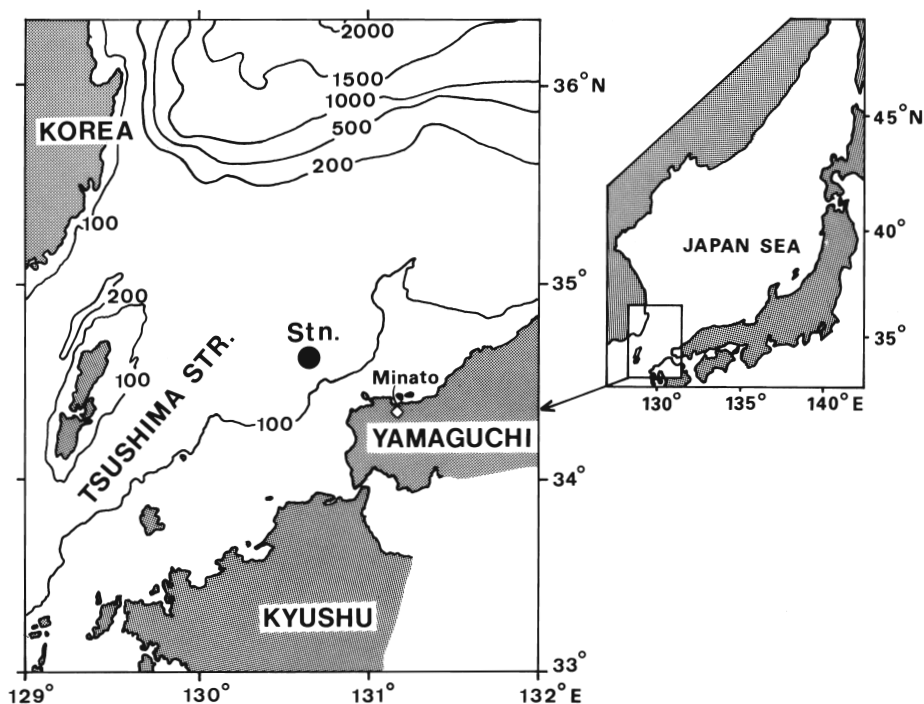


Fig. 1. Maps showing the location of the Tsushima Straits and environs (right panel), and position of the present sampling station off Yamaguchi Prefecture (left panel). Bathymetric contours (100, 200, 500, 1000, 1500 and 2000m) are also shown.

seasonal variations published by HIRAKAWA *et al.* (1995).

2 Catch data

The catch data of anchovy are derived from the report published by the YAMAGUCHI PREFECTURAL OPEN SEA FISHERIES EXPERIMENTAL STATION (1993). In coastal waters of the southwestern Japan Sea, “shirasu”, postlarval anchovy [TL (total length): 2-4cm] is an important target of dip-net and boat seine fisheries. The data used were based on the catch statistics of dip-net fisheries belonging to the Minato Port of Yamaguchi Prefecture (Fig. 1). The fishery operates in the coastal waters adjacent to the study area.

3 Gut content analysis

Anchovy larvae used for diet analysis were collected aboard the R/V “Mizuho-Maru” on the 19th of October, 1993 and the R/V “Kuroshio” on the 18th of May, 1994 at the same station. Collections were made using fish-larval nets (130cm or 200cm mouth diameter, 0.50mm mesh aperture), which were towed obliquely from ca. 50m depth to the surface during daylight hours (local time: 1200-1300). In other larval anchovy species (*E. mordax* and *E. ringens*), stomach content analyses have indicated that their feeding behaviour is

