Spatial variations in zooplankton community structure along the Japanese coastline in the Japan Sea: influence of the coastal current

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10   **Abstract.** This study evaluates spatial variations in zooplankton community structure and potential controlling factors along the Japanese coast under the influence of the coastal branch of the Tsushima Warm Current (CBTWC). Variations in the density of morphologically-identified zooplankton in the surface layer in May were investigated for a 15-year period. The density of zooplankton (individuals per cubic meter) varied between sampling stations, but there was no consistent west–east trend. Instead, there were different zooplankton community structures in the west and east, with that in Toyama Bay
15   particularly distinct: *Corycaeus affinis* and *Calanus sinicus* were dominant in the west and *Oithona atlantica* was dominant in Toyama Bay. Distance-based redundancy analysis (db-RDA) was used to characterize the variation in zooplankton community structure, and four axes (RD1–4) provided significant explanation. RD2–4 only explained <4.8% of variation in the zooplankton community and did not show significant spatial difference; however, RD1, which explained 89.9% of variation, did vary spatially. Positive and negative species scores on RD1 represent warm- and cold-water species, respectively, and
20   their variation was mainly explained by water column mean temperature, and it is considered to vary spatially with the CBTWC. The CBTWC intrusion to cold Toyama Bay is weak and occasional due to the submarine canyon structure of the bay. Therefore, the varying bathymetric characteristics along the Japanese coast of the Japan Sea generate the spatial variation in zooplankton community structure, and dominance of warm-water species can be considered an indicator of the CBTWC.

1. Introduction

25   Ocean currents transport water with heat and solved materials, and thus they are related to climate properties and distributions of dissolved and particulate matter (Thorpe, 2010). The biological importance of ocean currents has been accepted for a century, since Hjort (1914), and is especially applicable in coastal areas which only cover 7% of the ocean but support 90% of global fish catches (Pauly et al., 2002). Plankton community structure varies in accordance with currents (Russell, 1935), and changes in ocean currents cause fisheries regimes to shift, such as from sardine to anchovy and back (Chavez et al., 2003).

30   The ocean current is important for zooplankton abundance and community structure: the Gulf Stream is affected to abundance of copepods, *Calanus finmarchicus* and *C. helgolandicus*, in the European coastal seas (Frid and Huliselan, 1996; Reid et al., 2003), and the copepod species richness varies with amount of the inflow the source water in the California current (Hooff and Peterson, 2006). Not only ocean currents, water temperature, nutrient supply, and other many factors affect to zooplankton abundance and community structure, thus, monitoring results of zooplankton abundance and community usually represent
35   hydro-meteorological change (Beaugrand, 2005).

In the Japan Sea (Sea of Japan), which is a marginal sea of the western North Pacific, the Tsushima Warm Current (TWC) flows from west (connected to the East China Sea at the Tsushima Strait) to east (connected to the western North Pacific and

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the Okhotsk Sea at the Tsugaru and Soya straits, respectively). The TWC has three branches (Kawabe, 1982): the coastal (first) branch (CBTWC) flows along the Japanese coast following the shelf edge; the second branch flows on the offshore side of the first branch; the third branch (also known as East Korean Warm Current) flows along the Korean Peninsula up to ~39°N. As well as the other ocean currents, the TWC transports water properties such as heat, freshwater, nutrients, and phytoplankton and affects climate and marine systems in the Japan Sea and the Japanese Archipelago (Hirose et al., 1996; Isobe et al., 2002; Hirose et al., 2009; Onitsuka et al., 2010; Kodama et al., 2015; Kodama et al., 2016), and is the spawn and nursery field of important fisheries resources (Goto, 1998, 2002; Kanaji et al., 2009; Ohshimo et al., 2017).

