

Structure and Species Diversity of the Zooplankton Community of the Inland Sea of Japan

M. Madhupratap^a and Takashi Onbé

Faculty of Applied Biological Science, Hiroshima University, Fukuyama 720, Japan

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Seasonal fluctuations in composition and abundance of zooplankton of the Inland Sea of Japan were investigated in 1979–1980. Some of the areas in the environment were found to be eutrophic and sharp temperature variations occurred with seasons. In this scenario, zooplankton populations peaked in autumn. Copepods were the dominant component and six species of this group formed about 88% of the total zooplankton counts. Species groups are categorized based on distributional characteristics. Zooplankton composition was more or less homogeneous in each season within the area studied and a few oceanic species which occurred had only limited influence on community structure. Species diversity was low and competition among species was weak. The results indicated a poor quality biotope probably resulting from a deterioration of water quality and an environment which favours *r*-selection.

Introduction

The Inland Sea of Japan (33°17'–34°47'N; 130°55'–135°25'E) is an enclosed sea which partly skirts three major islands of Japan—Honshu, Kyushu and Shikoku. This scenic environment, speckled with many smaller islands, has recently become a centre of commercial and recreational activities. Thus, it is a receptacle of large quantities of industrial wastes and sewage, and this, along with many other man-made changes such as reclamations, has increased the vulnerability of the environment. To estimate the degree of changes in the ecology of the sea, periodic monitoring of the system is essential.

Considerable data on the distribution of zooplankton in the Inland Sea of Japan were collected in the 1950s and 1960s (Kado, 1950, 1954; Hirota, 1961, 1962, 1968*a,b*, 1969*a,b*; Yamazi, 1952, 1954) and since then the focus has shifted mainly to studies on the biology of some of those organisms such as copepods and cladocerans (Kasahara *et al.*, 1974, 1975*a,b*; Onbé, 1974, 1977, 1985; Uye, 1982; Uye *et al.*, 1979). Earlier studies indicated the presence of oceanic species of zooplankton in the area and investigators speculated on the influence of the Kuroshio Current in this environment. The present paper attempts to

^aPresent address: National Institute of Oceanography, Dona Paula 403004, Goa, India

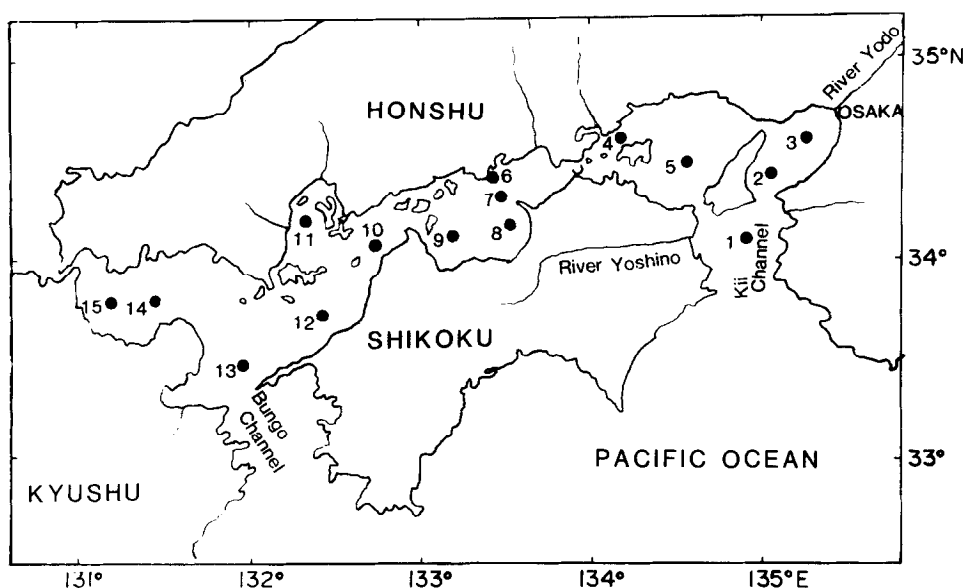


Figure 1. Map of the Inland Sea of Japan showing the location of stations.

analyse the zooplankton distribution based on a comprehensive set of data and to elucidate the structure of the zooplankton community in relation to environmental conditions.

Materials and methods

Zooplankton samples were collected during autumn (26 October–1 November, cruise I) in 1979, winter (19–25 January, cruise II), spring (17–23 April, cruise III) and the beginning of summer (20–26 June, cruise IV) in 1980 from 15 stations spreading over the Inland Sea of Japan (Figure 1). Vertical hauls from near bottom to surface were made with a Kitahara's net (mesh size 92 μ m). Vertical profiles of environmental data (salinity, water temperature and chlorophyll *a*) were simultaneously collected. Values obtained from the surface were used for analysis of environmental parameters. Zooplankton were identified and enumerated from whole samples or aliquots depending on the sample size.