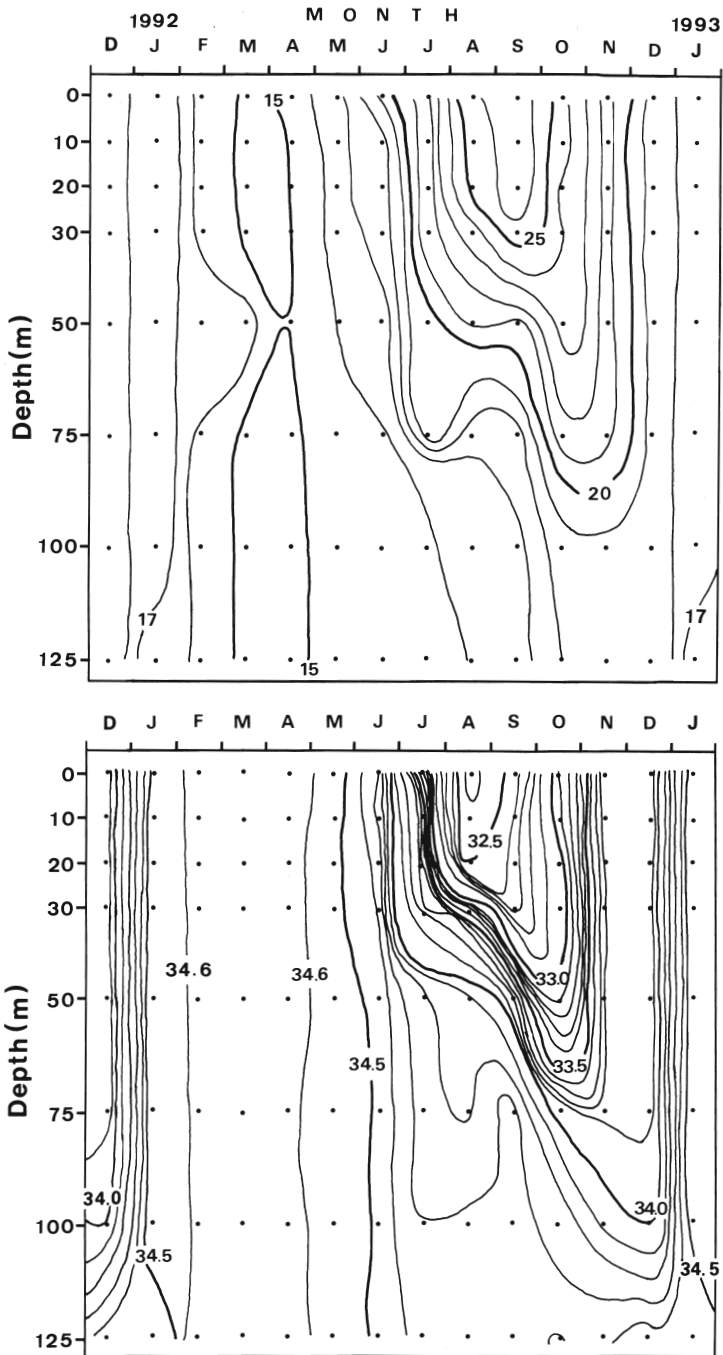


Fig. 2. Seasonal changes in temperature (upper, °C) and salinity (lower, PSU) in the upper 125m depth range at the station off Yamaguchi Prefecture from January to December 1992 (after HIRAKAWA *et al.* 1995).

confined to daylight hours: more than 90% of the total number of the larvae with food were caught during the day (BERNER 1959; de MENDIOLA 1974; ARTHUR 1976). In fact, at nighttime there were few anchovy larvae with gut contents in the present NORPAC net-samples (e.g. the May and September larvae). Specimens were preserved in 10% buffered formalin-seawater, and the guts of 461 larvae dissected to examine the food organisms inside.

Since UOTANI *et al.* (1988) reported that anchovy larvae smaller than 8.9mm in SL (standard length) fed mainly on copepod nauplii in Sagami Bay, we sorted undamaged specimens in the size category (SL: 4.0-8.9mm) from the samples and dipped them into methyl blue-lactic acid solution for staining. They were subsequently measured under a dissecting microscope (SL to nearest 0.10mm). After this, the guts of the anchovy larvae were removed and opened with needles. Food organisms in the gut contents were counted and classified into three fundamental groups [orders: Calanoida, Cyclopoida (-Poecilostomatoida) and Harpacticoida] as characterized by DIETRICH (1915) and BJÖRNBERG (1972). The diagnostic features used for the identification of family and genus levels, whenever possible, were the number and arrangement of the spine and/or setae at the caudal armature, as described by OGILVIE (1953), FABER (1966), BJÖRNBERG (1972) and KOGA (1984).

Results

1 Hydrography

Figure 2 shows the vertical temperature and salinity profiles over the whole water column at the station (Fig. 1) from January to December 1992. The water temperature varied from a minimum of 14.4°C at 125m depth in March to a maximum of 26.6°C in the upper 20m depths in September. The water column was thermally homogeneous during the cooling season from December to April. Surface warming occurred from May to September. During the warming season, a weak seasonal thermocline began to form in May and became distinct from July through September when the temperature of the upper mixed layer (<25m depth) reached 26°C. Surface cooling and subsequent vertical mixing began to break up the seasonal thermocline in October.

The salinity of the water column was nearly homogeneous from January to May, showing a high value above 34.5. High salinity water above 34.1 remained in deeper depths (>100m depth) throughout the year. Water with a maximum salinity over 34.6 occurred from February to April. In contrast, low salinity water (<34.0), termed the "Upper Water of the Tsushima Current" (MIYAZAKI 1953; YASUI *et al.* 1967), prevailed within the surface layer during the summer and autumn. The minimum salinity, below 32.4, was observed at the surface in August.

The most distinct feature of the hydrography in the study area is that there is a seasonal alternation of two major water masses: high temperature/low salinity water mass during the summer and autumn and low temperature/high salinity water mass during the

winter and spring, as reported by OGAWA (1983). This fact demonstrates that there is a large seasonal fluctuation in water mass, even in the same area, which changes the hydrographic environment experienced by the marine organisms.

2 Seasonal variations in the abundance and the species composition of copepods

Results of examinations of plankton samples are shown in Table 1 and Appendix 1. A total of 82 copepod species was identified (Table 1). They include 55 calanoid species, 22 poecilostomatoid species, four cyclopoid species and one harpacticoid species. Most of them are typical warm-water species.

Figure 3 (upper panel) shows the seasonal variations in individual number per m³ and the total number of copepod species. Numerically copepods showed two spring peaks in March and May, and one autumn peak in November. Copepods were most abundant (annual maximum: 456 ind/m³) in March after the annual minimum (54 ind/m³) in February. The number of copepods decreased to form a local minimum in summer, in August and then increased gradually in autumn, forming a third peak (260 ind/m³) in November. The spring peaks were composed of a total of 19–25 species. The total number of species increased remarkably from spring to autumn and reached an annual maximum (50 species) during the abundance peak in November.

Figure 3 (lower panel) shows the species composition of the dominant copepods in each month. The combination of only three dominant species (*Calanus sinicus*, *Paracalanus parvus* and *Ctenocalanus vanus*) contributed to form the early spring peak in March. The first two of these species are temperate species (T) and represented ca. 80% of the total number of individuals of the dominant species collected during this month. In contrast, the autumn peak in November had 12 dominant species (*Ctenocalanus vanus*, *Oithona plumifera*, *Clausocalanus arcuicornis*, *Euchaeta flava*, *Oncaea venusta*, *Paracalanus parvus*, *Euchaeta plana*, *Paracalanus aculeatus*, *Eucalanus subtenuis*, *Calanus minor*, *Undinula vulgaris* and *Clausocalanus furcatus*) which were mostly composed of temperate-subtropical species (TS) and each had a low relative abundance, rarely exceeding 10% of the total. Furthermore, the late spring peak in May was composed of the seven dominant species: four temperate-subtropical (TS), two cosmopolitan (C) and one temperate species (T). Five of these species also became dominant species in one or two of the other peaks. They were *Ctenocalanus vanus* in March and November, *Oithona plumifera*, *Clausocalanus arcuicornis* and *Eucalanus subtenuis* in November, and *Calanus sinicus* in March.