Zooplankton are transported by the TWC: the distributions of the giant jellyfish, *Nemopilema nomurai*, which originates from the Chinese coastal area of the East China Sea (Uye, 2008; Kitajima et al., 2015), and the giant salps, *Thetys vagina* (Iguchi and Kidokoro, 2006), depend on the TWC in the Japan Sea. However, studies of the relationship between the TWC and small zooplankton such as copepods are very limited, especially concerning their spatial distribution. In the TWC, zooplankton biomass varies interdecadally (Hirota and Hasegawa, 1999; Kang et al., 2002; Chiba et al., 2005), and community structure varies seasonally in accordance with water temperature, and interannually with the thickness of the TWC (Chiba and Saino, 2003); however, the advection of small zooplankton and its implication for communities have been not discussed, except for studies on tintinnid distributions in the Tsushima Strait (Kim et al., 2012).

Zooplankton biomass is homogeneous in the CBTWC area, along the Japanese coastline (Hirota and Hasegawa, 1999), but from two previous studies, (Iguchi and Tsujimoto, 1997; Iguchi et al., 1999), it can be identified heterogeneity in zooplankton community structure during spring bloom period: warm-water species (*Calanus sinicus*, *Corycaeus affinis,* and *Palacalanus parvus*) are dominant in Wakasa Bay, in the western part of the Japan Sea, while cold-water species (*Pseudocalanus newmani*, *Metridia pacifica*, and *Oithona atlantica*) are dominant in Toyama Bay, in the east. Although these observations were conducted in only one year and may not be representative of longer term trends in zooplankton community structure, the question of why this spatial difference of zooplankton community structure might occur in the western and eastern parts of the Japan Sea along the Japanese coast is important. Hence, in this study, we aim to provide a better understanding of the spatial variations in zooplankton community structure in spring along the Japanese coast in the Japan Sea and their causal mechanisms. In particular, the influence of the CBTWC is evaluated using a 15-year data set and multivariate analysis, which is useful for explaining the heterogeneity of zooplankton community structure (Field et al., 1982).

2. Materials and methods

2.1. On-board observations

On-board observations were conducted in May from 1999–2013, by T/V *Mizunagi* of Kyoto Prefecture (from 1999 to 2011) and R/V *Mizuho-maru* of the Japan Sea National Fisheries Research Institute (after 2012), at 26 stations (Stn. 1–26) set along the Japanese coast from Toyama Bay to Wakasa Bay (Fig. 1). Observations were conducted at each cruise for one week (Fig. 2a), in the middle of May until 2010, and at the end of May after 2011. The stations are located near the Japanese coast (<40 km from Honshu) and close to the continental shelf or the shelf edge, with water depths of 40–1230 m. The presence of a submarine canyon structure in Toyama Bay accounts for the relatively deep bottom depths of Stns. 3, 4, 5, and 8 (990, 700,

330, and 1230 m, respectively, Fig. 1). Additionally, Stns. 3–5 are in river mouths, and Stn. 7 is located in the mouth of Nanao Bay, which has a mean bottom depth of <20 m.

At each station, vertical profiles of temperature and salinity were recorded using an STD (Salinity-Temperature-Depth) sensor (Alec Electronics, AST1000) during the *Mizunagi* cruises (until 2011) or a CTD (Conductivity-Temperature-Depth) sensor (Seabird, SBE9plus) during the *Mizuho-maru* cruises (after 2012) from the surface to 150 m depth or 5 m above the bottom (but only 5 m pitch during 1999–2001). Temperature and salinity were omitted at two stations, Stn. 4 in 1999 and Stn. 14 in 2001, due to mechanical malfunction. As the temperature- and density-based depth of the mixed layer (Z_m) is similar in the Japa Sea (Lim et al., 2012), Z_m was defined as that at which the temperature is 0.5ºC below the temperature at 5 m depth, as modified from Levitus (1982).

