Comparison of copepod communities during upwelling and non-upwelling in the summers from 1992 to 2010 in Tosa Bay, western Japan

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Abstract: Copepods were collected using a Norpac net (0.315 mm mesh aperture, 0.45 m mouth diameter) in the summers from 1992 to 2010 at Stn A (700 m depth) in Tosa Bay, western Japan. Among the summer samples collected in July and August, there were 19 net samples during periods of upwelling and 27 net samples during periods of non-upwelling, judged by criteria of water temperature. Total abundance of adult copepods in the upwelling samples was not significantly different from the abundance in the non-upwelling samples, while the number of species and species diversity in the upwelling samples was lower than in the non-upwelling samples. Adults of four species (*Calanus sinicus*, *Clausocalanus parapergens*, *Paracalanus parvus* s.l. and *Corycaeus affinis*) in the upwelling samples were significantly more abundant than those in the non-upwelling samples. The changes of the copepod community structure during periods of upwelling may be produced because of increases of species preferring low water temperatures and decreases of species preferring warm water temperatures.

Key words: copepod community, Tosa Bay, summer upwelling

Introduction

Tosa Bay is an open bay facing the Pacific Ocean, western Japan. The water temperature at the surface of Tosa Bay shows conspicuous seasonal changes and becomes highest in August and September (Sakamoto 1981, Kuroda et al. 2014). Meanwhile, the water temperatures at depths of 50 m and 100 m in summer frequently are lower and do not show a clear seasonal pattern (Hirota et al. 2002, Hirota & Ichikawa 2012).

Upwelling in summer often has been observed on the onshore side of the Kuroshio, south of Japan (e.g. Nakamura 1977, Unoki & Unno 1983, Takeuchi et al. 1997, Kaneda et al. 2002). Kuroda et al. (2010) found that subsurface temperatures of three areas on shelf-slope regions around Shikoku, i.e., Bungo Channel, Tosa Bay and Kii Channel,

changed simultaneously over a mesoscale (400–500 km) range in summer. Some studies have indicated that the decrease of subsurface water temperature in summer is related to fluctuations of the Kuroshio axis. When the Kuroshio flows near Kyushu, cold-water tends to upwell in the Bungo Channel (Kaneda et al. 1996, 2002). The water temperature at 50 m and 100 m depths in summer subsequently becomes lower in the Bungo Channel, Tosa Bay and Kii Channel during large meanders of the Kuroshio axis (Kuroda et al. 2010). When the Kuroshio axis is located 30 miles or more from Cape Shionomisaki, subsurface water temperature in summer is low in the Kii Channel and adjacent waters (Sakamoto 1991, Takeuchi et al. 1997, Takashi et al. 2006, Kuroda et al. 2010).

After an upwelling occurs in summer and autumn when the nutrient concentrations in the surface layer are low, chlorophyll *a* (Chl *a*) has been shown to increase in the Bungo Channel, Tosa Bay and Kii Channel (Koizumi & Kohno 1994, Hashimoto et al. 1995, Takeuchi 2001, Hi-

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rota et al. 2002, Hayami et al. 2006, Hirota & Ichikawa 2012), and primary production increases (Ichikawa & Hirota 2004). Upwelling events play a significant role not only in increasing the production of the lower trophic level in summer but also maintaining the production which is enhanced in winter and spring (Takeuchi 2001). There are a few studies about the effect of upwelling on zooplankton in summer in waters off the central and western coast of Japan. Toda (1989) found that several phytoplankton patches developed in upwelled waters and eggs, nauplii, copepodites and adults of copepods were abundant in patches around the Izu Islands, central Japan, in summer. Ozaki et al. (2004) examined the interannual variability of zooplankton abundance in the Kii Channel of western Japan during 1987 to 1999 and considered that the decrease of copepods after 1995 was due to the weakening of bottom intrusions into the channel.

In the present study, we compared the total abundance of adult copepods, number of species, species diversity and abundance of copepod species between during periods of upwelling and during periods of non-upwelling in Tosa Bay in summer of 1992 to 2010. Our study aimed at examining the effect of upwelling on the abundance of copepod species and on the copepod community structure.