Figure 3 (lower panel) also indicates the characteristics of seasonal succession of the dominant copepods. *Ctenocalanus vanus*, *Oithona plumifera* and *Clausocalanus arcuicornis* predominantly occurred almost all the year-round. While *Euchaeta flava*, *Euchaeta plana*, *Paracalanus parvus*, *Paracalanus aculeatus* and *Oncaea venusta* became dominant species from summer to winter or from summer through to the following spring, *Calanus sinicus* predominated during the spring and summer.

The other 19 species predominated in turns, every one to three species from spring to early winter: *Corycaeus affinis* in April, *Rhincalanus nasutus*, *Mesocalanus tenuicornis* and

Table 1. List of copepod species identified in the NORPAC net samples obtained at the station off Yamaguchi Prefecture from January to December 1992.

Order CALANOIDA	<i>Labidocera acuta</i> (DANA)
Family Calanidae	Family Candaciidae
<i>Calanus minor</i> (CLAUS)	<i>Candacia bipinnata</i> (GIESBRECHT)
<i>Calanus sinicus</i> BRODSKY	<i>Candacia catula</i> (GIESBRECHT)
<i>Mesocalanus tenuicornis</i> (DANA)	<i>Candacia truncata</i> (DANA)
<i>Neocalanus gracilis</i> (DANA)	<i>Candacia</i> sp.
<i>Cosmocalanus darwini</i> (LUBBOCK)	Family Temoridae
<i>Undinula vulgaris</i> (DANA)	<i>Temora discaudata</i> GIESBRECHT
<i>Canthocalanus pauper</i> (GIESBRECHT)	<i>Temoropia mayumbaensis</i> T. SCOTT
Family Eucalanidae	Family Metridinidae
<i>Eucalanus attenuatus</i> (DANA)	<i>Pleuromamma gracilis</i> (CLAUS)
<i>Eucalanus crassus</i> GIESBRECHT	<i>Pleuromamma robusta</i> (F. DAHL)
<i>Eucalanus mucronatus</i> GIESBRECHT	Family Lucicutiidae
<i>Eucalanus pileatus</i> ? GIESBRECHT	<i>Lucicutua flavicornis</i> (CLAUS)
<i>Eucalanus subcrassus</i> GIESBRECHT	Family Acartiidae
<i>Eucalanus subtennis</i> GIESBRECHT	<i>Acartia danae</i> GIESBRECHT
<i>Rhincalanus nasutus</i> GIESBRECHT	<i>Acartia erythraea</i> GIESBRECHT
Family Phaennidae	<i>Acartia negligens</i> DANA
<i>Xanthocalanus</i> sp. ?	<i>Acartia omorii</i> BRADFORD
Family Mecynoceridae	<i>Acartia pacifica</i> STEUER
<i>Mecynocera clausi</i> THOMPSON	
Family Paracalanidae	Order POECILOSTOMATOIDA
<i>Paracalanus aculeatus</i> GIESBRECHT	Family Corycaeidae
<i>Paracalanus parvus</i> (CLAUS)	<i>Corycaeus affinis</i> MCMURRICH
(= <i>P. quasimodo</i> BOWMAN)	<i>Corycaeus agilis</i> DANA
<i>Acrocalanus gibber</i> GIESBRECHT	<i>Corycaeus andrewsi</i> FARRAN
<i>Acrocalanus gracilis</i> GIESBRECHT	<i>Corycaeus catus</i> F. DAHL
Family Calocalanidae	<i>Corycaeus crassiusculus</i> DANA
<i>Calocalanus pavo</i> (DANA)	<i>Corycaeus dahli</i> TANAKA
<i>Ischnocalanus plumulosus</i> (CLAUS)	<i>Corycaeus flaccus</i> GIESBRECHT
Family Pseudocalanidae	<i>Corycaeus gibbulus</i> (GIESBRECHT)
<i>Clausocalanus arcuicornis</i> (DANA)	<i>Corycaeus longistylis</i> DANA
<i>Clausocalanus farrani</i> SEWELL	<i>Corycaeus pacificus</i> F. DAHL
<i>Clausocalanus furcatus</i> (BRADY)	<i>Corycaeus speciosus</i> DANA
<i>Clausocalanus</i> sp.	<i>Corycaeus</i> spp.
<i>Ctenocalanus vanus</i> GIESBRECHT	Family Oncaeidae
Family Euchaetidae	<i>Oncaea conifera</i> GIESBRECHT
<i>Euchaeta concinna</i> DANA	<i>Oncaea media</i> GIESBRECHT
<i>Euchaeta flava</i> GIESBRECHT	<i>Oncaea mediterranea</i> (CLAUS)
<i>Euchaeta longicornis</i> GIESBRECHT	<i>Oncaea venusta</i> PHILIPPI
<i>Euchaeta plana</i> MORI	Family Sapphirinidae
<i>Euchaeta wolfendeni</i> A. SCOTT	<i>Sapphirina angusta</i> DANA
<i>Euchaeta</i> sp.	<i>Sapphirina gemma</i> DANA
Family Scolecithricidae	<i>Sapphirina intestinata</i> GIESBRECHT
<i>Scolecithricella bradyi</i> (GIESBRECHT)	<i>Sapphirina nigromaculata</i> CLAUS
<i>Scolecithricella longispinosa</i> CHEN and ZHANG	<i>Copilia longistylis</i> MORI
<i>Scolecithricella</i> sp.	<i>Copilia mirabilis</i> DANA
<i>Scolecithrix danae</i> (LUBBOCK)	<i>Copilia quadrata</i> DANA
<i>Scolecithrix nicobarica</i> SEWELL	
<i>Scolecithrix</i> sp.	Order CYCLOPOIDA
Family Aetideidae	Family Oithonidae
<i>Aetideus giesbrechti</i> CLEVE	<i>Oithona atlantica</i> FARRAN
Family Cantropagidae	<i>Oithona longispina</i> NISHIDA
<i>Centropages abdominalis</i> SATO	<i>Oithona plumifera</i> BAIRD
<i>Centropages bradyi</i> WHEELER	<i>Oithona setigera</i> DANA
<i>Centropages furcatus</i> (DANA)	<i>Oithona</i> sp.
<i>Centropages orsinii</i> GIESBRECHT	
<i>Centropages yamadai</i> MORI	Order HARPACTICOIDA
Family Pontellidae	Family Miraciidae
<i>Calanopia minor</i> A. SCOTT	<i>Macrosetella gracilis</i> (DANA)

Eucalanus subtennis in May, *Candacia bipinnata*, *Oithona longispina* and *Oncaea mediterranea* in June, *Temora discaudata*, *Acartia danae* and *Calanus minor* in July, and *Clausocalanus farrani* and *Calocalanus pavo* in August, etc. This species succession followed a similar pattern to that seen in subtropical or tropical waters (FARRAN 1949; MOORE 1949; LEGARÉ 1964; REEVE 1964).