Two-way analysis of variance (ANOVA) (Sokal & Rohlf, 1981) was performed to find out temporal and spatial variations in environmental data and zooplankton composition. The data were log transformed for computations and this ensured additivity of treatment effects. Clustering of stations (based on zooplankton composition) and copepod community (based on their species composition) was done using Mountford's (1962) technique. Species diversity was calculated using the following two indices: *D* (Margalef, 1968) which gives species richness and *E* (Heip, 1974) which derives an equitability component based on information theory.

Results

Environment

The Inland Sea of Japan is connected to the Pacific Ocean through the Kii Channel in the east and the Bungo Channel in the west (Figure 1). A narrower connection exists in the

TABLE 1. Surface values of water temperature, salinity and chlorophyll *a* during the four cruises (CR I–IV) in the Inland Sea of Japan

Stations	Temperature (°C)				Salinity (‰)				Chlorophyll <i>a</i> (µg l ⁻¹)			
	CR I	CR II	CR III	CR IV	CR I	CR II	CR III	CR IV	CR I	CR II	CR III	CR IV
1	22.2	13.1	12.1	20.7	32.9	33.5	32.6	32.0	1.1	1.0	1.0	2.1
2	22.7	12.9	11.9	20.3	32.9	33.1	31.6	30.9	3.4	0.9	4.2	2.3
3	21.9	7.6	11.3	21.2	31.8	28.4	30.2	25.6	11.6	5.4	4.5	9.4
4	22.1	8.5	12.0	20.3	30.2	31.4	31.0	31.0	2.2	2.7	4.4	3.0
5	22.1	10.6	11.6	21.3	31.9	32.1	31.9	30.9	2.6	1.8	3.2	2.3
6	21.9	9.2	13.8	22.6	29.8	31.9	31.3	30.2	9.3	1.9	3.5	9.6
7	22.1	9.4	12.9	22.6	30.5	32.1	32.5	31.8	5.4	2.3	1.8	1.2
8	22.1	10.2	12.6	23.2	30.9	32.3	32.7	31.3	3.1	3.0	1.0	1.8
9	22.5	10.7	12.8	22.2	31.3	32.4	32.8	31.6	2.0	2.0	0.9	1.2
10	22.5	12.3	12.9	19.0	32.1	32.8	33.0	32.8	1.7	1.8	1.7	1.2
11	21.7	11.4	12.6	21.3	32.0	32.5	32.3	30.7	3.0	6.9	1.7	1.0
12	21.9	12.7	13.2	20.3	32.7	33.3	33.3	32.2	1.3	1.2	1.3	1.4
13	21.6	14.0	12.9	20.3	32.8	33.7	33.4	32.7	2.2	0.9	2.8	0.8
14	21.4	10.0	12.8	22.2	31.8	32.7	32.7	31.8	3.2	1.5	2.1	1.0
15	22.0	8.6	12.9	23.0	32.2	32.4	32.6	30.9	1.6	4.8	2.0	1.9

Data from the Laboratory of Aquatic Environmental Biology, Hiroshima University (Courtesy of Prof. T. Endo).

north-west through the Kanmon Strait. These connections facilitate exchange of water with the oceanic environment, although the currents are mainly of tidal origin (Yanagi *et al.*, 1982; Murakami *et al.*, 1985). Depth of the area investigated varied from about 10 m at station 6 to 60 m at station 1. ANOVA showed variations occurring in the environment to be highly significant ($P < 0.001$) between seasons for surface temperature and between stations for surface chlorophyll *a*, whereas less significant ($P < 0.05$) variations, both spatial and temporal, occurred for surface salinity.

Environmental data are presented in Table 1. Water temperature in the area is known to attain higher values by late summer (*ca* 28 °C in August; Okaichi, 1985*b*). Vertical profiles of temperature showed that the water column was well mixed from autumn to spring, while mild stratification occurred in summer. The temperature difference from surface to bottom in this season was about 5 °C at the deeper stations. Salinity was generally higher in the Kii and Bungo Channels with a weak gradient towards interior regions. Lower values were recorded at station 3 where the River Yodo joins the Osaka Bay. From the distribution of chlorophyll *a*, it can be presumed that some of the areas such as stations 3 and 6 were highly eutrophic. Recent reviews on environmental conditions of the Inland Sea of Japan also indicate that the area is subject to considerable pollution, causing frequent outbreaks of red-tides (Okaichi, 1985 *a, b*; Okaichi *et al.*, 1983).

