Spatiotemporal distribution of planktonic copepod communities in Tokyo Bay where *Oithona davisae* Ferrari and Orsi dominated in mid-1980s

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The spatiotemporal distributions of the planktonic copepod communities in Tokyo Bay in 1986–1987, when it was in a more eutrophicated condition than at present, were examined using zooplankton samples collected by vertical hauls of Kitahara’s quantitative net (mesh opening, 0.1 mm) from 19 stations in July, August, October, December 1986 and February 1987. The total abundance of copepods ranged from $3 \times 10^4$ to $2750 \times 10^4$ ind. m$^{-2}$ with peaks in July and August and a remarkable decrease in October. *Oithona davisae* dominated most samples with the subdominant species *Acartia omorii* in the inner and central areas in December and February, and *Paracalanus parvus* s.l. in the outer area in October, December and February. The copepod communities in the inner and central areas were classified into 2–4 groups in July, August and October, whereas they mostly comprised a single group in December and February. These differences in distribution pattern might be related to seasonal changes in environmental factors such as river discharge, intrusion of high-salinity outer-bay water, and hypoxic water. In comparison with the community in July 1948, the area of dominance of *O. davisae* had expanded to the whole bay and *A. omorii* had decreased in the inner area in July 1986, while other copepods such as *P. parvus* s.l. and *Microsetella norvegica* had decreased in the whole bay.

**Keywords:** spatiotemporal distribution; copepod community; *Oithona davisae*; Tokyo Bay; eutrophication; hypoxic water

**Introduction**

Tokyo Bay, surrounded by metropolitan areas, is one of the most highly eutrophicated inlets in Japan. Although water pollution increased through the 1960s with a nutrient peak and lowest transparency in the early 1970s, it has shown a recovery in recent years (Kanda et al. 2008; Ishii et al. 2008a). However, anoxia in the bottom layer and the Aoshio phenomenon (upwelling of anoxic water) continue to the present (Unoki 2011).

Although the distribution of the community of planktonic copepods, which play an important role as the primary consumers in the bay, was investigated in the whole bay area in 1948 (Yamazi 1955), there was no additional information for c.20 years after that study. Since 1970, many scientists have studied seasonal fluctuations (Anakubo and Murano 1991; Nomura and Murano 1992; Nomura et al. 1992; Itoh and Aoki 2010; Tachibana et al. 2013), vertical distribution (Anakubo and Murano 1991; Itoh et al. 2011) and long-term fluctuations (Marumo and

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Murano 1973; Nomura 1993), but such studies were conducted at a few restricted stations. Tokyo Bay extends 80 km north to south, and is an estuarine environment due to discharge from the Tamagawa River, Arakawa River and Edogawa River, etc., in the innermost area and connects with the Pacific oceanic environment via the entrance area. Although investigation of the whole bay is necessary for understanding this diverse bay ecosystem, previous studies were restricted to data obtained in July 1948 (Yamazi 1955), November 1970 (Yamazi 1973) and August 1989 (Uye 1994).

In order to get basic information for monitoring, we investigated the horizontal distribution of planktonic copepod communities in Tokyo Bay in summer, autumn and winter on the basis of samples collected during July 1986–February 1987, applying the same sampling method as in Yamazi (1955). We also compared species composition and copepod abundance patterns between 1948 and 1986 and discussed seasonal differences in relation to environmental factors.

Material and method

Field surveys were conducted on 1 July, 25 August, 27 October, 24 December 1986 and 19 February 1987 at 17 stations located in the inner and central area (the area north of the line linking the Capes-Kannonzaki and Futtsumisaki) in the bay, and at two additional stations in the outer area (Figure 1). Plankton samples were collected by vertical tows from the bottom to the surface of Kitahara’s quantitative net (Japan meteorological agency 1970; mouth diameter, 22.5 cm; mesh opening, 100 μm) which is same Hensen-type net as in Yamazi (1955). Although mounting a flow meter on this net is difficult due to its small mouth, a large filtering ratio can be ensured by fitting the canvas headpiece with a hoop. The samples were immediately fixed and preserved in buffered 5% formalin seawater solution. Environmental data such as temperature, salinity, dissolved oxygen (DO) and transparency at the time of sampling were obtained from other reports of water quality (Investigation Committee for Fisheries Impacts of Trans-Tokyo Bay Highway and Japan Fisheries Resources Conservation Assoc 1987).

In the laboratory, each original sample was sieved into large and small fractions with a 330-μm mesh net. The copepods in the large fraction were fully counted under a stereo-microscope, while those in the small fraction were counted from a 1/50 to 1/200 aliquot under a compound microscope. Copepods were identified to the lowest possible taxonomic level. Adults and immature copepodids were enumerated separately. The count data were converted to abundance per unit area (ind. m$^{-2}$) assuming a 100% filtration efficiency. We used individual number per square metre as a unit of copepod abundance in this paper, because use of abundance per unit volume (ind. m$^{-3}$), as averages over the depth of stations, tend to underestimate the abundance of the species that limited to particular layers (e.g. near-surface, near-bottom), particularly those at deeper station near the mouth of the bay as compared with those at inner station.

Grouping of communities was performed by using abundance data (ind. m$^{-2}$) for adults of the 18 species for which the frequency of occurrence exceeded 10%. Bray–Curtis similarity indices between samples (communities) were calculated using transformed abundance [log (x + 1)] in accordance with the method of Field et al. (1982). Cluster analysis was conducted by the unweighted pair-group method using arithmetic means and ordination on a two-dimensional map by non-metric
multidimensional scaling (NMDS). Dendrogram construction and NMDS were performed with the add-in software Cluster analysis Ver. 3.3 (Hayakari 2001) and Systat 11 (HULINKS, Inc., Tokyo, Japan), respectively. Environmental variables which have a significant correlation to ordination of the derived community groups on the NMDS plot were examined by multiple regression analysis, where ordination scores for each sample (x, y) were the independent variables and each environmental value was the dependent variable (cf. Kruskal and Wish 1978).