Zooplankton were collected with vertical hauls of a long Norpac net (Nytal 52GG, 335 µm mesh, 0.45 m mouth diameter, Rigo) from 150 m depth or 5 m above the bottom to the surface. A Rigo flowmeter, calibrated before and after every cruise, was installed at the mouth of the net for estimation of filtered water volume. Since macrozooplankton generally show diel vertical migration, our observations were mainly conducted during daytime (from 6 AM to 7 PM); with observations at six stations conducted after 7 PM (Fig. 2b). Zooplankton samples were fixed soon after sampling with neutral formalin and stored at room temperature until morphological identification. Individuals were identified to species level based on Chihara and Murano (1997), and then the density of each zooplankton species was calculated (individuals per cubic meter, inds. m^{-3}). In 1999, samples were lost at Stns. 10 and 13 due to decay.

2.2. Other hydrographic data

Daily sea surface absolute height (SSH) and absolute current velocity data were derived from merged satellite data provided by AVISO (http://aviso.altimetry.fr) between 1999–2013 at a spatial resolution of 0.25º × 0.25º.

No primary productivity parameters were measured during the *Mizunagi* cruises, and thus, the monthly composite sea surface chlorophyll *a* (SSChl *a*) concentration was derived from GlobColour (http://hermes.acri.fr), which uses merged sensor GSM (Garver-Siegel-Maritoren) products (Maritorena et al., 2010). The spatial resolution was 4 × 4 km, and the SSChl *a* concentration of a station was taken from the nearest neighbor data point. The validation of daily SSChl *a* data in Toyama Bay has already been reported by Terauchi et al. (2014). The monthly composite data was chosen in our study to avoid having many data blanks.

Sea surface net heat flux (Qnet) was calculated by using data sets derived from the Japanese 55-year Reanalysis (JRA-55, http://jra.kishou.go.jp), with a spatial resolution of approximately 0.5º × 0.5º, and the temporal resolution was set as monthly in this study. Qnet was calculated using the following equation shown in the atlas of JRA-55 (http://ds.data.jma.go.jp/gmd/jra/atlas/en/index.html);

$$Qnet = Qdswr + Qdlwr - (Quswr + Qulwr + Qlh + Qsh) \qquad \qquad \dots(1)$$

In (1), Qdswr, Qdlwr, Quswr, Qulwr, Qlh, and Qsh represent downward short-wave radiation, downward long-wave radiation, upward short-wave radiation, upward long-wave radiation, latent heat flux, and sensible heat flux, respectively.

2.3. Statistical analysis

Hypothesis-driven canonical analysis was used to evaluate the zooplankton community and environmental influences on zooplankton community structure. The calculation was performed using R software (R Core Team, 2017). Canonical analysis is a combination of an ordination technique and regression analysis. Four approaches are applicable for reduced space ordination applied to zooplankton community structures: principal component analysis (PCA), correspondence analysis (CA), nonmetric multidimensional scaling (NMDS), and principal coordinate analysis (PCoA) (Ramette, 2007). PCA is most frequently used in exploratory analysis as well as for clustering (Ramette, 2007), however, there are some prerequisites: the data must be quantitative, have a small number of blanks (null data), and show multivariate normality (Legendre and Legendre, 2012). Our plankton community data was quantitative, and to avoid too many blanks (null data), populations were excluded from the analysis if they met any of the following rules: 1) never above 5% of total numerical abundance in all samples; 2) absent at all 26 stations in one-third of the observation periods (five years); and 3) not able to be identified to species level. However, *Mardia*'s test in MVN package (Korkmaz et al., 2014) demonstrated our community data were not multivariate normal ($p < 0.001$), therefore, PCoA was applied. The NMDS approach was also appropriate, but for comparison of the environmental parameters using canonical analysis, PCoA was considered to be superior.