Zooplankton composition and distribution

Significant seasonal variations ($P < 0.001$) in total zooplankton counts were observed, but variations occurring between stations were less pronounced ($P < 0.05$). On the average, zooplankton counts were higher in autumn (aver. 20 891 m⁻³), followed by summer 13 326 m⁻³). In samples of winter and spring, when the environmental conditions were more or less similar to each other, the average counts were almost equal (8172 m⁻³ and

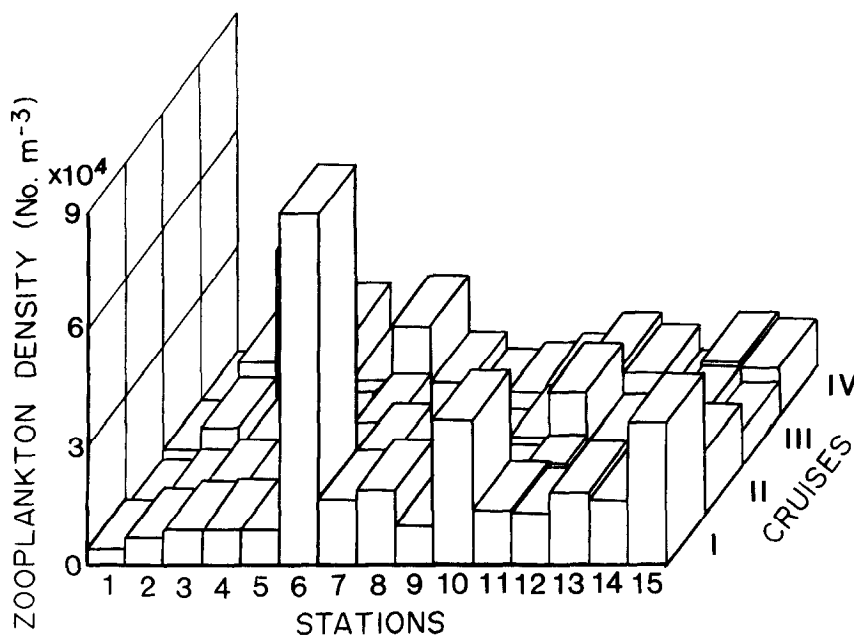


Figure 2. Distribution of total zooplankton in the Inland Sea of Japan in 1979–1980.

TABLE 2. Numerical abundance (averages from 15 stations) and percentages (all stations combined) of major zooplankton groups in 1979–1980 in the Inland Sea of Japan

Cruise	Copepoda		Invertebrate larvae		Chaetognatha		Appendicularia		Cladocera	
	No. m ⁻³	%	No. m ⁻³	%	No. m ⁻³	%	No. m ⁻³	%	No. m ⁻³	%
I (autumn)	19963	95.6	174	0.8	193	0.9	460	2.2	58	0.3
II (winter)	7643	93.5	253	3.1	51	0.6	214	2.6	3	0.04
III (spring)	7231	89.4	255	3.1	37	0.4	148	1.8	413	5.1
IV (summer)	10723	80.4	1229	9.0	50	0.4	195	1.4	1092	8.0

8089 m⁻³, respectively). The autumn peak was mainly due to the increase in the abundance of zooplankton at a few stations (Figure 2). At station 6, where fairly eutrophic conditions prevailed, a small calanoid copepod *Paracalanus parvus*, contributed to the increase (population density of the species: 80 000 m⁻³). A similar situation was observed at station 3 in summer.

Average abundance and percentage of composition of major groups of zooplankton are presented in Table 2. Copepods were the dominant group forming about 90% of the total annual zooplankton population. Trends in seasonal and spatial variations in this group were similar to that of total zooplankton. Among the other groups, invertebrate larvae showed significant variations in abundance ($P < 0.001$) between seasons with a peak in summer, whereas appendicularians varied significantly ($P < 0.001$) between stations (maximum density: 695 m⁻³ at station 15). Invertebrate larvae were represented by polychaetes, echinoderms, decapods, cirripedes and other crustaceans. A few other groups which exhibited seasonal variations ($P < 0.05$) were siphonophores (higher