To define indicator species, an indicator value (IndVal) was calculated for each species within each community, in accordance with the method of Dufrene and Legendre (1997). In the present study, the top two species in order of IndVal were defined as indicator species in each community group. The Shannon–Wiener index ($H'$; Shannon and Weaver 1963) was also calculated for comparison of species diversity.

Comparisons of environmental variables and copepod abundance among seasons or community groups were performed using Bonferroni multiple comparison
procedure. Transformed abundance \[\log (x + 1)\] was used in calculations, because abundance is not normally distributed in general.

To compare with results in 1948 (Yamazi 1955), copepod abundance per unit area (ind. m\(^{-2}\)) was converted into abundance per unit volume of water (ind. m\(^{-3}\)) by dividing by depth (m). To compare between 1948 and 1986, Student’s \(t\)-test and the Mann–Whitney \(U\)-test were used for environmental variables and for copepod abundance, respectively.

Results

Hydrography

The monthly mean water temperature ranged from 9.8 to 25.7°C in the surface layer (0.5 m; Figure 2) and from 11.2 to 18.7°C in the bottom layers (1 m above sea floor). The difference between the surface and bottom layers was large in July and August \((p < 0.01)\), reflecting stratification of the water column, but small in October, December and February, as a result of vertical mixing. Areal differences were not significant in July, August and October, but values in the outer area were higher than those in the central and inner areas in December and February.

The monthly mean salinity ranged from 26.1 to 32.1 psu in the surface and from 33.1 to 33.7 psu in the bottom layer (Figure 2). Low values (<25 psu) were found in the surface layer in the western inner area in July and August, suggesting large river discharge. High values (>34) were found in bottom layer from the outer to central areas in every month except February (Figure 2), suggesting inflow of outer bay water. The difference between surface and bottom layers was larger in July and August than in the other months \((p < 0.01)\).

The monthly mean DO ranged from 6.3 to 10.8 and from 2.8 to 8.4 mg l\(^{-1}\) in the surface and bottom layers, respectively (Figure 2). Although the values in the bottom layer were more than 5 mg l\(^{-1}\) in the outer area, hypoxic water (DO < 2 mg l\(^{-1}\)) was found in the inner area in July, August and October and in the central area in August (Figure 2). In December, the hypoxic water disappeared and mean DO exceeded 6 mg l\(^{-1}\) in all areas.

The monthly mean transparency ranged from 1.6 to 6.4 m (Figure 2), with lower values (<2 m) in July and August than in the other months \((p < 0.01)\). In December and February, the values in the outer area were higher than in the other areas.

Copepod species

Through the five cruises, three orders, 30 families, 42 genera and 98 species of adult copepods were identified (Table 1). Two forms (medium and small forms) of *Oncaea venusta* Philippi, 1843 were treated as two different species because they represent different genetic lineages, according to recent molecular analysis (Elvers et al. 2006). The species number was 25 in the inner area, 65 in the central area and 77 in the outer area. Of these, 14 species of Calanoida and 16 species of Cyclopoida were collected only in the outer area, while the other 68 species (38 species of Calanoida, 23 species of Cyclopoida and seven species of Harpacticoïda) occurred in the central and inner areas, including those occurring in the outer area as well. The latter 68 species comprise inhabitants of various habitats including fresh water (e.g. *Eucyclops* sp.,
Mesocyclops sp.), brackish water (e.g. Sinocalanus tenellus, Acartia sinjiensis), inlet water (e.g. A. omorii, Centropages abdominalis, Labidocera rotunda), coastal water (e.g. Calanus sinicus, Paracalanus parvus s.l.) and oceanic water (e.g. Paraeuchaeta russelli, Pleuromamma gracilis, Temoropia mayumbaensis) (cf. Chihara and Murano 1997; Ishida 2002).
Table 1. Mean abundance, areal occurrence and frequency of occurrence of adult copepods recorded from Tokyo Bay in the present study.