Materials and Methods

The station (Stn A, 33°12.2'N, 133°45.8'E, 700 m depth)

is located in Tosa Bay (Fig. 1). Samples were obtained in the daytime from 1992 to 2010 during cruises of the *Kotaka-Mar* and *Shirafuji-Mar* which were conducted once or twice a month. Twenty samples in July and 26 samples in August were collected with a Norpac net (mesh aperture 0.315 mm, mouth diameter 0.45 m) which was hauled vertically from 150 m depth from 1992 to 1996 and from 200 m depth from 1997 to 2010. A flow-meter (Cat. No. 5571, Rigosha & Co. Ltd.) was installed in the mouth of the net. The average of the filtered volume was 36.4 m³ (range from 20.7 m³ to 70.4 m³). Samples were fixed in 5% buffered formalin sea water immediately after collection.

Subsamples from 1/67 to 1/6 of samples were drawn by using a Stempel pipette and more than 200 individual copepods were enumerated. Adult copepods were identified to the species and copepodites of *Calanus sinicus* Brodsky, 1965 were identified to the species and each stage. Copepodite CIII to copepodite VI of *Calanus pacificus* Brodsky, 1948 and *Calanus jashonovi* Hulsemann, 1994 did not occur in the present study. As Nonomura et al. (2011) found copepodites of *Cala. pacificus* were absent in the epipelagic zone of the Kuroshio region, it is probable that copepodite CI and copepodite CII of *Cala. pacificus* have not occurred in the present study. However, we can't deny the possibility that copepodite CI and copepodite CII of *Cala. jashonovi* have been included in the abundance estimates of *Cala. sinicus*. Identification of copepod species basically followed Chihara & Murano (1997) and additionally oth-

Fig. 1. The location of the sampling station (Stn A) in Tosa Bay on the Pacific side of western Japan.

Fig. 2. Vertical profiles of temperature (a), salinity (b) and chlorophyll *a* (c) at Stn A in Tosa Bay in July and August from 1992 to 2010. Upwelling: the average of observation values during upwelling, non-upwelling: the average of observation values during non-upwelling periods, all: the average of observation values during upwelling and non-upwelling periods.

er references (e.g. Chen & Zhang 1965, Park 1995, 2000, Böttger-Schnack 1999, 2000). Three forms (large, medium and small forms) of *Oncaea venusta* Philippi, 1843 which were distinguished from each other by differences in body length, shape of the second thoracic segment and morphology of the genital double-somite (see Böttger-Schnack & Huys 2004) occurred and were treated as separate taxa.

The significance of differences in the abundance of total adults, the number of species, species diversity (Shannon–Wiener diversity index H'), the adult abundance of species and stages of *Cala sinicus* copepodites were compared between the upwelling samples and the non-upwelling samples. To test the significance of differences between the upwelling samples in July or August and the samples collected within about one month (31 to 50 days) after each upwelling, an additional five samples from September were used. Total abundance of mesopelagic species, which was judged by the characteristics of their vertical distribution according to Chihara & Murano (1997) and Razouls et al. (2005–2016), between upwelling and non-upwelling samples were compared. After a normality test, the existence of significant differences between the upwelling samples and the non-upwelling samples about one month after upwelling were tested using a paired *t* test or the Wilcoxon signed-ranks test. Other comparisons in the present study were tested using a *t* test or the Mann-Whitney *U* test.

For comparisons of species composition among the samples (Q-mode analysis) and grouping of species (R-mode analysis), cluster analysis and non-metric multidimensional scaling (NMDS) with Bray-Curtis similarity indices were performed for the dominant species that exceeded 1% of total adult copepods in July and August from 1992 to 2010. The abundances of species were fourth-root transformed to normalize the variance. Ward's method of clustering was

carried out to construct the dendrogram. Calculation of the index, construction of the dendrogram and NMDS were performed with programs in the R language (R-3.02. <http://www.okada.jp.org/RWiki/>).