For hypothesis-driven canonical analysis, we used distance-base redundancy analysis (db-RDA), with PCoA as the ordination technique (Ramette, 2007). Before the db-RDA, multicollinearity in the environmental factors was checked using the variance inflation factor (VIF). Usually, VIF values of 10 are taken as the threshold of multicollinearity (Borcard et al., 2011), but in this study, the threshold was applied more strictly: only parameters with a VIF <3 were selected. The environmental parameters are listed in Table 1: temperature at 5 m depth (SST), water column mean temperature (from 0 to 150 m or bottom-5 m depth; mean T), minimum temperature (corresponding to temperature at 150 m or bottom-5 m depth; mini T), salinity at a 5 m (SSS), water column mean salinity (mean S), maximum salinity (max S), Z_m, and SSChl a as the water quality; bottom depth as the geographical information; and haul depth, and observation time of day as the station information. Year is possible explanatory parameter, but as this study focused on spatial variations, the effect of year was removed using partial db-RDA as a categorical variable. Initially, the VIF values of mean T, SST, mini T, mean S, max S, and haul depth were >3 (Table 1); this means they exhibited similar spatio-temporal variations. Since temperature is important for the zooplankton physiology, one of three temperature parameters should be kept in analysis at least. When we removed the parameters with highest VIF values until VIF values of the remained parameters were <3, all of three temperature parameters were removed. Therefore, we kept the mean T as the representative parameters of the others (SST, mini T, mean S, max S, and haul depth) for the db-RDA, and discarded the other high VIF parameters. As a result, VIF values of the remaining parameters were <2.0 (Table 1). We then checked that the parameters significantly explained the zooplankton community variations based on AIC (Akaike information criterion) (Blanchet et al., 2008); as a result, time of sampling was excluded from the analysis. Therefore, the remaining environmental parameters comprised mean T, SSS, Z_m, and bottom depth.

After the remaining environmental factors were standardized to Z-scores, scaling to a mean of 0 and standard deviation of 1, db-RDA (including preprocessing) was conducted using the VEGAN package (Oksanen et al., 2007), and detailed codes were based on Borcard et al. (2011). The distance between species was calculated by the Bray method. The db-RDA outputs scores for environmental parameters, stations, and species. The contribution of environmental factors to the axes was evaluated in terms of the coefficient values of the explanatory equations. Aside from this main analysis, we supplementarily do another

partial db-RDA with environmental parameters comprised SST, max S, Z_m and bottom depth; the only coefficient values of the supplemental analysis were shown in the discussion session of this study.

3. Results

3.1. Environmental conditions

5 Mean T varied from 10.96–17.28 ºC and showed a decreasing tendency from west–east along the coastline (Fig. 2c). The 15-years mean T was 16°C at Stn. 26 and lowered to <12°C at Stns. 1–2, and the west–east decrease in mean T was reproduced in every year. The spatial trends in mini T, SST, mean S, and max S were similar to mean T (data not shown), as shown by the high VIF values (Table 1). SSS ranged from 29.0–34.58; lower values (<33) were often observed at Stns. 1–9, which are located in Toyama Bay where large rivers flow (Fig. 2d). Z_m ranged from 5–118 m (Fig. 2e) and did not show significant

10 spatial variation (ANOVA, $p = 0.78$). The greatest Z_m was observed in 2007, which is shown as outliers in Fig. 2e. Monthly high SSChl a concentration (>2 mg m^{-3}) was only observed at stations in Wakasa and Toyama bays (Fig. 2f), and mainly remained 0.2–0.5 mg m^{-3}.

SSH was lower in Toyama Bay than any of the other areas, with an area of high SSH extending from the Noto Peninsula to the north–east, and current velocity was <15 cm s^{-1} (Fig. 3). The CBTWC was explicitly observed from of Wakasa Bay to the

15 Noto Peninsula, however, it was ambiguous in Toyama Bay. The monthly mean Qnet changed from negative to positive in April (Fig. 4a), and the mean Qnet in March–May showed no spatial differences (Fig. 4b).