| Species                          | Mean abundance (ind. m$^{-2}$) | Areal occurrence | Frequency of occurrence** (%) |
|----------------------------------|-------------------------------|------------------|--------------------------------|
|                                  | July  | August | October | December | February | I   | C   | O   |
| Calanoida                        |       |        |         |          |          |     |     |     |
| Acaritidae                       |       |        |         |          |          |     |     |     |
| Acartia (Acanthacartia) sinjiensis|     240 |       3 |         |          |          | *   | *   | *   |
| Mori                             |       |        |         |          |          | 16.8|     |     |
| Acartia (Acartia) danae           |     4  |       1 |         |          |          | *   | *   | 3.2 |
| Giesbrecht                       |       |        |         |          |          |     |     |     |
| Acartia (Acartia) negligens Dana  |     1  |       1 |         |          |          |     | *   | 1.1 |
| Acartia (Acartiura) omorii       |   14600 | 1000  | 38      | 3300     | 28900    | *   | *   | *   |
| Bradford                         |       |        |         |          |          | 91.6|     |     |
| Calanidae                        |       |        |         |          |          |     |     |     |
| Calanus sinicus Brodsky          |     120 |       8 | 7       | 10       |          | *   | *   | *   |
| Undinula vulgaris (Dana)          |       |        |         |          |          |     | *   | 1.1 |
| Candaciidae                      |       |        |         |          |          |     |     |     |
| Candacia bipinnata Giesbrecht    |     7  |       1 |         |          |          |     | *   | 3.2 |
| Centropagidae                    |       |        |         |          |          |     |     |     |
| Centropages abdominalis Sato     |     80 |       2400| 3800    |          |          | *   | *   | *   |
| Centropages tenuiremis Thompson  |       |        |         |          |          |     | *   | 51.6|
| & Scott                          |       |        |         |          |          |     |     |     |
| Sinocalanus tenellus (Kikuchi)   |     3  |       |         |          |          |     | *   | 2.1 |
| Clausocalanidae                  |       |        |         |          |          |     |     |     |
| Clausocalanus arcuticornis (Dana)|     4  |       |         |          |          | *   | *   | 3.2 |
| Clausocalanus farrani Sewell     |     3  |       1 |         |          |          | *   | *   | 3.2 |
| Clausocalanus furcatus (Brady)   |     3  |       9 |         |          |          | *   | *   | 4.2 |
| Clausocalanus lividus Frost &    |       |        |         |          |          |     | *   | 1.1 |
| Fleminger                       |       |        |         |          |          |     |     |     |
| Clausocalanus mastigophorus      |     1  |       |         |          |          |     | *   | 1.1 |
| (Claus)                          |       |        |         |          |          |     |     |     |
| Clausocalanus minor Sewell       |     1  |       1 |       1 |          |          |     | *   | 3.2 |
| Clausocalanus parapergens Frost  |     1  |       5 |       1 | 10        | 30        | *   | *   | *   |
| & Fleminger                      |       |        |         |          |          | 12.6|     |     |
| Clausocalanus paululus Farran    |       |        |         |          |          |     | *   | 3.2 |
| Clausocalanus pergens Farran     |     7  |       8 |       5 | 40        |          | *   | *   | 8.4 |
| Ctenocalanus vanus Giesbrecht    |    20  |     60 |       3 | 8         | 3         | *   | *   | 17.9|

(Continued)
Table 1. (Continued).

| Class          | Genus                     | Species                        | Author       | Size (μm) | Abundance |
|----------------|---------------------------|--------------------------------|--------------|-----------|-----------|
| Eucalanidae    | Subeucalanus pileatus     | (Giesbrecht)                   |              |           |           |
| Euchaetidae    | Euchaeta plana            | Mori                           |              |           |           |
|                | Paraechueta russelli      | (Farran)                       |              |           |           |
| Fossphanidae   | Temoropia mayumbaensis    | T. Scott                        |              |           |           |
| Lucicutiidae   | Lucicutia flavicornis     | (Claus)                         |              |           |           |
| Mecynoceridae  | Mecynocera clausi         | Thompson                        |              |           |           |
| Metridinidae   | Pleuromamma gracilis      | (Claus)                         |              |           |           |
|                | Pleuromamma piiseki       | Farran                          |              |           |           |
| Paracalanidae  | Acrocalanus longicornis   | Giesbrecht                      |              |           |           |
|                | Calocalanus curtus        | Andronov                        |              |           |           |
|                | Calocalamus gracilis      | Tanaka                          |              |           |           |
|                | Calocalamus minutus       | Andronov                        |              |           |           |
|                | Calocalanus plumulosus    | (Claus)                         |              |           |           |
|                | Calocalamus styliremis    | Giesbrecht                      |              |           |           |
|                | Calocalamus tenuis        | Farran                          |              |           |           |
|                | Delius nudus (Sewell)     |                                 |              |           |           |
|                | Paracalanus aculeatus     | Giesbrecht                      |              |           |           |
|                | Paracalanus gracilis      | Chen & Zhang                    |              |           |           |
|                | Paracalanus nanus         | Sars                            |              |           |           |
|                | Paracalanus parus (Claus) | s. l.                           |              |           |           |
|                | Parvocalanus crassiostri  | Dahl                            |              |           |           |
|                | Parvocalanus elegans      | Andronov                        |              |           |           |
| Pontellidae    | Labidocera japonica      | Mori                            |              |           |           |
|                | Labidocera rotunda        | Mori                            |              |           |           |
| Pseudodiaptomidae | Pseudodiaptomus inopinus | Burckhardt                      |              |           |           |
| Rhinalanidae   | Rhinalanus nasatus        | Giesbrecht                      |              |           |           |
| Scolecitrichidae | Scolecithricella dentata | (Giesbrecht)                    |              |           |           |
|                | Scolecithrix bradyi       | Giesbrecht                      |              |           |           |
| Stephidae      | Stephos sp.               |                                 |              |           |           |
Table 1. (Continued).

| Species | Mean abundance (ind. m$^{-2}$) | Areal occurrence | Frequency of occurrence** (%) |
|---------|-------------------------------|-----------------|-------------------------------|
|         | July | August | October | December | February | I | C | O |
| Temoridae |     |        |         |          |          |   |   |   |
| Temora discaulata Giesbrecht | **3** | * | * | * | * | 1.1 |
| Temora turbinata (Dana) | 1 | 170 | * | * | * | 9.5 |
| Cyclopoida |     |        |         |          |          |   |   |   |
| Clausidiidae |     |        |         |          |          |   |   |   |
| Hemicyclops japonicus Itoh & Nishida | **5** | * | * |   |   | 2.1 |
| Corycaeidae |     |        |         |          |          |   |   |   |
| Corycaeus (Agetus) flaccus Giesbrecht | **4** | 1 | * |   |   | 3.2 |
| Corycaeus (Agetus) typicus (Kroyer) | 1 | * |   |   |   | 1.1 |
| Corycaeus (Corycaeus) speciosus Dana | **3** | * |   |   |   | 1.1 |
| Corycaeus (Ditrichocorycaeus) affinis McMrrich | **50** | **70** | **3** | **160** | * | * | * | 21.1 |
| Corycaeus (Ditrichocorycaeus) andrewsi Farran | 1 | * |   |   |   | 1.1 |
| Corycaeus (Ditrichocorycaeus) dahl Tanaka | **4** | * |   |   |   | 1.1 |
| Corycaeus (Onychocorycaeus) catus F. Dahl | **3** | * |   |   |   | 1.1 |
| Cyclopina sp. | 1 | 1 | * |   |   | 2.1 |
| Eucyclops sp. | **1** | * |   |   |   | 1.1 |
| Mesocyclops sp. | **1** | * |   |   |   | 1.1 |
Table 1. (Continued).