Thus, the spring copepod assemblage mainly consists of a few major temperate species with a higher abundance and lower species diversity, while the autumn copepod assemblage consists of temperate-subtropical species with a lower abundance and higher species diversity. This difference is attributed to the seasonal succession from temperate species to temperate-subtropical species. The species diversity of zooplankton community becomes higher in the warm, southern waters than in the cold, northern waters (HATTORI and MOTODA 1983; KANG and HONG 1995). In terms of the seasonal succession, it is suggested that the seasonal succession of copepod assemblage is accompanied by seasonal alternations in the water masses, as shown in Fig. 2. The spring copepod assemblage occurs with the low temperature and high salinity water mass, while the autumn copepod assemblage appears with the high temperature and low salinity water mass. The high species diversity and its succession pattern, in the study area, are closely linked to the inflow of warm-water mass during summer and autumn.

3 Seasonal variations in the abundance of postlarval anchovy

Figure 4 indicates the seasonal variations in the number of the early postlarval anchovy (SL: 3.5–10.5mm, middle panel) and the commercial catch of the late postlarval anchovy termed “shirasu” (lower panel) in relation to those in the copepod naupliar abundance and phytoplankton biomass (upper panel). The early postlarval anchovy peaked numerically in May, July and September and were absent from the study area in August and from November to the following March.

Of the three annual peaks of the early postlarval abundance, the May and July peaks followed the March and June peaks of copepod naupliar abundance, respectively. Although such a time lag in the larval peak of abundance was not seen in autumn, the September larvae could feed on timely copepod nauplii which were increasing in number prior to their October peak. These naupliar peaks were due to the copepod breeding activity, which accelerated consistently in February–March, May–June and September–October—being able to quickly respond to seasonal blooms of phytoplankton and exploit new food resources (HIRAKAWA *et al.* 1995). The major reproductive period of the temperate species group synchronized with the early spring phytoplankton bloom in February, while the temperate-subtropical species group spawned mainly during the autumn phytoplankton bloom in September.

The “shirasu” catches showed two annual peaks in June and November, following the early postlarval peaks in May and September. Except for the July peak of postlarvae, Figure 4 (middle and lower panels) suggests a clear relation between the occurrence of peaks in the early postlarval abundance and the size of the “shirasu” catches.

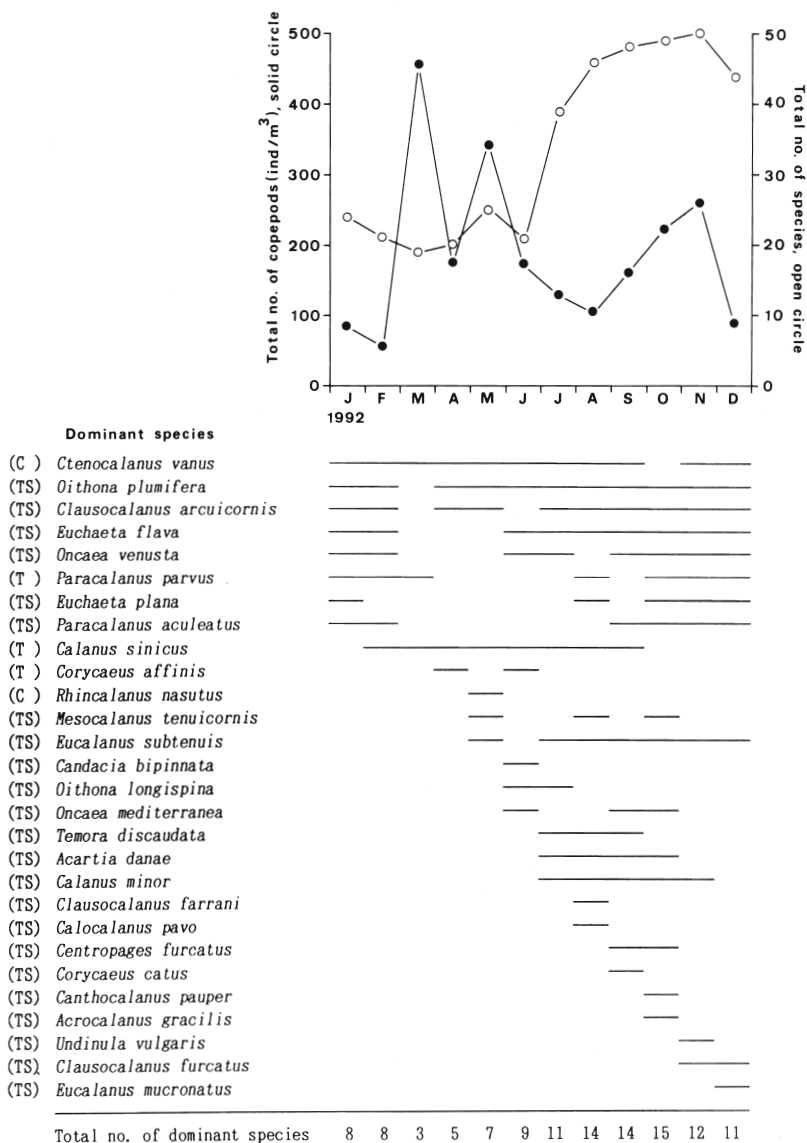


Fig. 3. Seasonal variations in the total number of individuals/m³ and number of species of copepods (upper panel), and the dominance of copepod species by month (lower panel) at the station off Yamaguchi Prefecture from January to December 1992. Dominant species were determined for each sample using the definition and formula of HOSOKAWA *et al.* (1968) as follows:

$$\text{Dominant species: } Ni > (1/S) \sum_{i=1}^S Ni$$

where Ni is the number of the i -th species and S is the total number of species. Grouping of species according to geographic distribution (T: Temperate species, C: Cosmopolitan, TS: Temperate-subtropical species) was based on published papers and unpublished data as follows: GIESBRECHT (1892), MORI (1937), VERVOORT (1949), BOWMAN (1955, 1971), TANAKA (1956a, b, 1957), CHEN and ZHANG (1965), FROST and FLEMINGER (1968), HEINRICH (1969), MULLIN (1969), FLEMINGER and HULSEMANN (1973), CHEN *et al.* (1974), FLEMINGER (1975), GREENWOOD (1978), GARDNER and SZABO (1982), NISHIDA (1985), HIROMI (1987; unpubl.), HULSEMANN (1994), BRADFORD-GRIEVE (1994), HERON and BRADFORD-GRIEVE (1995).

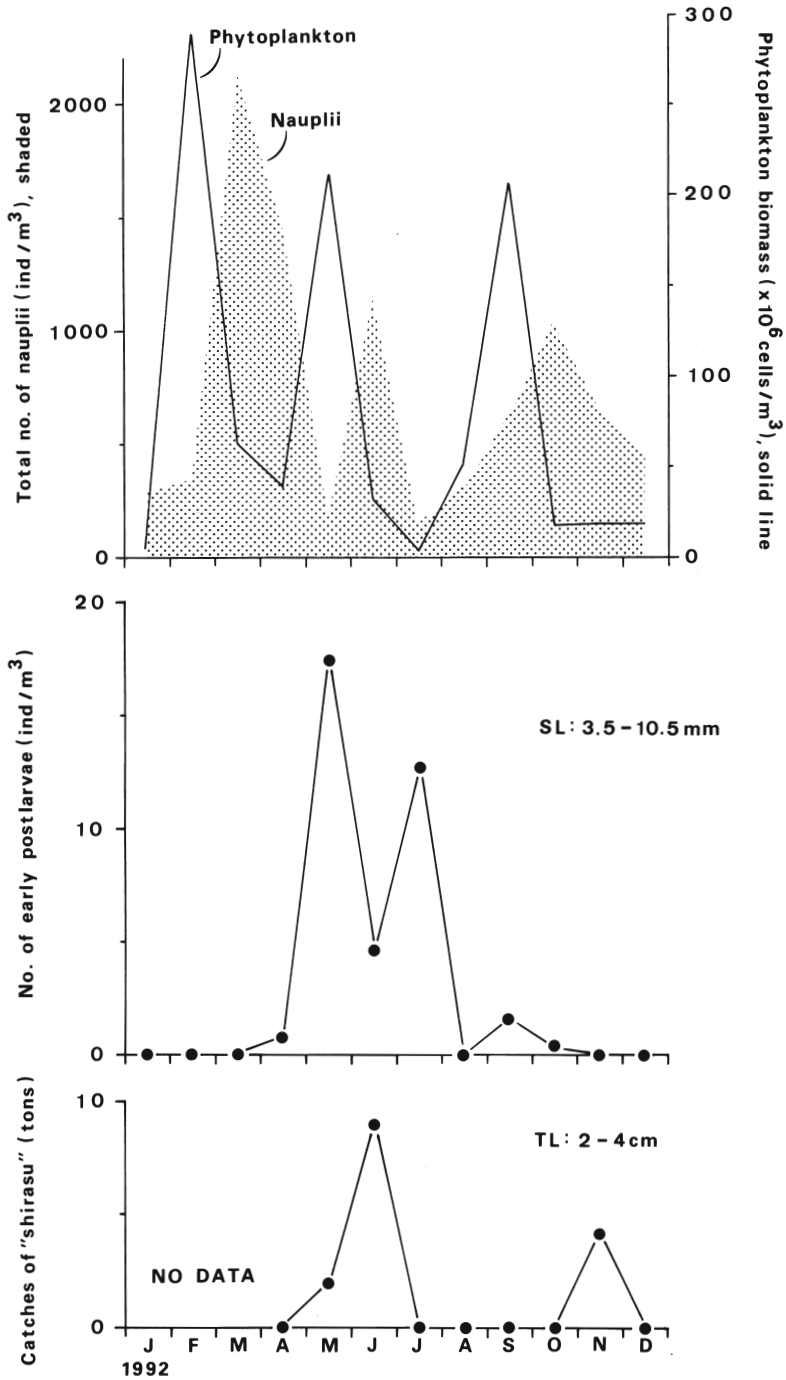


Fig. 4. Seasonal variations in the number of copepod nauplii and in the phytoplankton biomass (upper panel, modified from HIRAKAWA *et al.* 1995), and in the number of the early postlarval anchovy (middle panel), and in the catch of "shirasu" (lower panel, YAMAGUCHI PREFECTURAL OPEN SEA FISHERIES EXPERIMENTAL STATION 1993). There were no catch data from January to March 1992.

According to NAKAI *et al.* (1955), approximately two months are necessary for anchovy growth from the early postlarvae of 7.0 mm in SL to the “shirasu” of 30.0 mm in SL. Considering this growth time and the distributions of the pre- and postlarval anchovies in the Tsushima Straits and adjacent waters (NAKAHARA *et al.* 1985), the peak catches of “shirasu” in June and November are dependent on the spring and autumn groups appearing as the early postlarval peaks in May and September, respectively.