3.2. Zooplankton abundance and community structures

Overall, 78 species were identified from 388 samples. Some specimens were limitedly identified to genus level, since key parts for identification were destroyed. The top 10 dominant species from an average of all stations contained seven copepods

20 (*Corycaeus affinis*, *Oithona atlantica*, *Calanus sinicus*, *Ctenocalanus vanus*, *Paracalanus parvus* s.l., *Oithona plumifera,* and *Pseudocalanus newmani*), plus one each of Appendicularia (*Oikopleura longicauda*), Euphausiacea (*Euphasia pacifica*), and Cladocera (*Evadne nordmanni*). Spatially, the dominant species differed in the west and east: in the west, *C. affinis* and *C. sinicus* were the first and second most dominant species on average, while *O. atlantica* was most dominant in the east, apart from Stn. 7 (Fig. 5a). *C. affinis* and *E. nordmanni* showed the largest temporal variation (Fig. 5b): *C. affinis* was abundant in

25 2006 and 2010, and *E. nordmanni* was dominant in 2004.

Total abundance largely varied from 48–2933 inds. m^{-3} (mean ± SD: 649 ± 418 inds. m^{-3}); there was no clear west–east tendency in abundance (Fig. 5c). The highest mean abundances were recorded at Stns. 3 and 7 in Toyama Bay, with 1009 ± 613 and 975 ± 800 inds. m^{-3}, respectively, and Stn. 24 in Wakasa Bay recorded the lowest with 361 ± 125 inds. m^{-3}. There was no trend in the temporal variation of total abundance (Fig. 5d). The species richness (S), the number of appeared species

30 at a station, ranged 7 to 32: the lower and upper quartile values were 15 and 19, respectively (Figure 5e). The interannual variation of S had a peak in 2001, and high after 2009 to 2013 (Figure 5f).

3.3. Multivariate analysis

After preprocessing, 25 zooplankton species remained for multivariate analysis. In addition to the top 10 species, there were two Chaetognatha (*Sagitta minima* and *S. nagae*), two Cladocera (*Podon leuckarti* and *Penilia avirostris*), nine copepods (*Metridia pacifica*, *Acartia omorii*, *Candacia bipinnata*, *Centropages bradyi*, *Mesocalanus tenuicornis*, *Neocalanus plumchrus*, *Clausocalanus pergens*, *Oncaea mediterranea,* and *Oncaea venusta)*, one Hyperiidea (*Themisto japonica*) and one Appendicularia (*Fritillaria pellucida*). The 25 species accounted for 94% of total abundance on average, although only ~70% at some stations. At the latter stations, *Oithona longispina* and/or *Oithona* spp. were highly abundant after 2010.

The db-RDA results for total, conditioned, and constrained inertial were 112.63, 18.64, and 17.08, respectively. Three axes of zooplankton community structure variation were significantly explained in the db-RDA (ANOVA, $p < 0.05$): the eigenvalues of the first, second and third axes (RD1–3, respectively) explained 89.9, 4.9, and 2.5% of zooplankton community structure variability, respectively.

The relationship between species and environmental parameters is shown in Fig. 6, after scaling the site score using biplot diagrams (Fig. 6); the site score was removed from Fig. 6 since their plot was invisible due to their numbers ($n = 388$). First, on the combination of RD1 and RD2, the absolute values of mean T were large in RD1 but small in RD2 (Fig. 6a). The absolute values of SSS in RD1 and RD2 were same level; that in RD2 was largest among the five parameters. Bottom depth was the parameter which RD1was largely negative. Of the zooplankton species, *C. affinis* and *O. atlantica* plotted in the second and third quadrant: the RD1 values were opposite to each other, but both of those RD2 values were plotted negative. *C. vanus* was plotted in the first quadrant, *C. sinicus* and *O. longicauda* were plotted in the second quadrant, and the other species were located near the origin. Second, in the combination of RD1 and RD3, *E. nordmanni* was plotted far away from the axis of RD3 = 0 (Fig. 6b). Bottom depth and SSChl *a* were negatively large, and Z_m was positive on RD3.