| Family     | Species                        | Author | Length (mm) | Width (mm) | Height (mm) | Mass (mg) | Volume (μL) | Cones | Length (μm) | Width (μm) | Height (μm) | Mass (μg) | Notes |
|------------|--------------------------------|--------|-------------|------------|-------------|-----------|-------------|-------|-------------|------------|-------------|-----------|-------|
| Oithonidae | Oithona atlantica               | Farran | 1           | 8          | 1           | *         | *           | *     | 6.3         |            |             |           |       |
|            | Oithona attenuata               | Farran | 1           | 1          | 1           | *         | *           |       | 2.1         |            |             |           |       |
|            | Oithona brevicornis             | Giesbrecht | 260 70    |             | 5           | *         | *           |       | 3.2         |            |             |           |       |
|            | Oithona davisi               | Ferrari & Orsi | 907000 3040000 34200 110000 196000 | *       | *         | 100.0     |            |       |             |            |             |           |       |
|            | Oithona decipiens              | Farran | 30          |             |             | *         | *           |       | 2.1         |            |             |           |       |
|            | Oithona fallax                  | Farran | 10          | 10          |             | *         | *           |       | 4.2         |            |             |           |       |
|            | Oithona longispina              | Nishida, Tanaka & Omori | 30 20    | 3           | 1           | *         | *           |       | 9.5         |            |             |           |       |
|            | Oithona nana                    | Giesbrecht | 3 50      | 30          |             | *         |             |       | 4.2         |            |             |           |       |
|            | Oithona plumifera               | Baird   | 30          | 1           | 7           | *         | *           |       | 7.4         |            |             |           |       |
|            | Oithona pseudofrigida           | Rosendorn | 5        |             |             |           |             |       | 1.1         |            |             |           |       |
|            | Oithona setigera (Dana)         |         | 3           | 1           |             |           |             |       | 3.2         |            |             |           |       |
|            | Oithona similis                 | Claus   | 1700 14000 80 20 200 | *       | *         | 37.9     |            |       |             |            |             |           |       |
|            | Oithona simplex                 | Farran   | 100         | 20          |             |           |             |       | 3.2         |            |             |           |       |
|            | Oncaea clevei                   | Früchti  | 100         | 1           | 4           | *         | *           |       | 5.3         |            |             |           |       |
|            | Oncaea media                    | Giesbrecht | 100 8      |             | *         | *           |       | 4.2         |            |             |           |       |
|            | Oncaea mediterranea             | (Claus)  | 1           | 20          |             |           | *         | *     | 6.3         |            |             |           |       |
|            | Oncaea scottidicarloi           | Heron & Bradford-Grieve | 20 9         | 40       | 13          | 40     | *         | *     | 11.6        |            |             |           |       |
|            |                                |         |             |             |             |           |             |       |             |            |             |           |       |
|            | Oncaea venusta                  | Philippi small form | 20  | *       | 2.1         |            |             |       |             |            |             |           |       |
|            | Oncaea venusta                  | Philippi medium form | 4 3 | 1       | 5.3         |            |             |       |             |            |             |           |       |
|            | Oncaea venusta                  | Philippi medium form | 4 3 | 1       | 5.3         |            |             |       |             |            |             |           |       |
|            | Oncaea waldemari                | Bersano & Boxshall | 100 200 70 | *       | *         | 10.5    |            |       |             |            |             |           |       |
|            | Oncaea zernovi                  | Shmeleva | 400 5       | 5           | 5           | *         | *           |       | 5.3         |            |             |           |       |
|            | Spinoncaea ielvi (Shmeleva)     |         | 1           |             |             |           |             |       | 1.1         |            |             |           |       |
|            | Triconia conifera               | (Giesbrecht) | 1 8      | 1           | 1           | *         | *           |       | 8.4         |            |             |           |       |
|            | Triconia denticula              | Wi, Shin & Soh | 1 1         |             |             |           | *         |       | 2.1         |            |             |           |       |
|            | Triconia furcula                | (Farran)  | 1           |             |             |           |           |       | 1.1         |            |             |           |       |
|            | Triconia minutula               | Giesbrecht | 3  | *       | 2.1         |            |             |       |             |            |             |           |       |

(Continued)
### Table 1. (Continued).

| Species                        | Mean abundance (ind. m$^{-2}$) | Areal occurrence | Frequency of occurrence** (%) |
|-------------------------------|---------------------------------|------------------|------------------------------|
|                               | July  | August | October | December | February | I | C | O |
| *Triconia parasimilis* Böttger-Schnack | 1     | *      | *       | *        | *        | 1.1 |
| *Triconia umerus* (Böttger-Schnack & Boxshall) | 4     | 1      | 3       | *        | *        | 4.2 |
| **Harpacticoida**              |       |        |         |          |          |    |
| Danielssenidae                 |       |        |         |          |          |    |
| *Danielssenia typica* Boeck    | 100   | 40     | 400     | 14200    | *        | * | * | * | 23.2 |
| Ectinosomatidae                |       |        |         |          |          |    |
| *Microsetella norvegica* (Boeck) | 5     | 200    | 30      | 40       | *        | * | * | * | 11.6 |
| *Microsetella rosea* (Dana)    | 1     | 40     | 30      | 3        | *        | * | * | * | 10.5 |
| Euterpinidae                   |       |        |         |          |          |    |
| *Euterpina acutifrons* (Dana)  | 300   | 30     |         |          |          | * | * | * | 4.2 |
| Harpacticidae                  |       |        |         |          |          |    |
| *Harpacticus* sp.              | 3     | 1      | *       |          |          | 2.1 |
| Miraciidae                     |       |        |         |          |          |    |
| *Macrosetella gracilis* (Dana) | 1     | 5      | *       | *        |          | 4.2 |
| Tisbidae                       |       |        |         |          |          |    |
| *Tisbe* sp.                    | 1     | 5      | *       | *        |          | 2.1 |