TABLE 3. Results of ANOVA performed on data for abundance of species identified

	Between stations	Between seasons	Maximum abundance	
			station	month
Copepoda				
<i>Calanus sinicus</i>	**	NS	1,2	
<i>Eucalanus attenuatus</i>	NS	NS		
<i>E. mucronatus</i>	NS	NS		
<i>E. crassus</i>	NS	NS		
<i>E. subcrassus</i>	NS	NS		
<i>Rhincalanus rostrifrons</i>	NS	NS		
<i>R. nasutus</i>	NS	NS		
<i>Acrocalanus gracilis</i>	NS	NS		
<i>A. gibber</i>	NS	NS		
<i>Paracalanus parvus</i>	NS	***		Oct–Nov, Jun
<i>Euchaeta plana</i>	**	**	1,2,5	Jan
<i>E. longicornis</i>	NS	NS		
<i>Centropages abdominalis</i>	NS	***		Apr
<i>C. yamadai</i>	NS	NS		
<i>Pseudodiaptomus marinus</i>	NS	NS		
<i>Temora turbinata</i>	*	*	15	Oct–Nov
<i>Lucicutia flavicornis</i>	NS	NS		
<i>Candacia bipinnata</i>	NS	NS		
<i>Calanopia thompsoni</i>	NS	***		Oct–Nov
<i>Labidocera rotunda</i>	NS	NS		
<i>Acartia omorii</i>	NS	***		Apr
<i>A. pacifica</i>	NS	***		Oct–Nov
<i>A. erythraea</i>	NS	NS		
<i>Tortanus forcipatus</i>	NS	***		Oct–Nov
<i>Microsetella norvegica</i>	NS	***		Oct–Nov
<i>Clytemnestra rostrata</i>	NS	**		Oct–Nov
<i>Euterpina acutifrons</i>	NS	NS		
<i>Oithona</i> spp.	NS	***		Oct–Nov, Apr
<i>Oncaea media</i>	**	***	10,12,15	Oct–Nov
<i>Corycaeus affinis</i>	NS	NS		
Cladocera				
<i>Penilia avirostris</i>	NS	***		Jun
<i>Evadne tergestina</i>	NS	***		Jun
<i>E. nordmanni</i>	NS	***		Apr
<i>Podon polyphemoides</i>	NS	***		Jun
<i>P. leuckarti</i>	NS	***		Apr
Chaetognatha				
<i>Sagitta crassa</i>	***	**	6,7	Oct–Nov
<i>S. enflata</i>	NS	*		Oct–Nov

NS, not significant; *, significant at 5% level; **, significant at 1% level; ***, significant at 0.1% level.

abundance in October–November; average density: 36 m^{-3}) and fish eggs and fish larvae (higher abundance in June; average density: 10 m^{-3} for each group). Chaetognaths occurred in all seasons, whereas cladocerans proliferated in summer. Hydromedusae, Amphipoda, Isopoda, Ostracoda and Thaliacea were the other groups of zooplankton which occurred in low densities. Results of ANOVA performed on the species identified are presented in Table 3.

Within the Copepoda, 24 species of calanoids belonging to 15 genera, 3 species of harpacticoids and 2 species of poecilostomatoids, each belonging to a separate genus,