Mean T had the highest coefficient on RD1, 0.0525 (Table 2), and those of the other parameters were at least one-sixth that of mean T; the second highest were 0.0079 for SSS. On RD2, SSS had the largest absolute coefficient value (0.0517), and the absolute values of the other three parameters (mean T, Z_m and bottom depth) were same level (0.022–0.026). On RD3, bottom depth was largest (-0.046), and Z_m and mean T were next (-0.034).

In terms of spatial features, RD1 show west-east trend: it was low in relative from Stn. 1 to 8 except 7, corresponding to Toyama Bay, and relatively high from Stn. 16 to 26, corresponding to the western part of Noto Peninsula to Wasaka Bay (Fig. 7a). RD1 values in Toyama Bay (Stns. 1–8, except 7) were significantly different from those in the northern part of the Noto Peninsula to Wakasa Bay (Stns. 9–26) (*Tukey*'s test, $p < 0.001$). The RD1 of Stn. 7 was significantly different from the other Toyama Bay stations, and similar to Stns. 9–15, corresponding to northern part of Noto Peninsula. The RD2–3 did not show west–east trends, and showed high or low values in Stns. 2 and 8 comparing to the other stations (Fig. 7b, c).

4. Discussion

In our study, zooplankton abundance differed between the stations (Fig. 5), however, there was no clear west–east gradient. This finding is similar to that of a previous study by Hirota and Hasegawa (1999), which found that zooplankton abundance (wet weight) is homogenous along the Japanese coast at a spatial resolution of 1° × 1°.

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4.1. Interpretation of multivariate analysis

Since the equations with coefficient values calculated from db-RDA are only "hypothesis", the db-RDA results need to be interpreted in terms of the species score. Before the analysis, some environmental parameters were dropped based on the VIF and AIC values. The sampling time was removed from the explanatory variables based on the AIC values, but some previous studies show the dial migration of zooplankton in Toyama Bay: the wet-weight of zooplankton in the 0–150 m is high in the nighttime (Hirota and Hasegawa, 1999), and the evident dial vertical migrations in spring are reported on *E. pacifica* (Iguchi, 1995) and *M. pacifica* (Takahashi and Hirakawa, 2001). We considered that the sampling time is rejected from the explinaed values because the sampling was mostly done in the day-time (Fig. 2b), and the shallow bottom depth in the western part of our sampling site (Fig. 1). On the other hand, our results were shown the day-time zooplankton community structure: the variation of night-time may be different from our results.

From the db-RDA with mean T, SSS, Z_m, SSChl a and bottom depth, variations in zooplankton community structure were mainly distributed along three axes, and most of the variance was explained by RD1. The coefficients (Table 2) show that the variation in RD1 is largely controlled by mean T. Zooplankton species that recorded positive (*C. affinis*, *C. sinicus*, *C. vanus*, and *O. longicauda*) and negative (*O. atlantica*, *E. pacifica*, and *P. newmani*) scores for RD1 (Fig. 8) are classified in the Japan Sea as warm- and cold-water species, respectively (Iguchi and Tsujimoto, 1997; Iguchi et al., 1999; Chiba and Saino, 2003). Therefore, this axis is interpreted as explaining spatial differences owing to water temperature, and the equations on RD1 are considered to describe the zooplankton variation well.

Although RD2 and 3 was shown the minor contribution to the spatial variation of zooplankton community structure, the interpretation was tried. RD2, which explained 4.9% of variation, is highly explained by SSS (Table 2), which is negatively related to *C. affinis* and *O. atlantica* (Fig. 8b). However, we cannot reasonably explain this axis. The low SSS indicated the supply of river discharge, and river discharged water contains large amount of phytoplankton (Terauchi et al., 2014), while coefficient of SSChl a was low in this axis. Since *O. atlantica* is a suspension feeder (herbivorous), it was possible to be explained reasonably that low SSS increase *O. atlantica* abundance. However, *C. affinis* is carnivorous, and thus the eutrophication did not directly have an influence on the population.