*occurrence, I: inner area, C: central area, O: outer area. **(Number of samples containing the species) ×100/ (total number of samples).
Abundance and species diversity

The total abundance of copepods including immature copepodids ranged from $3 \times 10^4$ to $2750 \times 10^4$ ind. m$^{-2}$. The monthly mean was higher ($>240 \times 10^4$ ind. m$^{-2}$) in July and August than in the other months ($<70 \times 10^4$ ind. m$^{-2}$) ($p < 0.01$; Figure 3). Especially in the outer area, the total abundance became less than $10^5$ ind. m$^{-2}$, showing remarkable difference between the central and outer areas. *Oithona davisae* accounted for more than 90% of total copepod abundance in most stations in July and August (Figure 3), and more than 60% except for the outer area in December and the inner area in February. The proportion of *O. davisae* decreased with the increase of *Acartia omorii* in the inner and central areas in February, and that of *Paracalanus parvus* s.l. in the outer area in October, December and February.

Species number per sample ranged from 2 to 37 and was mostly less than 10 in the inner area (Figure 3). Relatively high numbers ($>20$) were found in the central area in

![Figure 3](image-url)
July and August and in the outer area in August and December. The species diversity index ($H'$) was low in July and August, and higher after October ($p < 0.05$). Especially in October and December, high values were observed in the outer area.

**Horizontal distribution of copepod communities**

The 95 samples were grouped into two clusters at the 0.5 dissimilarity level (Figure 4). One cluster consisted of samples collected in October, and the other from all other months; these clusters were further classified into four and seven clusters at 0.3 dissimilarity, respectively. Accordingly, we defined 10 clusters as community groups A–E4 (hereafter simply referred to as ‘groups A–E4’: Figure 5). Groups A and B consist mainly of December/February and July samples, respectively. Groups C1–D and groups E1–E4 consist of August and October samples, respectively. The directions of the arrows in the NMDS plot (Figure 5) indicate that surface salinity, DO at bottom layer and transparency are positively correlated with group A, while surface water temperature and salinity at bottom layer are positively correlated with groups C2 and D. The distribution of copepod communities in each month is summarized as follows.

**July:** Groups C1 and B were distributed in the main part of the inner area and from the central to outer areas, respectively (Figure 6). In these two communities, *Oithona davisae* accounted for more than 90% followed by *Acartia omorii*. Difference between these two communities was due to relative abundance of *Paracalanus parvus* s.l., whose IndVal was higher in group B (45.5%) than C1 (0.1%: Table 2).

**August:** Groups C3 and C2 were distributed in the northern part of the inner area and from the southern part of the inner area to the central area, respectively. Groups C1 and D were distributed in the north-eastern part of the central area and from the central area to the outer area, respectively (Figure 6). In these four communities, *O. davisae* accounted for more than 95%. Group C3 was characterized by *A. sinjiensis*.

Figure 4. Grouping results for adult copepod community in Tokyo Bay by a cluster dendrogram. Letters and numerals near symbols indicate sample name (month–station no.).
group C2 by *Pseudodiaptomus marinus*, group C1 by *A. omorii* and group D by *Oithona similis* with relatively high IndVal (Table 2). Among them, group C3 was distributed in the hypoxic area and showed the lowest $H'$ with the highest proportion (99.8%) of *O. davisae* to total copepod abundance. In contrast, group D was distributed mostly in high salinity areas and included many species that inhabited the outer area in spite of low $H'$.

October: Group E1 was distributed in the northern part of the inner area and groups E2 and E3 were distributed from the southern part of the inner area to the central area. Group E4 was distributed from the central to outer areas (Figure 6). In these four communities, *O. davisae* accounted for more than 75% associating with *Parvocalanus crassirostris* which is peculiar to this season. Group E2 was characterized by *Microsetella rosea*, group E3 by *Oncaea waldemari* and *M. norvegica* and group E4 by *O. waldemari* and *O. scottodi Carloi* (Table 2). Group E4 showed the highest value of $H'$ and their distribution area showed the highest surface salinity and transparency (Table 2).
December: Group A was distributed across the whole inner and central areas (Figure 6), with lower proportion of *O. davisae* than in the other communities and a higher abundance of *A. omorii*. The community was characterized by *Centropages abdominalis* and *Danielssenia typica*. The communities at two stations in the outer area showed a high proportion of *P. parvus* s.l. and were distinct from the communities in the inner and central areas (Figure 3).

February: Group A was distributed in the inner and central areas, but group B, which occurred in July and was characterized by *P. parvus* s.l., was found at two stations in the central and outer areas (Figure 6).