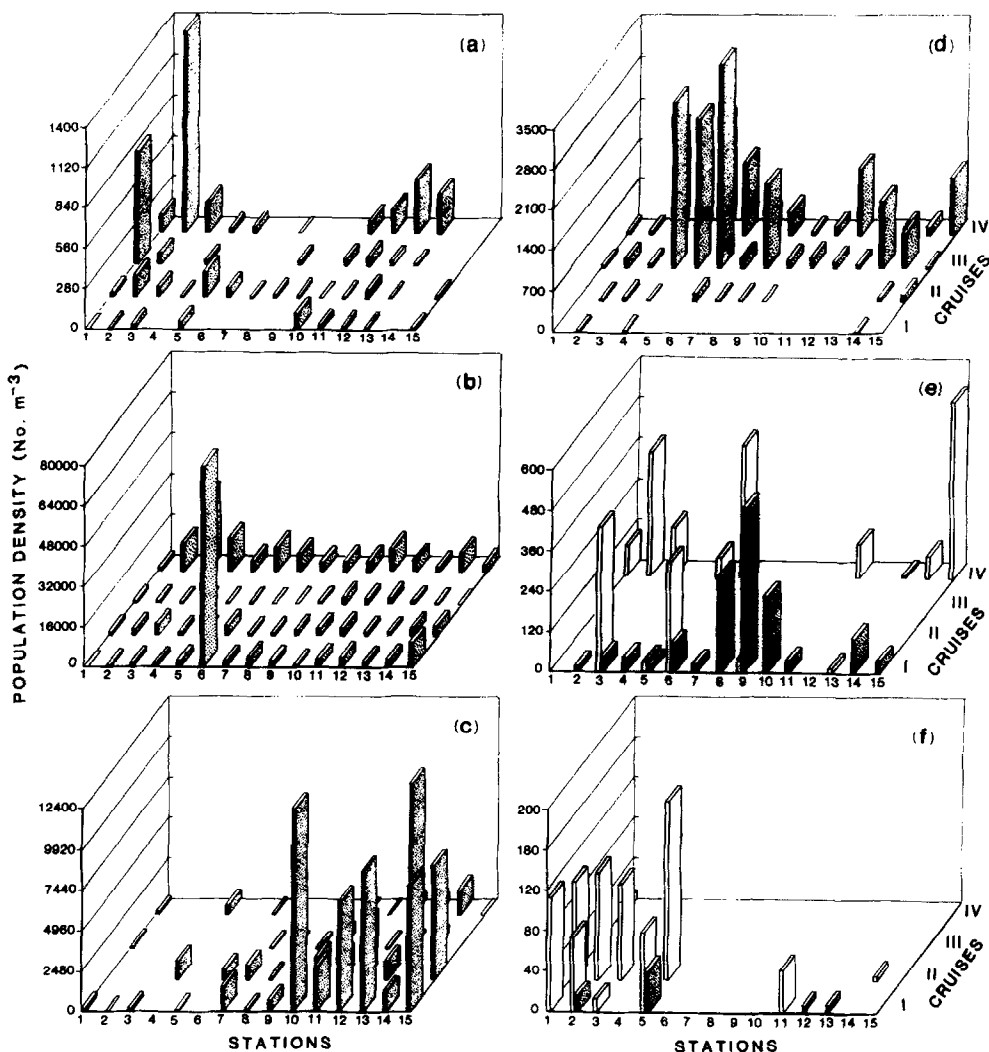


Figure 3. Distribution of selected species in the Inland Sea of Japan in 1979-1980: (a) *Calanus sinicus*, (b) *Paracalanus parvus*, (c) *Oncaea media*, (d) *Acartia omorii*, (e) *Acartia pacifica*; *Eudne tergestina* (not shaded), (f) *Sagitta enflata*; *Euchaeta plana* (not shaded).

plus cyclopoids *Oithona* spp., occurred in the present study. Six of these species, viz. *Paracalanus parvus* (41.6%), *Microsetella norvegica* (18.6%), *Oithona* spp. (16.9%), *Oncaea media* (11.3%), *Corycaeus affinis* (5.9%) and *Acartia omorii* (3.3%), comprised 97.6% of the total copepod population (88% of the total zooplankton counts). Based on distribution, and results of ANOVA, species belonging to the Copepoda could be classified into the following 5 categories.

1. Species occurring year-round without seasonal peaks

Calanus sinicus, a distinct neritic species, occurred in all seasons, albeit not being abundant. Although this species was more abundant in the Kii Channel [Table 3, Figure 3(a)], it also occurred in the interior stations. *Corycaeus affinis*, a relatively more abundant species, was another species of this category.

2. Species occurring year-round with seasonal peaks

Four common and abundant species, viz. *Paracalanus parvus*, *Microsetella norvegica*, *Oithona* spp. and *Oncaea media*, occurred in all seasons. However, all these species showed significant seasonal variations in population structure [Table 3, Figure 3(b,c)]. Among these, only *O. media* showed significant spatial variations and was more abundant in the western parts of the Inland Sea.

3. Seasonally occurring species

Acartia omorii was predominant in spring and early summer, and was almost absent in autumn [Figure 3(d)]. *Centropages abdominalis* occurred in the colder seasons of winter and spring. Species like *Acartia pacifica* [Figure 3(e)], *Tortanus forcipatus* and *Calanopia thompsoni* were present only in October–November samples. *Labidocera rotunda* and *Centropages yamadae* also are species occurring in warmer months and were collected mostly in October–November and in June.

4. Oceanic species

Some of the distant neritic/oceanic species like *Eucalanus attenuatus*, *E. mucronatus*, *E. subcrassus*, *Rhincalanus rostrifrons*, *R. nasutus*, *Acrocalanus gracilis*, *A. gibber*, *Euchaeta plana* [Figure 3(f)], *E. longicornis*, *Lucicutia flavicornis*, *Candacia bipinnata* and *Clytemnestra rostrata* occurred in the samples. These species were generally collected from stations located in the Kii or Bungo Channels. However, they usually occurred irregularly in very low numbers (formed only 0.17% of the total copepods collected in the four cruises) and did not show significant variations in the ANOVA with exceptions of *Euchaeta plana* and *Clytemnestra rostrata* (Table 3).

5. Other (neritic) species

Temora turbinata was also more frequent in the channel waters, but was a relatively more abundant species. *Euterpina acutifrons* infrequently occurred in channel waters as well as in interior regions albeit in low numbers. *Pseudodiaptomus marinus* was occasionally found in interior regions. However, the abundance of this epibenthic species could not be ascertained from day samples. *Acartia erythraea*, which is reported to be common in the interior regions of the Inland Sea during warmer months (Uye *et al.*, 1984), occurred only in low numbers in the present study.

Among the chaetognaths, *Sagitta crassa* was common in all seasons with peak abundance in October–November at stations located in interior regions. This species could be assigned to category 2. *S. enflata*, an oceanic chaetognath often encountered in neritic waters, occurred in October–November in low numbers in the channel waters [Figure 3(f)].

All five species of cladocerans occurred seasonally. *Podon polyphemoides* and *Penilia avirostris* were the more abundant species in summer, whereas *Evadne nordmanni* and *Podon leuckarti* had population peaks in spring. *E. tergestina* occurred in autumn and in summer [Figure 3(e)].