However, it is noticeable that there is no “shirasu” catch in summer, in spite of the occurrence of a summer group as the second peak of the early postlarvae in July. The precise reason why no “shirasu” catch corresponding to the July peak of postlarvae occurred in summer is not clear, at present. A possible explanation is that the summer group was under unfavorable food conditions for their growth and survival. This is due to the summer decline (Fig. 3) in the populations of copepods (copepodids and adults), which are the most significant food source for “shirasu” with a TL of 16–34mm (MITANI 1988). Thus, there are two distinct “shirasu” groups which occur in spring and autumn.

4 Gut contents of the early postlarval anchovy

Food incidence (percentage of larvae containing at least one food particle for a particular sample) was 24.4% in spring and 40.6% in autumn. Table 2 shows that both spring (May) and autumn (October) larvae fed mainly on copepods (>90% of the total) of different developmental stages, particularly as nauplii (46–52% of the total), and on unidentified crustacean remains. Dinoflagellates and ciliates were also found, but only occasionally and rarely.

Table 3 shows the species composition of copepod nauplii found in the guts of larvae. Most of the nauplii were in poor condition making species identification difficult, although some were identified to genus. Nauplii, represented by *Calanus-Paracalanus* type and *Oithona* spp., were dominant dietary components of larvae, accounting for 93% in May and 62% in October in total. In addition to these dominant groups, nauplii which consisted of

Table 2. Composition of food found in the guts of anchovy larvae (standard length: 4.0–8.9mm) collected at the station in October 1993 and May 1994. Numbers denote their relative abundance as a percentage of the total (*N*).

Food item	May 18, 1994 (<i>N</i> = 127)	October 19, 1993 (<i>N</i> = 127)
COPEPODA	92.9	98.4
Developmental stages		
eggs	37.8	1.6
nauplii	46.4	51.9
copepodids	7.9	37.0
adults	0.8	7.9
DINOPHYCEAE (Peridineaceae)	0.8	
CILIATA (<i>Codonellopsis</i> sp.)		0.8
Unidentified	6.3	0.8

Table 3. Composition of copepod nauplii found in the guts of anchovy larvae (standard length: 4.0–8.9mm) collected at the station in October 1993 and May 1994. Numbers denote their relative abundance as a percentage of the total (N).

Copepod nauplii	May 18, 1994 ($N=59$)	October 19, 1993 ($N=66$)
CALANOIDA		
<i>Calanus-Paracalanus</i> type ^{a)}	52.5	37.9
<i>Eucalanus</i> spp.		6.1
<i>Temora</i> spp.		1.5
Pontellidae		1.5
<i>Acartia</i> spp.		1.5
CYCLOPOIDA		
<i>Oithona</i> spp.	40.7	24.3
POECILOSTOMATOIDA		
<i>Oncaea</i> spp.		1.5
<i>Corycaeus</i> spp.		1.5
HARPACTICOIDA		
<i>Microsetella</i> spp.		4.5
<i>Euterpina acutifrons</i>		7.6
Unidentified	6.8	12.1

^{a)} including Calanidae, Paracalanidae and Pseudocalanidae.

various calanoids (*Eucalanus* spp. *Temora* spp. Pontellidae and *Acartia* spp.), poecilostomatoids (*Oncaea* spp. and *Corycaeus* spp.) and harpacticoids (*Microsetella* spp. and *Euterpina acutifrons*) were recognized in the guts of the autumn larvae. Even though their individual quantities were small, their combined numerical abundance represented more than 26% of the total, including some unidentified remains.

The results of gut content analysis revealed that the food of the autumn larvae showed a greater variety of copepod nauplii than that of the spring larvae (Table 3). This demonstrates that the larval food composition clearly reflects the seasonal succession of copepod assemblage in the study area (Fig. 3) under the influence of the alternation of water masses, as shown in Fig. 2. The spring larvae depend on the higher peak abundance of a comparatively simple copepod assemblage with only a few temperate species supported by the large spring phytoplankton bloom in the low temperature, high salinity water mass. The autumn larvae, however, depend on the lower peak abundance of a more highly diversified copepod assemblage of the temperate-subtropical species associated with the small autumn phytoplankton bloom under high temperature and low salinity conditions of water.

Discussion

Our results not only confirm the previous researches that copepods and their nauplii are essential food items for anchovy larvae (BERNER 1959; CIECHOMSKI 1967; de MENDIOLA 1974; ARTHUR 1976; UOTANI *et al.* 1988 etc.), but also have an important implication for the study of population dynamics of anchovy.

In the seas around Japan, the anchovy population contains two separate groups, a spring race and an autumn race—due to the difference of main spawning seasons (WATANABE 1960; ASAMI 1962; NAKAHARA and OGAWA 1979; FUNAKOSHI 1992 etc.). Even though these two races of anchovy coexist, each race is quite distinct. The autumn race lives in restricted coastal waters, makes short migrations and displays small population fluctuations when its population level is low. The spring race migrates over wide areas and displays large, long-term fluctuations in its population levels. This is well known as a so-called dominant species alternation, which is also seen in pelagic fish community from the “anchovy era” to the “sardine era” (e.g. NAKAHARA and OGAWA 1979), for example.

In terms of the long-term population fluctuations of anchovy, our results imply a possible mechanism by which the abundance of the spring race shows such large, long-term fluctuations in comparison with those of the autumn race. The spring copepod assemblage, on which the spring race depends, consists of a few dominant species, although its abundance is high (Fig. 3). If a simple assemblage with only a few species is not always as stable as compared to the more highly diversified assemblage latter in the year, it is probable that the food conditions for the spring race may show more considerable interannual fluctuations. Although we have no direct evidence to confirm this, there are several cues, related to the biological process at the lower trophic levels, which suggest that this implication is plausible.

For example, the transparency can be a practical and useful index of phytoplankton biomass in the seas around Japan (NAGATA 1996). According to NAGATA *et al.* (1996), the transparency of water in the seas around Japan remarkably decreases in spring and its coefficient of variation shows a peak at the same time. This signifies that the spring phytoplankton bloom, on which the spring copepod assemblage depends, shows large year-to-year fluctuations. Thus, food conditions for the spring copepod assemblage are not always stable because of the large phytoplankton fluctuations in spring. This may be a trigger event that leads to large, long-term fluctuations in the spring race of anchovy.