Vertical profiles of temperature and salinity were measured with a STD (AST-1000, Alec Electronics Co. Ltd., Japan) and a CTD (SBE 9 plus Sea-Bird Electronics Inc. USA, Neil Brown MK3B or ICTD Falmouth Scientific Inc., USA). Water transparency was measured with a Secchi disc. Chl *a* concentration was measured using the water sampled with 1.7 L Niskin bottles. Samples were collected at 10, 20, 30, 50, 75, 100, 150 and 200 m depths. Surface water was collected with a bucket. Sampled seawater was filtered with glass fiber filters (Whatman GF/F) for extracting Chl *a* with 90% acetone for 24 hours. Chl *a* concentration was then measured with a fluorometer (112, Turner until 1997; 10-Au-005, Turner Designs Inc. USA after 1998).

Results

Oceanographic conditions

The average water temperature in July and August was 27.0°C (SD±1.6) at 0 m depth and decreased with depth. Average temperatures were 25.9°C (SD±1.7) at 10 m depth, 20.6°C (SD±2.6) at 50 m depth, 16.8°C (SD±2.2) at 100 m depth and 11.4°C (SD±1.5) at 200 m depth (Fig. 2a). The fluctuation in temperature was low at each depth near the surface layer but largest at 44 m depth (SD±2.7°C, minimum temperature 16.4°C and maximum temperature 26.6°C). The monthly average temperature at 200 m depth at Stn A between 1992 and 2010 fluctuated from 13.5°C (January) to 11.3°C (July) and the annual average temperature was 12.4°C (Fig. 3, Hirota unpublished data). In the

present study, cases where the temperature at 50 m depth became less than 21°C, the temperature at 100 m depth became less than 17°C and the temperature at 200 m depth became less than 12°C are regarded as an upwelling regime by reference to the average temperatures. There were 19 samples in the periods of upwelling and 27 samples in the periods of non-upwelling. There was no significant difference among the monthly average temperatures at 200 m depth, excluding the data in the periods of upwelling in July and August (ANOVA and post hoc test).

The average salinity during the periods of upwelling became higher with depth and was highest (34.587) at 80 m depth. Meanwhile, salinity became lower with depth in the layer deeper than 80 m depth and was 34.385 at 200 m depth (Fig. 2b). The average salinity during the periods of non-upwelling was maximum (34.635) at 101 m depth. The average transparency during the period of upwelling that was 18.9 m (SD±4.0) and was significantly lower than the average during the period of non-upwelling, which was 25.3 m (SD±4.8) (*t* test, $p < 0.001$).

The average Chl *a* concentration during the periods of upwelling was highest (0.799 mg m⁻³) at 30 m depth while the average during the periods of non-upwelling was highest (0.567 mg m⁻³) at 50 m depth (Fig. 2c). The averages of Chl *a* concentration at the layers of 10 m depth, 20 m depth and 30 m depth during the periods of upwelling were all significantly higher than averages during the periods of non-upwelling (*U* test, $p < 0.01$).

Fig. 3. Seasonal changes of temperature at 200 m depth at Stn A in Tosa Bay from 1992 to 2010 (Hirota unpublished data). Black circles: observation values during upwelling in July and August. Open triangles: the monthly average temperature.

Abundance and species composition

The average abundance of total adult copepods in the 46 samples was 2.43×10^4 inds. m⁻² (SD±0.93×10⁴) (Table 1). Average abundance of adult copepods in periods of upwelling was 2.37×10^4 inds. m⁻² (SD±0.94×10⁴) and average abundance in periods of non-upwelling was 2.47×10^4 inds. m⁻² (SD±0.93×10⁴). There were no significant differences between the upwelling and non-upwelling periods. We have identified 148 species and three forms of adult copepods. One hundred and six species and the three forms were identified in the upwelling samples, while 138 species and three forms were identified in the non-upwelling samples. The average number of species during the upwelling was 35.5 species sample⁻¹ (SD±5.2), which was significantly less than the average during the non-upwelling periods, which was 43.7 species sample⁻¹ (SD±7.1) ($p < 0.001$). During the upwelling, *Paracalanus parvus* (Claus, 1863) s.l. was most abundant (22.3% of total abundance of adult copepods) and *Paracalanus aculeatus* Giesbrecht, 1888 was second most (8.6%). *Ctenocalanus vanus* Giesbrecht, 1888 (6.3%) and *Oithona plumifera* Baird, 1843 (5.0%) were also abundant (Table 2). On the other hand, during the non-upwelling periods, *Para. aculeatus* and *Oith. plumifera* were the most abundant and accounted for 9.6% and 8.0%, respectively. Next to these species, *Oncaea venusta* small form (6.3%), *Clausocalanus furcatus* (Brady, 1883) (6.1%) and *Clausocalanus minor* Sewell, 1929 (5.6%) were abundant. The average of the diversity index (*H'*) was 3.02 (SD±0.26) (Table 1). The average during the upwelling of 2.83 (SD±0.25) was also significantly less than the average during the non-upwelling periods, which was 3.16 (SD±0.17) ($p < 0.001$).