**Horizontal distribution of indicator species (adults)**

*Oithona davisae* was an indicator of the inner-area communities found in July, August and October, and occurred in all 95 samples (Table 2) at a high proportion (>80%) with respect to adult copepods in 82 samples excluding 13 samples from the outer area in December and the inner area in February. The monthly mean population density ranged from $3.4 \times 10^4$ to $304 \times 10^4$ ind. $m^{-2}$ (Table 1), and was higher in July and August than in the other months ($p < 0.01$). Areal differences are not remarkable.
Table 2. Average values of environmental factors, number of species, diversity indices, abundance and indicator values of adult copepods in each community group classified by the cluster analysis. In the abundance column, underlined values were significantly different from maximum value (bold) (Bonferroni’s post-hoc test $p < 0.05$). In the IndVal column, bold numerals indicate values of indicator species (top two species).

| Environmental factor       | Community group | A   | B   | C1  | C2  | C3  | D   | E1  | E2  | E3  | E4  |
|----------------------------|-----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Number of samples          |                 | 33  | 13  | 10  | 7   | 3   | 7   | 4   | 9   | 2   | 3   |
| Depth (m)                  |                 | 20.3| 25.7| 15.7| 18.6| 10.6| 28.1| 13.3| 18.7| **29.5**| 26.7|
| Temperature (°C) at 0.5-m layer |              | 10.5| 19.5| 21.9| 25.4| **26.0**| 25.8| 17.3| 17.6| 17.5| 17.7 |
| Temperature (°C) at bottom layer |               | 12.1| 15.8| 17.0| 19.0| **19.7**| 18.0| 18.1| 18.2| 18.0| 18.1 |
| Salinity (psu) at 0.5-m layer |                | 31.7| 29.3| 27.0| 26.2| 21.8| 27.5| 30.8| 31.4| 31.3| **32.5**|
| Salinity (psu) at bottom layer |               | 32.9| 33.9| 33.5| 33.4| 32.9| **34.1**| 32.4| 33.1| 33.7| 33.8 |
| DO (mg l$^{-1}$) at bottom layer |              | **7.9**| 5.3 | 2.7 | 2.3 | 0.3 | 4.4 | 4.0 | 4.9 | 4.7 | 5.8 |
| Transparency (m)            |                 | 4.7 | 2.4 | 1.9 | 1.5 | 1.3 | 1.6 | 5.3 | 5.1 | 5.8 | **6.2**|
| Total abundance ($\times 10^4$ ind. m$^{-2}$) |         | 20.2| 96.4| 67.6| 289.1| 147.8| **461.3**| 2.4 | 5.1 | 1.8 | 2.2 |
| Number of species           |                 | 6.0 | 10.6| 3.5 | 8.1 | 5.0 | **23.7**| 2.0 | 5.2 | 5.5 | 13.7 |
| Species diversity index ($H'$) |                | 0.62| 0.45| 0.11| 0.09| 0.02| 0.13| 0.30| 0.52| 0.79| **1.38**|
| Proportion of *Oithona davisae* wrt total copepods (%) |       | 87.6| 91.0| 98.4| 98.0| **99.8**| 97.8| 94.3| 90.0| 86.1| 77.1 |

(Continued)
| Community group                  | A  | B    | C1  | C2  | C3   | D  | E1 | E2 | E3 | E4 |
|----------------------------------|----|------|-----|-----|------|----|----|----|----|----|
| Abundance (ind. m$^{-2}$)        |    |      |     |     |      |    |    |    |    |    |
| *Acartia omori*                  | 17,100 | **20,000** | 6300 | 540 | 2000 | 1200 | 40 | 100 | 30 |
| *Acartia sinjiensis*             |     |      |     |     |      |    |    |    |    |    |
| *Calanus sinicus*                | 5  | 180  | 4   |     |      | 18 |    |    |    |    |
| *Centropages abdominalis*        | **3400** | 450  | 10  |    |      |    |    |    |    |    |
| *Clausocalanus parapergens*      | 6  | **30** |      |    |      |    |    |    |    |    |
| *Ctenocalanus vanus*             | 1  | 40   | 7   |    |      | 160|    |    |    |    |
| *Parvocalanus crassirostris*     | 200|      |     |    |      |    | 1300| **4700**| 1700| 600 |
| *Paracalanus parvus s. l.*       | 2000| **5700** | 40  | 200 | 20  | 4000| 200| 100 | 400 |
| *Labidocera rotunda*             | 6  | 10   | 8   |    |      | 32 |    |    |    |    |
| *Pseudodiaptomus marinus*        | 300| 2700 | 600 | 3700|      |    |    |    |    |    |
| *Oithona davisae*                | 171,000| 930,000| 671,000| 2,860,000| 1,470,000| **4,570,000**| 22,700| 45,300| 15,100| 18,700 |
| *Oithona similis*                | 10 | 2700 | 8   | 400 |      | 38,000| 3  | 300 | 200 |
| *Microsetella norvegica*         | 3  | 8    |     |    |      | 600 |    |    |    |    |
| *Microsetella rosea*             | 2  | 2    |     |    |      | 120 |    |    |    |    |
| *Danielssenia typica*            | 8350| 190  |     |    |      |    | 60 |    |    |    |
| *Corycaeus affinis*              | 77 | 107  | 4   |    |      | 197 |    |    |    |    |
| *Oncaea scottodicarloi*          | 1  | 40   |     |    |      | 30  |    |    |    |    |
| *Oncaea waldemari*               | 4  | 400  |     |    |      | 400 |    | 700 |    |    |

(Continued)
Table 2. (Continued).