Relationship between stations

Cluster analysis based on zooplankton composition (Figure 4) showed high affinities between stations. The lowest correlation coefficient value was 0.595; no negative values resulted when the cruises were treated separately. Stations were somewhat linked spatially, although variations in the pattern of linkage were apparent in various seasons (not presented). The results, contrary to expectation, did not show complete affinity

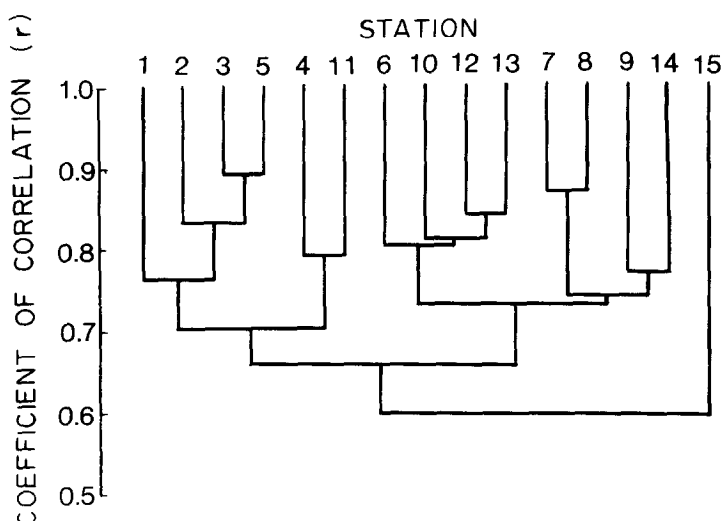


Figure 4. Dendrogram showing affinity between stations (all 4 cruises combined).

among similarly placed stations (stations in channels *versus* stations in interior regions). This was probably because the oceanic species occurred irregularly and in low numbers in the channels.

Species diversity

Species richness and equitability were generally low in the Inland Sea [Figure 5(a,b)]. Species richness showed higher values at stations located in the channels; this was due to the presence of oceanic species detected in these areas. Diversity was generally low in winter. Equitability was found to be inversely related to the density of the zooplankton population; it was generally low in October–November and somewhat higher values were observed in winter and spring. Naturally, the lowest values were observed at stations where the zooplankton population peaked as a result of increases in the density of one or a few species (e.g. stations 6 and 10 in October–November; station 3 in June).

Associations of copepod species

Linkage of copepod species occurring in the area under investigation is presented in Figure 6(a–d). The most striking features were the low affinity indices between most species. Common species which occurred year-round also did not cluster in a consistent pattern and were usually loosely linked or sometimes negatively correlated. This lack of correlation showed that the occurrence and abundance of these species were independent of one another. Any common factor controlling the distribution appears to be absent. However, associations of the oceanic species could be recognized and these were generally weakly or negatively correlated with other species.

In autumn, some neritic seasonal species like *Centropages abdominalis*, *C. yamadai*, *Labidocera rotunda*, etc. were also associated with oceanic species since they occurred in low numbers during the period. Three species, *Calanopia thompsoni*, *Acartia pacifica* and *Tortanus forcipatus*, which were collected only in autumn, were grouped together in this season. *Acartia omorii* and *Centropages abdominalis* which were more common in colder seasons were weakly or negatively correlated with most other species in winter and spring.

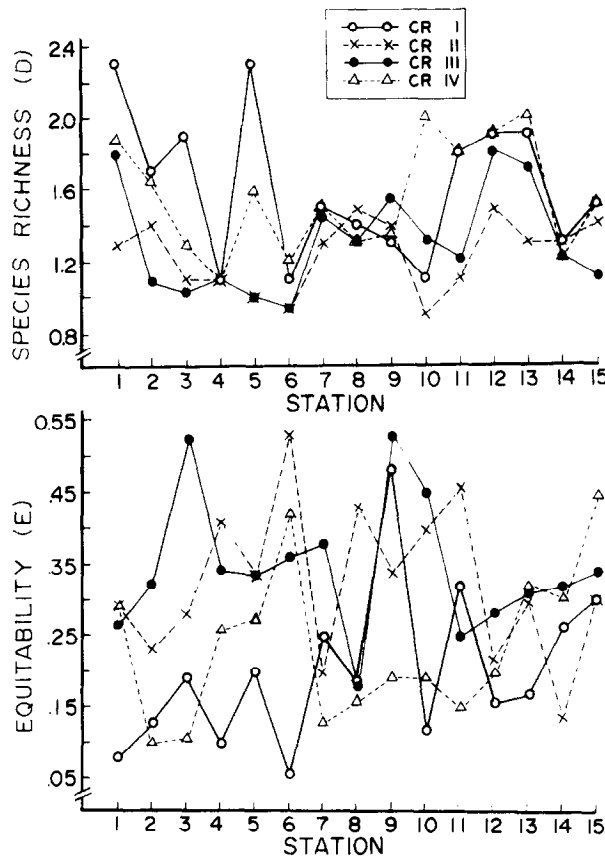


Figure 5. Species diversity indices (species richness and equitability) in the Inland Sea of Japan in 1979–1980.