RD3, which explains 2.5% of total variation, is positively affected by Z_m and negatively affected by bottom depth and mean T (Table 2), and *E. nordmanni* was recorded positive. These mean that deep mixing with low temperature, and shallow bottom depth increase the abundance of *E. nordmanni*. Abundance of *E. nordmanni* is increased in the cold season when SST is < 20˚C in Toyama Bay, but not observed before February (Onbé and Ikeda, 1995). *E. nordmanni* spend during the bad condition period as the resting egg which sinks to sea bottom, and the resting eggs sink to the deep bottom will not hatch (Onbé, 1985); the shallow bottom depth was important to recover its abundance. Therefore, we considered that the equation of this axis shows the spatial variation of *E. nordmanni* abundance following its life cycle and physiology.

4.2. Influence of the CBTWC

RD1 was the only axis that showed differences between the stations and expressed the main feature (89.9%) of spatial variation in the zooplankton community structure in our investigation area. The axis showed greater spatial variation (Fig. 6). RD1 was interpreted as representing the dominance of warm- and cold-water species in Wakasa and Toyama bays, respectively, which

is similar to the findings of previous studies at the same sites (Iguchi and Tsujimoto, 1997; Iguchi et al., 1999). Therefore, this feature is considered highly reproducible with temperature variation in our investigated area in May.

However, the environmental difference between Toyama Bay and the other areas were not limited to temperature: the bottom depth with the submarine canyon was deep (Fig. 1), and SSS was low (Fig. 2d) because of the river input in Toyama Bay. These are affected to the zooplankton community as well as temperature. For example, the subsurface canyon is the habitat of zooplankton, and the zooplankton migrate to shallow layer (Herman et al., 1991), and cold-water species are dominant in the deep layer of the Toyama Bay (Takahashi and Hirakawa, 2001). The river input should change amount of phytoplankton, and then affects to zooplankton amount in the Mediterranean (Espinasse et al., 2014). In our study area, river input to the Toyama Bay raise the sea surface chlorophyll *a* concentration (Terauchi et al., 2014), and thus these should be considered as the factors which were affected to the difference on the zooplankton community structure in Toyama Bay and other areas.

The results of RD1 were contained the bottom depth in the regression analysis, but the coefficient of bottom depth was significantly lower than the mean T (Table 2). This indicated that the bottom depth was not directly contributed to the zooplankton community structure, while the deep layer is the habitat of zooplankton which migrate to shallower depth in the other studies (*e.g.* Herman et al., 1991). We considered the sampling time is the one of the reasons why the bottom depth has only a minor contribution in RD1: our sampling time was mainly day-time, and thus zooplankton such as *E. pacifica*, *M. pacifica*, and *T. japonica*, which are present in the deep layer in day-time and migrate to surface layer in night time (Ikeda et al., 1992; Iguchi, 1995; Takahashi and Hirakawa, 2001), were limited to be collected.

Pollution (eutrophication) and river discharge are sometimes considered to determine community structure in areas such as the Mediterranean (Siokou-Frangou et al., 1998), the Brazilian coast (Valentin and Monteiroribas, 1993), the coastal area of Taiwan (Chou et al., 2012), and coast of North America (Pepin et al., 2015); however, the low coefficient values of SSS and SSChl *a* in our db-RDA results show that eutrophication is not the principal determinant of zooplankton community structure in the Japan Sea. The cause of this is not clear in this study, but we consider there are two possible explanations: 1) the observation period was at the end of the spring bloom, and local upwelling along the shelf edge in our study area occurs during summer (Nakada and Hirose, 2009); thus the area was not oligotrophic, and the food condition was not important; 2) less-saline water was only present at the surface (< 10 m depth), and most of the water column was not affected by the less-saline eutrophic water. However, difference on the feeding habits of the dominant zooplankton (*i.e.* carnivore *C. affinis* and herbivore *O. atlantica*) may depend on the difference of primary productivity among areas. In addition, *Oithona* prefer the stratified condition for feeding (Saiz et al., 2003); less saline surface water possibly contribute the stratification, and thus *O. atlantica* may increase in Toyama Bay.