In comparison with the large coefficients of variation of the transparency in spring, those in autumn are small (NAGATA *et al.* 1996). This signifies that there is only a small year-to-year fluctuation in the autumn phytoplankton bloom, on which the autumn copepod assemblage depends. Even so, the degree of the autumn decrease in transparency reflects a lower bloom peak in autumn than that in spring. Thus, this cue implies that a small, but stable phytoplankton bloom in autumn feeds and stabilizes the autumn copepod assemblage with a high species diversity but a lower peak level of abundance. This may explain why the autumn race of anchovy shows smaller long-term fluctuations in population even at a

lower population level.

FUNAKOSHI (1990) also reported examples that “shirasu” catches fluctuated in response to the changing structure of copepod assemblage in coastal waters along the Pacific Ocean. In order to reveal the precise mechanism regulating anchovy populations, it is necessary to monitor the long-term fluctuations in the copepod assemblage as a major food item of anchovy in relation to fluctuations in the hydrographic conditions and phytoplankton biomass. The key mechanism consists of at least three major biotic/abiotic elemental processes. They are (1) a process regulating phytoplankton biomass under changing hydrographic conditions, (2) a process regulating not only the abundance but also the structure of copepod assemblages as a food resource for anchovy under changing hydrographic conditions and linked to the fluctuations in primary production, and (3) a process regulating the survival of anchovy during the early stages of its development under changing hydrographic and food conditions.

In addition, there is a further point which needs to be examined. This is the so-called “diversity-stability rule” (e.g. WILSON and BOSSERT 1971) for copepod assemblage. As for the diversity-stability relationships in a community, it is summarized, at present, that diversity and stability tend to be parallel to each other, although there is no clear law of causation between them (KOBAYASHI 1980). If this is the case, the high diversity of the autumn copepod assemblage tends to parallel to high stability, while the lower diversity of the spring copepod assemblage tends to parallel its lower stability. However, it is also necessary to monitor year-to-year changes in not only the abundance, but also the structure of copepod assemblage to verify this diversity-stability rule.

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日本海南西部におけるカイアシ類群集の特性とそれが カタクチイワシ個体群動態にもつ意味

平川和正・小川嘉彦

1992～1994年山口県沖定点で、カタクチイワシ仔魚の餌料としてのカイアシ類群集の季節変化を生物・非生物的環境との関連で調べた。仔魚の餌料組成は、水塊の季節的交替に伴うカイアシ類群集の季節的遷移を反映している。春季仔魚は、低温・高塩分水下で植物プランクトン大増殖に同調した単純な種組成を示す温帯性カイアシ類群集の大きな出現ピークに依存する。他方、秋季仔魚は、高温・低塩分水下での小規模な植物プランクトン増殖に伴う種多様性に富む温帯～亜熱帯性カイアシ類群集の小さな出現ピークに依存する。この結果はカイアシ類群集の経年変動がカタクチイワシ個体群の数量変動に重要な役割を果たしている可能性を示唆している。

Appendix 1. Individual numbers (per m³) of copepods collected with the NORPAC net at the station off Yamaguchi Prefecture from January to December 1992.

Species	Sampling date	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Nov.
	8 1992	5	10	8	1	2	2	7	3	1	5	30	
CALANOIDA													
<i>Calanus minor</i>	1.2	0.5	0.0	0.0	0.0	0.0	0.0	3.9	5.3	7.8	29.6	8.8	1.4
<i>Calanus sinicus</i>	1.2	2.6	226.6	48.9	141.1	10.3	11.4	7.5	12.9	3.8	2.0	1.2	
<i>Mesocalanus tenuicornis</i>	1.6	0.2	4.0	1.5	16.7	2.4	2.4	2.8	3.0	5.5	1.4	0.6	
<i>Neocalanus gracilis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Cosmocalanus darwini</i>	0.4	0.0	0.0	0.0	0.0	0.0	3.1	0.0	2.2	1.6	2.7	1.2	
<i>Undinula bulgaris</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	5.4	0.6	
<i>Canthocalanus pauper</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	7.7	3.4	0.2	
<i>Eucalanus attenuatus</i>	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Eucalanus crassus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.7	0.6	
<i>Eucalanus mucronatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.1	0.7	3.1	
<i>Eucalanus pileatus</i> ?	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	
<i>Eucalanus subcrassus</i>	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.6	0.0	3.3	0.7	0.0	
<i>Eucalanus subtenius</i>	0.0	0.0	6.1	2.4	18.9	0.6	5.5	8.9	9.0	22.5	6.8	2.5	
<i>Rhincalanus nasutus</i>	0.0	0.0	0.0	0.5	14.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	
<i>Xanthocalanus</i> sp. ?	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	
<i>Mecynocera clausi</i>	0.0	0.2	7.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.7	0.0	
<i>Paracalanus aculeatus</i>	15.1	12.4	11.1	1.9	1.1	3.6	1.6	1.4	12.9	14.2	35.2	16.0	
<i>Paracalanus parvus</i> (= <i>P. quasimodo</i>)	9.1	5.5	87.0	4.4	3.3	5.5	0.8	2.8	0.0	13.1	18.3	1.9	
<i>Acrocalanus gibber</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	3.3	0.7	0.0	
<i>Acrocalanus gracilis</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.4	1.4	3.0	5.5	3.4	0.6	
<i>Calocalanus pavo</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.8	2.8	2.6	1.1	0.7	0.0	
<i>Ischnocalanus plumulosus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.6	0.4	0.0	0.7	0.2	
<i>Clausocalanus arcuicornis</i>	4.0	3.1	2.0	10.7	15.6	3.0	14.9	6.4	16.8	17.5	13.5	2.5	
<i>Clausocalanus farrani</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.9	0.0	0.0	0.8	
<i>Clausocalanus furcatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	1.3	1.1	12.9	4.5	
<i>Clausocalanus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	
<i>Ctenocalanus vanus</i>	7.5	7.6	45.5	25.7	36.7	43.2	14.6	12.8	9.0	0.5	11.5	4.1	
<i>Euchaeta concinna</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0	
<i>Euchaeta flava</i>	4.4	8.6	10.1	2.4	3.3	14.6	8.7	5.5	16.4	6.0	22.3	14.4	
<i>Euchaeta longicornis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	
<i>Euchaeta plana</i>	9.9	1.4	6.0	1.0	5.6	4.9	2.0	3.6	2.6	8.2	31.8	7.6	
<i>Euchaeta wolfendeni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	
<i>Euchaeta</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	
<i>Scolecithricella bradyi</i>	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	
<i>Scolecithricella longispinosa</i>	0.8	0.0	1.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.7	0.0	
<i>Scolecithricella</i> sp.	0.0	0.0	0.0	0.0	2.2	0.0	0.4	0.0	0.9	0.5	0.7	0.0	
<i>Scolecithrix danae</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	2.0	1.0	
<i>Scolecithrix nicobarica</i>	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.4	
<i>Scolecithrix</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.9	0.0	0.0	0.0	
<i>Aetideus giesbrechti</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.0	0.0	0.7	0.0	
<i>Centropages abdominalis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.0	
<i>Centropages bradyi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	
<i>Centropages furcatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	3.4	19.2	0.0	0.2	
<i>Centropages orsinii</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	
<i>Centropages yamadai</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.5	0.0	0.0	
<i>Calanopia minor</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	