A. omorii was also frequent in early summer and was linked with *Corycaeus affinis*, another common species. Very few of the positive associations between the frequently occurring species were significant.

Discussion

The Inland Sea of Japan, despite its proximity to the open ocean, has intrinsic characteristics derived from its geography and man-made changes. Some of the interior regions, close to industrial centres, appear to be heavily eutrophic in spite of tidal flushings. This situation, along with a weak salinity gradient, appears to effectively limit the incursion of distant neritic and oceanic zooplankton species. Temperature appears to be another environmental parameter controlling the temporal abundances.

The common copepod species occurring in the area included herbivores (*Paracalanus parvus*, *Oithona* spp.), omnivores (*Acartia omorii*, *Microsetella norvegica*) and carnivores (*Oncaea media*, *Corycaeus affinis*). Although the abundance of the herbivorous species increased dramatically at times in some of the heavily eutrophicated stations, consistent agreement between population peaks and chlorophyll *a* distribution could not be demonstrated. Such high population densities usually result from a series of discrete generations (Miller, 1983) and an *r*-selected strategy of opportunistic species living in an

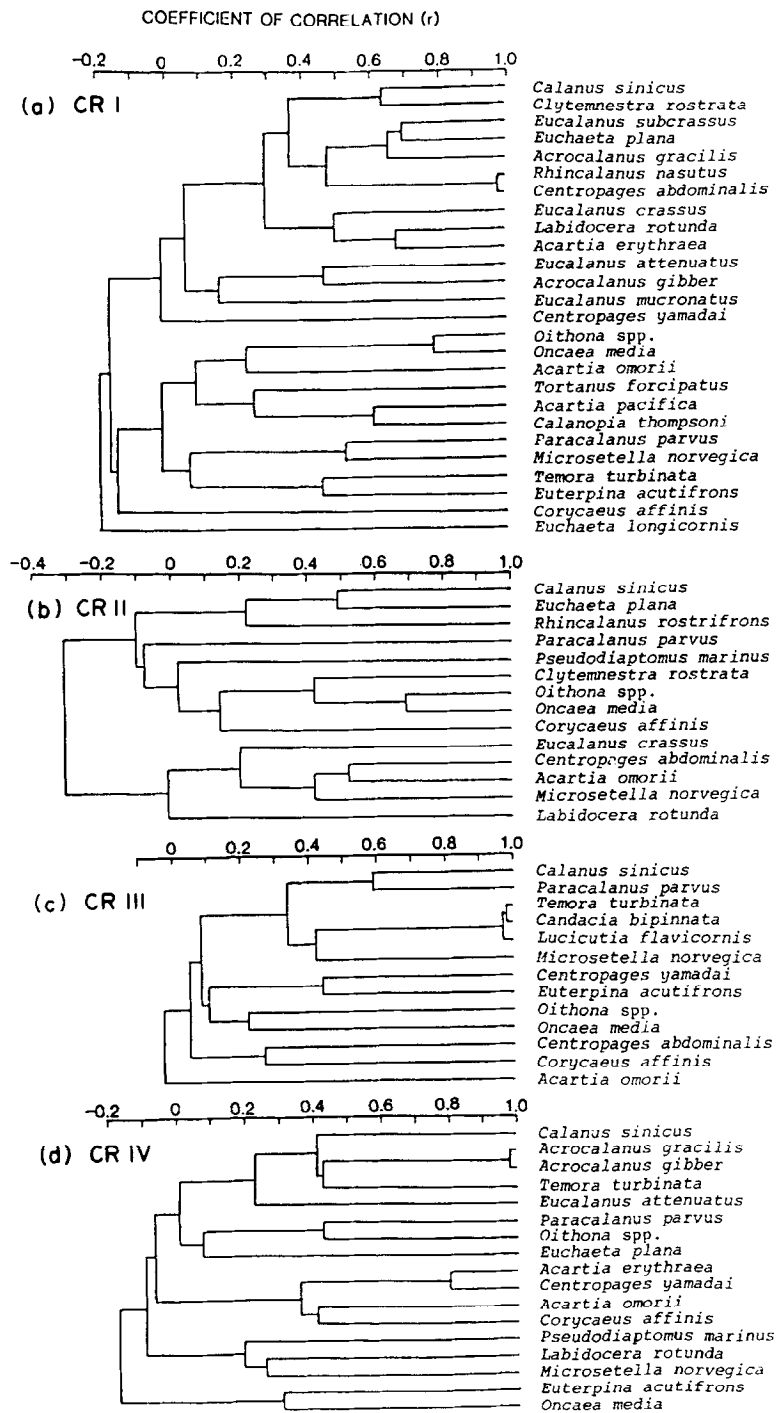


Figure 6. Dendrograms showing correlation between copepod species occurring in the Inland Sea of Japan: (a) autumn, (b) winter, (c) spring, (d) summer.

unstable environment. Relatively higher numerical abundance and dominance are often considered to be measures of successful adaptation (cf. Briggs, 1974). The aforementioned species have been reported to be abundant in the area in earlier studies (Hirota, 1961, 1962, 1968a,b, 1969a,b) and appear to be well tuned to the fluctuations in the environment.