The abundance of species during the upwelling and non-upwelling periods

Adults of four species, *Cala. sinicus*, *Clausocalanus parapergens* Frost & Fleminger, 1968, *Para. parvus* s.l. and *Corycaeus affinis* McMurrich, 1916 in the upwelling samples had significantly higher densities compared to those in the non-upwelling samples (Table 2). The abundance of each copepodite stage of *Cala. sinicus* in the upwelling samples was significantly more abundant than in the non-upwelling samples. In contrast, the abundance of nine species and three forms, *Canthocalanus pauper* (Giesbrecht, 1888), *Lucicutia flavicornis* (Claus, 1863), *Tri-*

Table 1. Total abundances, numbers of species and Shannon–Wiener *H'* of copepods in upwelling and non-upwelling periods at Stn A in Tosa Bay in July and August from 1992 to 2010. n: number of samples. *p*: probability of significant difference using the Mann–Whitney *U* test. Values in bold type were significantly higher than underlined values.

	All (n=46)	Upwelling samples (n=19)	Non-upwelling samples (n=27)	<i>p</i>
Total abundance ($\times 10^4$ ind. m ⁻²)	2.43	2.37	2.47	0.516
Number of species	40.3	<u>35.5</u>	43.7	<0.001
Shannon–Wiener <i>H'</i>	3.021	<u>2.831</u>	3.155	<0.001

Table 2. Average abundances of the dominant copepod species (>1% of total adult abundance) and other species that showed a significant difference in abundances between upwelling period and non-upwelling periods at Stn A in Tosa Bay in July and August from 1992 to 2010. n: number of samples. *p*: probability of significant difference using the Mann–Whitney *U* test. Values in bold type were significantly higher than underlined values.