Appendix 1. Continued.

Species	Sampling date	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Nov.
	8 1992	5	10	8	1	2	2	7	3	1	5	30	
CALANOIDA													
<i>Labidocera acuta</i>	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.6	2.6	2.2	0.0	0.0
<i>Candacia bipinnata</i>	0.0	0.0	1.0	1.0	13.3	12.8	2.0	0.6	1.7	1.6	0.0	0.0	
<i>Candacia catula</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.9	1.1	0.0	0.0	
<i>Candacia truncata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	
<i>Candacia</i> sp.	0.0	1.0	2.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.2	
<i>Temora discaudata</i>	0.0	0.0	0.0	0.0	0.0	0.6	5.9	3.9	5.2	1.1	0.0	0.0	
<i>Temoropia mayumbaensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	
<i>Pleuromamma gracilis</i>	0.0	0.2	0.0	1.5	4.4	0.6	0.8	0.0	0.4	0.0	2.0	0.0	
<i>Pleuromamma robusta</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	2.0	0.2	
<i>Lucicutua flavicornis</i>	0.8	0.2	1.0	0.0	1.1	0.0	1.6	0.6	0.4	0.0	0.7	0.2	
<i>Acartia danae</i>	0.8	0.0	0.0	0.0	1.1	0.0	5.9	10.3	6.5	6.6	2.0	0.6	
<i>Acartia erythraea</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	
<i>Acartia negligens</i>	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.6	0.4	0.5	1.4	0.4	
<i>Acartia omorii</i>	0.0	0.0	0.0	1.9	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Acartia pacifica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	
POECILOSTOMATOIDA													
<i>Corycaeus affinis</i>	1.2	2.4	0.0	35.4	7.8	14.6	2.0	0.6	0.0	0.0	0.0	0.0	
<i>Corycaeus agilis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.7	0.0	0.0	0.0	0.0	
<i>Corycaeus andrewsi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	
<i>Corycaeus catus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	4.3	2.7	0.0	0.2	
<i>Corycaeus crassiusculus</i>	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.1	2.0	1.9	
<i>Corycaeus dahli</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.4	
<i>Corycaeus flaccus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	
<i>Corycaeus gibbulus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.2	0.5	0.0	0.0	
<i>Corycaeus longistylis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	
<i>Corycaeus pacificus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	1.1	0.0	0.4	
<i>Corycaeus speciosus</i>	0.4	0.0	0.0	0.0	1.1	0.0	1.6	0.3	1.7	0.5	0.0	1.0	
<i>Corycaeus</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	2.7	0.7	0.6	
<i>Oncaea conifera</i>	0.4	0.0	0.0	0.0	2.2	0.6	1.2	0.3	0.0	0.0	0.7	0.0	
<i>Oncaea media</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.2	
<i>Oncaea mediterranea</i>	0.8	0.0	1.0	1.0	6.7	10.3	3.1	1.7	5.2	6.6	2.7	1.9	
<i>Oncaea venusta</i>	8.7	3.3	2.0	1.0	4.4	9.1	11.8	1.9	4.3	12.1	12.9	4.7	
<i>Sapphirina angusta</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	
<i>Sapphirina gemma</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.4	0.0	0.0	0.0	
<i>Sapphirina intestinata</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.3	0.0	0.0	0.0	0.0	
<i>Sapphirina nigromaculata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.5	0.0	0.0	
<i>Copilia longistylis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.7	0.0	
<i>Copilia mirabilis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.7	0.0	
<i>Copilia quadrata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	
CYCLOPOIDA													
<i>Oithona atlantica</i>	1.2	0.7	10.1	2.4	13.3	0.0	0.0	0.6	2.2	0.5	2.0	0.6	
<i>Oithona longispina</i>	2.0	0.0	16.2	1.5	5.6	9.1	6.3	0.3	0.4	0.5	4.1	0.2	
<i>Oithona plumifera</i>	8.7	2.6	11.1	27.1	20.0	24.3	8.7	2.5	6.5	5.5	23.7	6.6	
<i>Oithona setigera</i>	0.4	0.2	0.0	0.0	1.1	0.0	0.4	0.0	0.4	1.1	1.4	0.6	
<i>Oithona</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	
HARPACTICOIDA													
<i>Macrosetella gracilis</i>	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.7	0.2	
Copepod nauplii	0.0	0.0	5.1	1.5	0.0	0.0	0.0	2.5	1.7	1.1	0.0	0.0	