| IndVal (%) | *Acartia omorii* | 36.1 | **42.2** | 13.5 | 0.7 | 4.3 | 2.0 | 0.1 | 0.1 | 0.1 |
|------------|------------------|------|----------|------|-----|-----|-----|-----|-----|-----|
|            | *Acartia sinjiensis* |      |          |      |     |     |     |     |     |     |
|            | *Calanus sinicus* | 0.2  | 40.6     | 9.1  | 0.1 |     |     |     |     |     |
|            | *Centropages abdominalis* | **88.2** | 10.7 | 0.1 |     |     |     |     |     |     |
|            | *Clausocalanus parapergens* | 1.4  | 9.3      | 0.1  |     |     |     | 9.3 |     |     |
|            | *Ctenocalanus vanus* | <0.1 | 8.0      | 0.1  |     |     |     |     |     |     |
|            | *Parvocalanus crassirostris* | 0.6  |          |     |     |     |     |     |     |     |
|            | *Paracalanus parvus* | 15.2 | **45.5** | 0.1  | 0.9 | <0.1| 24.5| 1.4 | 0.9 | 3.4 |
|            | *Labidocera rotunda* |      | 2.2      | 10.1 | 4.6 |     |     |     |     |     |
|            | *Pseudodiaptomus marinus* | 0.3  | 4.6      | 0.9  |**47.5**| 7.1 |     |     |     |     |
|            | *Oithona davisa* | 1.6  | 8.7      | 6.2  |15.2 |13.7 |33.0 |0.2 | 0.4 |0.1|
|            | *Oithona similis* | <0.1 | 5.5      | <0.1 |0.3 |     |     |**71.1**| 0.0 |0.8 |
|            | *Microsetella norvegica* | <0.1 | 0.1      |     |     |     |     |     |     |     |
|            | *Microsetella rosea* | <0.1 | 0.1      |     |     |     |     |     |     |     |
|            | *Danielssenia typica* | **52.5**| 0.2 |     |     |     |     |     |     |     |
|            | *Corycaeus affinis* | 1.2  | 16.3     |     |     |     |     |     |     |     |
|            | *Oncaea scottodi carloi* | <0.1 | 3.6      |     |     |     |     |     |     |     |
|            | *Oncaea waldemari* |      |          |     |     |     |     |     |     |     |

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in July and August, but low density was found in the outer area in December and February (Figure 7A–E).

**Centropages abdominalis** and *Danielssenia typica* were indicators of group A found in December and February. The former was distributed across the whole area with a maximum monthly mean of 3800 ind. m$^{-2}$ in February. It was absent from the shallow inner area and whole area in July and August, respectively (Figure 7I–J). The latter was abundant in the eastern inner area in February (Figure 7K).

Figure 7. Horizontal distribution of 12 indicator species of copepod communities in Tokyo Bay.
Acartia omorii was an indicator of July communities (groups B, C1), and occurred in all months. The monthly mean ranged from 38 to 28,900 ind. m\(^{-2}\) and was higher in July and February than in the other months (\(p < 0.01\)). High densities were observed in the inner and central areas in February, but decreased in the innermost area in July and it was absent from shallow areas in October (Figure 7F–H).

Pseudodiaptomus marinus and Acartia sinjiensis were indicators of August communities (groups C2 and C3). The former occurred in all months (monthly mean: 4–15,400 ind. m\(^{-2}\)) and was abundant in July and August (\(p < 0.01\)) with a centre of distribution in the western central area (Figure 7L). The latter occurred in August and October and was abundant in the inner area in August (Figure 7M).

Parvocalanus crassirostris was an indicator of October communities (groups E1 and E2) and was almost absent in other months. It was distributed across the whole area and abundant in the central area (Figure 7P).

The following seven species were distributed mainly in the central and outer areas, suggesting that they were transported from the outer area by outer bay water. Paracalanus parvus s.l. (Figures 7N, O) was an indicator of group B found in July and February and occurred in all other months. The monthly mean ranged from 200 to 4800 ind. m\(^{-2}\) and was higher in February (\(p < 0.01\)). Corycaeus affinis (Figure 7Q) and Oithona similis (Figure 7R) were indicators of group D found in August and occurred in almost all other months. Microsetella norvegica (Figure 7S), M. rosea, Oncaea scottodicarloi and Oncaea waldemari (Figure 7T) were indicators of October communities (groups E2–4) and occurred sporadically in the central and/or outer areas in the other months.

**Comparison with 1948**

In the inner and central areas, the difference in seawater density between surface and bottom layers in July 1986 was larger than in 1948 (\(p < 0.01\)) (Table 3), reflecting salinity differences between surface and bottom water in these years. This was associated with lower transparency (\(p < 0.01\)), higher DO at the surface (\(p < 0.01\)), and the presence of near-bottom hypoxic water (<2 mg l\(^{-1}\)) in 1986.

| Year                        | 1948 Average | SD  | 1986 Average | SD  |
|-----------------------------|--------------|-----|--------------|-----|
| Temperature (0 m)           | °C           |     |              |     |
| Temperature (bottom)        | °C           |     |              |     |
| Salinity (0 m)              | psu          |     |              |     |
| Salinity (bottom)           | psu          |     |              |     |
| \(\sigma_t\) (difference between bottom and 0 m) |           |     |              |     |
| DO (0 m)                    | mg l\(^{-1}\) |     |              |     |
| DO (bottom)                 | mg l\(^{-1}\) |     |              |     |
| Transparency                | m            |     |              |     |

**Table 3. Comparison of environmental factors in July in the inner and central areas of Tokyo Bay between 1948 and 1986.**
The population density of *Oithona davisae* in the central area in 1986 was higher than in 1948 ($p < 0.05$), in spite of there being no significant difference in the inner area ($p > 0.05$) (Figure 8). In contrast, *Acartia omorii* decreased in the inner area ($p < 0.05$), with no significant difference in the central area ($p > 0.05$). Population densities of *Paracalanus parvus* s.l., *Oithona similis* and *Microsetella norvegica* in 1986 were lower than in 1948 in both the inner and central areas ($p < 0.05$).