R-mode cluster	Species	All (n=46)		Upwelling samples (n=19)		Non-upwelling samples (n=27)		<i>p</i>
		$\times 10^4$ ind. m^{-2}	Percentage (%)	$\times 10^4$ ind. m^{-2}	Percentage (%)	$\times 10^4$ ind. m^{-2}	Percentage (%)	
C	<i>Acartia danae</i>	0.04	1.8	0.03	1.4	0.05	2.1	0.242
A	<i>Acartia negligens</i>	0.03	1.2	0.03	1.2	0.03	1.1	0.652
A	<i>Acrocalanus gracilis</i>	0.02	1.0	0.02	0.8	0.03	1.2	0.144
C	<i>Calanus sinicus</i>	0.04	1.7	0.07	3.0	<u>0.02</u>	0.9	<0.001
A	<i>Canthocalanus pauper</i>	0.03	1.3	<u>0.01</u>	0.4	0.05	1.8	<0.001
C	<i>Clausocalanus arcuicornis</i>	0.06	2.5	0.06	2.7	0.06	2.3	0.582
C	<i>Clausocalanus farrani</i>	0.06	2.3	0.04	1.8	0.06	2.6	0.089
B	<i>Clausocalanus furcatus</i>	0.12	4.9	<u>0.07</u>	3.1	0.15	6.1	0.023
B	<i>Clausocalanus minor</i>	0.11	4.4	<u>0.06</u>	2.7	0.14	5.6	<0.001
C	<i>Clausocalanus parapergens</i>	0.04	1.6	0.06	2.4	<u>0.02</u>	1.0	0.001
C	<i>Corycaeus affinis</i>	0.03	1.2	0.05	2.3	<u>0.01</u>	0.5	0.010
C	<i>Corycaeus pacificus</i>	0.05	2.2	0.05	2.1	0.06	2.2	0.992
B	<i>Ctenocalanus vanus</i>	0.13	5.4	0.15	6.3	0.12	4.7	0.459
A	<i>Farranula gibbula</i>	0.02	1.0	0.02	0.7	0.03	1.3	0.152
A	<i>Lucicutia flavicornis</i>	0.03	1.4	<u>0.02</u>	1.0	0.04	1.6	0.024
B	<i>Oithona longispina</i>	0.09	3.9	0.09	3.9	0.10	3.9	0.818
B	<i>Oithona plumifera</i>	0.16	6.8	<u>0.12</u>	5.0	0.20	8.0	0.003
B	<i>Oithona setigera</i>	0.09	3.6	0.07	3.0	0.10	4.0	0.089
B	<i>Oncaea mediterranea</i>	0.07	3.1	0.06	2.6	0.08	3.4	0.219
A	<i>Oncaea venusta</i> large form	0.06	2.5	<u>0.03</u>	1.3	0.08	3.4	<0.001
B	<i>Oncaea venusta</i> medium form	0.08	3.3	<u>0.07</u>	2.9	0.09	3.5	0.003
B	<i>Oncaea venusta</i> small form	0.13	5.4	<u>0.10</u>	4.0	0.16	6.3	0.001
B	<i>Paracalanus aculeatus</i>	0.22	9.2	0.20	8.6	0.24	9.6	0.095
C	<i>Paracalanus parvus</i> s.l.	0.25	10.5	0.53	22.3	<u>0.06</u>	2.5	<0.001
A	<i>Temora turbinata</i>	0.03	1.2	0.03	1.1	0.03	1.3	0.617
A	<i>Triconia conifera</i>	0.04	1.7	<u>0.02</u>	1.0	0.05	2.1	<0.001
	Others	0.96	39.5	1.11	46.8	0.85	34.6	
	<i>Acrocalanus longicornis</i>	0.02	0.7	<u>0.01</u>	0.4	0.02	1.0	0.033
	<i>Calocalanus pavo</i>	0.02	0.6	<u>0.01</u>	0.4	0.02	0.8	0.025
	<i>Candacia catula</i>	0.01	0.4	<u>0.01</u>	0.3	0.01	0.5	0.011
	<i>Calanus sinicus</i> CI	0.02		0.04		<u>0.00</u>		0.003
	<i>Calanus sinicus</i> CII	0.06		0.12		<u>0.02</u>		0.004
	<i>Calanus sinicus</i> CIII	0.06		0.09		<u>0.04</u>		0.006
	<i>Calanus sinicus</i> CIV	0.06		0.07		<u>0.05</u>		0.049
	<i>Calanus sinicus</i> CV	0.10		0.15		<u>0.06</u>		0.014

conia conifera (Giesbrecht, 1891), *Oith. plumifera*, *Clausocalanus furcatus*, *Clausocalanus minor*, *Acrocalanus longicornis* Giesbrecht, 1888, *Calocalanus pavo* (Dana, 1849), *Candacia catula* (Giesbrecht, 1889), *Oncaea venusta* large form, *Oncaea venusta* medium form and *Oncaea venusta* small form, in the upwelling samples were significantly less than those in the non-upwelling samples.

The number of species and the species diversity of adult copepods in samples collected within about one month af-

ter each upwelling sample series were significantly higher than in samples during the upwelling (Table 3). The adult abundance of five species, *Calanus sinicus*, *Clausocalanus parapergens*, *Corycaeus affinis*, *Oithona longispina* Nishida, 1977 and *Paracalanus parvus* s.l., in the samples one month after the upwelling were also significantly less compared to in the samples during the upwelling (Table 4). Each density from copepodite II to copepodite V of *Calanus sinicus* in the samples one month after the upwelling was significantly

Table 3. Numbers of species and Shannon–Wiener H' of copepods in sequentially collected sample-sets ($n=10$) during upwelling and ca. one month (31–50 days) after upwelling at Stn A in Tosa Bay from 1992 to 2010. Numbers indicate probability of significant difference using the t test. Values in bold type were significantly higher than underlined values.