Although the common copepod species occurred year-round (with the exception of *Acartia omorii*), most of them exhibited seasonal peaks. Generally, a higher population density was observed in autumn for most of these and other warm-water species. Population densities of these species begin to increase by early summer and probably attain their peaks in mid or late summer which are sustained until autumn. This period was not sampled in the present study, but some earlier studies by Hirota (1961) and Joh & Uno (1983) support this view. This sequence also seems applicable to the chaetognath *Sagitta crassa*. On the other hand, among species adapted to colder environmental conditions, *Acartia omorii* showed an increase in population by winter and higher density was sustained until early summer. *Centropages abdominalis* appears to be a winter-spring form.

In the light of studies conducted on egg dormancy of seasonally occurring copepod species in the Inland Sea of Japan (Kasahara *et al.*, 1974, 1975a,b; Kasahara & Uye, 1979; Uye & Kasahara, 1978; Uye *et al.*, 1979, 1984), it is now possible to explain the life history strategies of these species in relation to temperature. Adults of warm-water species like *Calanopia thompsoni*, *Centropages yamadae*, *Labidocera rotunda*, *Acartia pacifica*, *A. erythraea* and *Tortanus forcipatus* produce resting eggs before disappearing from the planktonic population as the water becomes cold by the beginning of winter. These eggs remain quiescent in the sea bottom mud until temperature conditions become favourable in the following spring or summer. The cold-water species, *Acartia omorii* and *Centropages abdominalis*, produce resting eggs to survive the warmer periods of the year. Similarly, all species of cladocerans, which occur seasonally in this area, are also known to produce resting eggs to survive unfavourable conditions (Onbé, 1974, 1977, 1985). The temperature threshold may vary with species. Some species produce diapause eggs which undergo an obligatory resting period and do not hatch even when favourable temperature conditions are attained until the refractory period is completed. Thus the two successional groups of cold-water species alternating with warm-water species occur together with species which occur year-round. With them the less abundant oceanic species and other groups of zooplankton form the mosaic of a zooplankton community.

The high degree of correlation between stations clearly showed a considerable homogeneity in zooplankton composition within each season in the area investigated. Most of the frequently occurring species did not show significantly higher abundance at any particular station (Table 3). Their abundances shifted independently of one another and of station positions over different seasons. Thus, ecotones are barely distinguishable within the Inland Sea of Japan. For this reason, earlier classification of the Inland Sea of Japan into different areas based on zooplankton composition (Hirota, 1969a,b) does not appear tenable. As has been mentioned, oceanic species occurred in very low numbers and did not appear to influence the linkage.

It is perhaps difficult to classify strictly distant neritic species assemblages into neritic and oceanic species (see Tokioka, 1979, for a detailed discussion). Most of the oceanic species recorded in the present study had been reported in earlier studies (Hirota, 1961, 1969a,b). These studies speculated on the possible influx of oceanic water into the Inland Sea of Japan and the influence of the Kuroshio Current which approaches the main island of

Japan in autumn. However, only a few distant neritic/oceanic species occur in the Inland Sea. These species occurred in various seasons in the present study. On the whole, their populations appear to be expatriate, occurring irregularly in low abundances, and do not seem to influence the structure of the ecosystem. In some earlier studies, the abundances of a few oceanic copepod species occurring in this region were reported to be somewhat higher than those observed in the present observation. Hirota (1961) found the chaetognath *Sagitta enflata* to be frequent and abundant in the interior regions of the Inland Sea. However, in a later study (Hirota, 1979), he reported this species to be absent in this area. It is possible that a deterioration in the water quality of the environment limits the present day distribution of the oceanic species.

Species diversity and evenness in species distribution were generally low and the indices obtained were comparable or sometimes even less than values reported from species-impooverished lagoons and estuaries (Madhupratap, 1983). Judging from these circumstances, the system is a poor quality biotope. It is difficult to reason out the lack of niche diversification *a priori*. However, instability in the environment resultant from seasonal temperature fluctuations, coupled with poor water quality in the interior regions, probably leads to this situation. Despite a fairly high degree of isolation, no endemic species of zooplankton has been reported from this area. These features imply that any faunal specialization to exploit a resource gradient is absent.

The loose interactions between the species also reflect a less specialized biotope, which does not foster niche separation. Competition, if it exists, is weak and even the few congeners are virtually precluded from competing for a common resource spectrum. A paucity of species, a high degree of dominance by a few (opportunistic) species with rapid rates of population increase, non-equilibrium conditions and a lack of competition among species characterize the Inland Sea of Japan as an environment which favours *r*-selection.

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