Figure 8. Comparison of July's copepod abundance including immature copepodids in Tokyo Bay between 1948 and 1986.
Discussion
Communities of meso-size copepods in Tokyo Bay were classified into three seasonal categories: the winter–spring community consisting of *Acartia omorii* and *Centropages abdominalis*, early summer community consisting of *Pseudodiaptomus marinus* and *A. omorii*, and summer–fall community consisting of *Paracalanus parvus* s.l. and *Temora turbinata* (Tachibana et al. 2013). Judging from the indicator species, group A in the present study might correspond to the winter–spring community, and groups C1 and C2 might correspond to the early summer community. In this study, the specific communities were found in fall (October) as in Tachibana et al. (2013), but the indicator species were small copepods such as *Parvocalanus crassirostris*, *Oncaea waldemari* and *Microsetella norvegica*.

In the inner and central areas of Tokyo Bay, 2–4 groups of copepod communities occurred with sequential change in a north to south direction in July, August and October, but only a single community was present in December and February. In the stratified season (July and August), a remarkable environmental gradient was formed by the river discharge and hypoxic bottom water in the inner area and by the outer bay water at the bottom layer of the central area. This condition may have been a cause for the occurrence of the diverse communities including indicator species from various habitats. Of the indicator species of August communities which were placed from inner to outer areas, *Acartia sinjiensis* and *Pseudodiaptomus marinus* were categorized as belonging to the oligohaline neritic group that is distributed in brackish water, *Oithona davisae* to the eutrophic neritic group that is distributed in the innermost part of inlet, and *Acartia omorii*, *Paracalanus parvus* s.l. and *Oithona similis* to the mesotrophic neritic group that is distributed in the outer half of the inlet (Ueda 1991). Expansion of the oligohaline neritic and eutrophic neritic species into the outer areas and the intrusion of mesotrophic neritic species into the inner area of the bay might be caused by the estuary circulation (Fujiwara and Yamada 2002; Fujiwara 2007). In addition, hypoxic water formed in the inner area may disrupt the intrusion of mesotrophic neritic species. In the mixing season (December and February), a uniform community may have been formed by relaxation of environmental gradients with the decline of river discharge and outer bay water, and the recovery of hypoxic water. In October, the decline of the population of *O. davisae* had begun with vertical mixing, but moderately high water temperature permitted the occurrence of *Parvocalanus crassirostris* which was limited to this season (Anakubo and Murano 1991; Itoh and Aoki 2010). The inflow of outer bay water, induced by the north-eastern wind, might have formed the three communities characterized by oceanic species, as pointed out by Nomura (1996).

According to the comparison of July’s copepod community in Tokyo Bay between 1948 and 1986, and with reference to previous studies, it is suggested that *Oithona davisae* increased and other species decreased with the advanced eutrophication in the bay in the 1970s–1980s (Anakubo and Murano 1991; Nomura and Murano 1992; Nomura et al. 1992; Uye 1994; Itoh and Aoki 2010). According to classification of Japanese inlets on the basis of their copepod communities (Yamazi 1956), Tokyo Bay changed from the A–D′–E type which has strong tidal current to the A–B type which is stagnant with an hypoxic area. Unoki (2011) pointed out that the decrease of water area by land reclamation and the increase in depth by dredging caused a decline of the tidal current in Tokyo Bay. Decrease in salinity and
increase in phytoplankton (= decrease in transparency) which were shown between 1948 and 1986, might have formed suitable environmental conditions for the population of *Oithona davisae*. In addition, the reinforced stratification caused hypoxic water in the bottom layer, which is assumed to have increased the mortality of species that have no egg sacs, such as *Acartia omorii* and *Paracalanus parvus* s.l. as pointed out by Nomura and Murano (1992) and Uye (1994). There were large tidal flats and shallow areas in the inner area where *A. omorii* was abundant in 1948, but these areas were lost by reclamation and excavation, and replaced by areas of different topography, such as deep waterways and large depressions, resulting in the frequent occurrence of the Aoshio phenomenon (upwelling of anoxic water) in recent years (Furota 1997; Unoki 2011).

In the mid-1980s when Tokyo Bay was still highly eutrophic (Nomura 1995; Ishii et al. 2008a), copepod species number reached 98 (68 in the inner and central areas: this study). However, permanent residents were restricted to seven species: *Acartia omorii*, *Centropages abdominalis* *, Labidocera rotunda* *, Paracalanus parvus* s.l., *Pseudodiaptomus marinus*, *Oithona davisae* and *O. similis* (the two species with asterisks were known to maintain their population by resting eggs in Tokyo Bay: Itoh and Aoki 2010). Large seasonal fluctuations in temperature and salinity, and the formation of hypoxic water in Tokyo Bay can be severe environmental stressors for marine organisms (Furota 1997). In addition, the strong feeding pressure by *Aurelia* sp. might select species that can survive in the bay (Uye 1994; Ishii and Tanaka 2001; Itoh et al. 2011). Under such environmental conditions, *O. davisae* dominated all the year round and its adult population density exceeded 10^6 ind. m^{-2} (>95% of total adult copepods) in July and August. Recently, nutrients and transparency have shown a tendency toward recovery (Kanda et al. 2008; Ishii et al. 2008a) and the exhaustion of nutrients is becoming a serious problem for *Porphyra* culture which is an important industry in the bay (Ishii et al. 2008b). In the 1990s, the phytoplankton flora (Yoshida and Ishimaru 2008; Ogura et al. 2011) and cladoceran fauna (Sato 2011) showed changes, suggesting that change might be continuing in various constituents of the ecosystem including the copepod community. Continued monitoring is necessary for better understanding of the functional role and the prediction of the status, both present and future, of the copepod communities and the Tokyo Bay ecosystem.

**Geolocation information**

Study area (box): 35°37′N, 139°41′E to 35°14′N, 140°00′E

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