	Upwelling samples	Non-upwelling samples one month after upwelling	p
Number of species	<u>33.3</u>	45.0	<0.001
Shannon–Wiener H'	<u>2.848</u>	3.133	0.022

Table 4. Abundance of the species that showed a significant difference in abundance between samples ($n=10$) collected during upwelling and ca. one month (31–50 days) after upwelling at Stn A in Tosa Bay from 1992 to 2010. Numbers indicate probability of significant difference using the Wilcoxon test or paired t test. Values in bold type were significantly higher than underlined values.

Species	Upwelling samples ($\times 10^4$ ind. m^{-2})	Non-upwelling samples one month after upwelling ($\times 10^4$ ind. m^{-2})	p
<i>Calanus sinicus</i>	0.05	<u>0.01</u>	<0.001
<i>Clausocalanus parapergens</i>	0.05	<u>0.01</u>	0.002
<i>Corycaeus affinis</i>	0.05	<u>0.00</u>	0.003
<i>Oithona longispina</i>	0.11	<u>0.06</u>	0.041
<i>Paracalanus parvus</i> s. l.	0.48	<u>0.03</u>	<0.001
<i>Calanus sinicus</i> CII	0.10	<u>0.00</u>	0.035
<i>Calanus sinicus</i> CIII	0.11	<u>0.00</u>	0.010
<i>Calanus sinicus</i> CIV	0.10	<u>0.01</u>	0.003
<i>Calanus sinicus</i> CV	0.23	<u>0.03</u>	0.002
<i>Canthocalanus pauper</i>	<u>0.01</u>	0.08	0.004
<i>Clausocalanus furcatus</i>	<u>0.08</u>	0.21	0.010
<i>Clausocalanus minor</i>	<u>0.09</u>	0.18	<0.001
<i>Farranula gibbula</i>	<u>0.01</u>	0.05	0.016
<i>Oncaea venusta</i> large form	<u>0.02</u>	0.13	<0.001
<i>Oncaea venusta</i> medium form	<u>0.04</u>	0.13	0.008
<i>Oncaea venusta</i> small form	<u>0.06</u>	0.18	0.013

Fig. 4. Cluster diagram (a) and NMDS ordination (b) of community structure of adult copepod species (>1% of total abundance) at Stn A in Tosa Bay in July and August from 1992 to 2010. The sample names with “u” in the cluster diagram indicate the samples during upwelling periods.

less compared to in the samples during upwelling. The adult abundance of four species and three forms, *Cantho. pauper*, *Clauso. furcatus*, *Clauso. minor*, *Farranula gibbula* (Giesbrecht, 1891), *Onc. venusta* large form, *Onc. venusta* medium form and *Onc. venusta* small form, in the samples one month after the upwelling were significantly increased compared to abundance in the samples during upwelling.

Fifty species were judged as mesopelagic species. Their mean abundance and mean species number were not significantly different between the upwelling and non-upwelling samples.

Fig. 5. Cluster diagram (a) and NMDS ordination (b) of species associations of adult copepod species (>1% of total abundance) at Stn A in Tosa Bay in July and August from 1992 to 2010. Abbreviations of species names: Ada, *Acartia danae*; Agr, *Acrocalanus gracilis*; Ane, *Acartia negligens*; Caf, *Corycaeus affinis*; Car, *Clausocalanus arcuicornis*; Cfa, *Clausocalanus farrani*; Cfu, *Clausocalanus furcatus*; Cmi, *Clausocalanus minor*; Cpa, *Clausocalanus parapergens*; Cpf, *Corycaeus pacificus*; Cpp, *Canthocalanus pauper*; Csi, *Calanus sinicus*; Cva, *Ctenocalanus vanus*; Fgi, *Farranula gibbula*; Lfl, *Lucicutia flavicornis*; Olo, *Oithona longispina*; Ome, *Oncaea mediterranea*; Opl, *Oithona plumifera*; Ose, *Oithona setigera*; Ovl, *Oncaea venusta* large form; Ovm, *Oncaea venusta* medium form; Ovs, *Oncaea venusta* small form; Pac, *Paracalanus aculeatus*; Ppa, *Paracalanus parvus*; Tco, *Triconia conifera*; Ttu, *Temora turbinata*.

Community structure

Twenty-three species and three forms were judged as the dominant species for cluster and NMDS analyses, and these accounted for 84.9% of the total adult copepods. A cluster analysis (Q-mode analysis) produced 2 clusters (I and II) at the 1.03 dissimilarity level (Fig. 4a, dotted line). Fifteen of the 19 samples in Cluster I were collected during upwelling. These two clusters became distinct in a NMDS plot, although its stress value was relatively high (Fig. 4b). The dominant species were divided into three clusters: A, B and C at the 0.60 dissimilarity level by R-mode analysis (Fig. 5a). Cluster A was formed by seven species and one form, the abundances of which peaked in July to November in Tosa Bay (Hirota unpublished data). Cluster B was formed by eight species and two forms including abundant species during the non-upwelling periods. Abundances of these species belonging to Cluster B peaked from April to October (Hirota unpublished data). Cluster C was formed by eight species including *Cory. affinis*, *Clauso. parapergens*, *Cala. sinicus* and *Para. parvus* s.l., which were significantly more abundant during the upwelling. Abundances of the eight species peaked from March to July (Hirota unpublished data). Though the points of Cluster A and C spread, three clusters were distinct in the NMDS plot (Fig. 5b).

Discussion

Coastal upwelling systems are located off the west coast of the United States and Peru-Chile, off the southeast coast of Brazil, off the west coast of Namibia-South Africa, off the east coast of Somalia, off the southwest coast of Indonesia and off northeastern Taiwan etc. (Nasu 1970, Peterson 1998, Liao et al. 2006). Generally, zooplankton biomass and abundance of copepods in upwelling regions are higher than in adjacent regions (Valentin 1984, Timonin et al. 1992, Postel et al. 1995, Morgan et al. 2003, Gutiérrez et al. 2005, Escribano et al. 2015) while the species richness and species diversity in the upwelling regions are lower than in the adjacent region (Ayón et al. 2008a, Verheye & Kreiner 2009, Kozak et al. 2014). In addition, abundance of copepods during periods of upwelling has been shown to be higher than during periods of non-upwelling (Valentin et al. 1987, Postel et al. 1995, Escribano et al. 2007, Verheye & Kreiner 2009, Kozak et al. 2014). In Tosa Bay, the species richness and species diversity of copepods during upwelling periods were lower than during non-upwelling periods, while the abundance of copepods during the period of upwelling was not clearly different from during the period of non-upwelling.

In regions where upwelling is intense or in periods when upwelling is at the early stage, several workers have reported that the abundances of zooplankton and copepods were low because their populations in the upper-layers were exported offshore by advective currents of upwelling

(Hansen et al. 2005, Ayón et al. 2008b, Fitzek 2011, Bode et al. 2014). Additional nutrients supplied to the surface waters by upwelling results in an increase in phytoplankton production, which has been continuously observed for several days after the beginning of nutrient supply (Fawcett & Ward 2011, Van Oostende et al. 2015). This is suggested to be an important factor for the subsequent increases in zooplankton abundance (Thiel et al. 2007). In Tosa Bay, our result showed that Chl *a* concentrations in the sub-surface layers during upwelling were higher than concentrations during non-upwelling periods. Because of the increase of phytoplankton availability as food, the survival rates of each stage in copepods would have increased (VanderLugt 2005, Almeda et al. 2010, Santhanam & Perumal 2012). The generation time of these copepods is generally from 15 to 25 days in water temperatures between 15°C and 20°C (Jacobs 1961, Vuorinen 1982, Landry 1983, Uye 1988, Huntley & Lopez 1992, Calbet & Alcaraz 1997, Lee et al. 2003). Therefore, the high Chl *a* concentrations during the upwelling periods in the present study might have potential for promoting increases of copepod abundance. However, the duration of the upwelling period in Tosa Bay is unclear because observations using thermometers and current meters in the sub-surface layer and mesopelagic layer are few (Sakamoto 1990, 1994). For this reason, the time of initiation of upwelling, the intensity of upwelling and the extent of upwelling in the present study remain unknown. Even though the upwelling and non-upwelling samples in Tosa Bay were judged by the criteria of water temperature, the lack of differences in abundance of copepods between these samples may be caused by different sampling timing in various stages of the upwelling phenomenon.

There are several species that increase in abundance during upwelling in coastal upwelling zones. In the California Current, the abundances of *Calanus marshallae* Frost, 1974, *Pseudocalanus mimus* Frost, 1989 and *Acartia longiremis* (Lilljeborg, 1853) at the on-shelf stations were higher than those at the off-shelf stations during the upwelling season (Morgan et al. 2003). In the upwelling zones during the upwelling periods, *Centropages brachiatulus* (Dana, 1849) and *Eucalanus inermis* Giesbrecht, 1892 were abundant off Peru (Gutiérrez et al. 2005), *Calanus chilensis* Brodsky, 1959, *Paracalanus* cf. *indicus*, *Calanoides patagoniensis* Brady, 1883 were abundant off Chile (Pino-Pinuer et al. 2014, Escribano et al. 2015), *Calanoides carinatus* Krøyer, 1848 and *Cte. vanus* were abundant off Brazil (Valentin et al. 1987), and *Calanoides carinatus* and *Rhincalanus nasutus* Giesbrecht, 1888 were abundant in the Benguela Current (Hansen et al. 2005). These species occur throughout the year in each coastal zone (Peterson & Miller 1977, Peterson 1998, Hansen et al. 2005, Pino-Pinuer et al. 2014). In Tosa Bay, three (*Cory. affinis*, *Cala. sinicus* and *Para. parvus* s.l.) of four species that increased during the upwelling occur throughout the year (Hirota unpublished data). These three species, which are abun-

dant in the coastal zones around Japan (Chihara & Murano 1997, Ohtsuka & Ueda 1999) have a preference for low water temperatures and thus were abundant in winter to early summer on the onshore side of the Kuroshio (Itoh & Mizushima 1999, Uye 2000, Itoh et al. 2005, Ueda & Yuasa 2015, Hirota unpublished data). Although, the other species that increased during the upwelling, *Clauso. parapergens*, is widely distributed in the oceanic region (Frost & Fleminger 1968), this species also has a preference for low water temperatures and occurs in the layer deeper than seasonal thermocline in the stratification period in Suruga Bay, central Honshu, Japan (Itoh et al. 2005). Therefore, these four copepods were considered to be adapted to the low water temperatures occurring during the upwelling periods. Our result indicated that the upwelling community was clearly distinguishable as Cluster I (Fig. 4a) in the cluster and NMDS analyses, which was characterized by the copepods belonging to Cluster C (Fig. 5a) including the “cold water” four species.

The following seven species, *Canth. pauper*, *Tri. conifera*, *Clauso. furcatus*, *Clauso. minor*, *Acro. longicornis*, *Calo. pavo* and *Canda. catula* were significantly more abundant during the non-upwelling periods and are known to be the most abundant in summer or autumn on the onshore side of the Kuroshio Current, south of Japan (Furuhashi 1961, Itoh & Mizushima 1999, Itoh et al. 2005). Itoh et al. (2005) found that *Cantho. pauper*, *Clauso. minor*, *Canda. catula* and *Calo. pavo* were abundant in waters of >20°C at 5 m depth in Suruga Bay. Similarly, *Onc. venusta*, which previously had not been divided into three forms, was most abundant in summer or autumn in the onshore area of the Kuroshio Current, south of Japan (Furuhashi 1961, Itoh & Mizushima 1999, Itoh et al. 2005). *Clauso. furcatus*, *Calo. pavo* and *Onc. venusta* have been reported to be more abundant not only in the onshore area but also the offshore area of the Kuroshio Current, south of Japan (Kidachi 1974, Kidachi et al. 1983). In addition, *Far. gibbula*, which was significantly abundant in the samples collected one month after the upwelling are the most abundant in summer or autumn on the onshore side of the Kuroshio (Furuhashi 1961, Itoh & Mizushima 1999, Itoh et al. 2005). Morgan et al. (2003) found that ‘warm water’ species were distributed in the offshore waters of Oregon during upwelling periods. The changes of the copepod community structure during the periods of upwelling in Tosa Bay may be due to an increase in species that prefer low water temperatures and a decrease of species that prefer warm water temperatures.

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