As the results, spatial variations of zooplankton shown in RD1 is largely explained by mean T. Factors controlling temperature are likely to be responsible for spatial variations in zooplankton community structure. Three factors potentially control the spatial variation of water temperature: 1) Qnet, net heat flux; 2) mixing between cold deep-sea water; and 3) heat supply by horizontal advection. Qnet controls stratification of water column and the timing of spring phytoplankton bloom (Taylor and Ferrari, 2011), but increase of zooplankton abundance is not associated with change of Qnet in the English Channel (Smyth et al., 2014). The timing of the change from negative to positive Qnet (Fig. 5a) coincides with that of sea surface temperature increase in Toyama Bay, while it lags that in the other areas (Fig. 3). Additionally, no spatial differences in the Qnet were observed in the study area (Fig. 5b), which is consistent with previous studies (Hirose et al., 1996; Na et al., 1999). This suggests that Qnet is not the controlling factor on spatial variations in temperature except in Toyama Bay, and indicates that

other heat supply processes may be more important. The second potential factor, mixing between cold deep-sea water, initially seems to have greater potential as the bottom depth of stations in Toyama Bay was deeper than elsewhere. Bottom depth was a remaining significant explanatory factor, but its coefficient value was low on RD1 (Table 2). Therefore, mixing between cold deep-sea water is not considered to be the main factor controlling the spatial variation of temperature, although its influence cannot be completely discounted. As the results, we considered that zooplankton abundance and community structure is not usually explained "on-site" environmental variations: large ocean systems can be influenced on the local zooplankton community variations, which is also observed in the European seas (Frid and Huliselan, 1996; Reid et al., 2003; Smyth et al., 2014).

The final potential control on sea surface temperature is horizontal advection by the CBTWC. Previous studies have indicated that the heat content of the Japan Sea is largely affected by horizontal advection associated with the TWC, particularly from April to October (Hirose et al., 1996). In our study, SSH values suggest that the path of the CBTWC was parallel to the mouth of Toyama Bay (Fig. 4), and indicates that the intrusion of the CBTWC is weak and rare in Toyama Bay. Weak and rare intrusion of the CBTWC in Toyama Bay is supported by previous studies (Hase et al., 1999; Nakada et al., 2002), and is attributed to the break of continental shelf in Toyama Bay (Nakada et al., 2002; Igeta et al., 2017). The CBTWC is trapped on the continental shelf and flows along the isodepth from the Tsushima Strait to the Noto Peninsula (Kawabe, 1982); breaks in the continental shelf at Noto Peninsula can potentially alter the direction of the current. The spatial variation of site scores on RD1 corresponds to the bottom topography; higher scores were observed on the continental shelf (Stn. 7 and 9), and there were lower scores in the downstream reach of the submarine canyon.

Nakada et al. (2002) and Igeta et al. (2017) evaluated the effect of Toyama Bay topography (the submarine canyon, Fig. 1) on the CBTWC using a simple two-layer numerical model. They showed that breaks in the continental shelf induce cyclonic eddies at the edge of the Noto Peninsula, which were sometimes transported to the north, while if the continental shelf is unbroken, the coastal current spreads widely into Toyama Bay. In contrast, the continental shelf is wider at Wakasa Bay (Fig. 1), and water exchange is active during winter (Itoh et al., 2016); here, and along the western part of Noto Peninsula, the zooplankton community structure on RD1 was homogenous.

The importance of ocean currents to zooplankton community structure has also been demonstrated in coastal areas facing the open ocean, such as the Kuroshio off Japan (Sogawa et al., 2017), and on the Pacific and Atlantic coasts of North America (Mackas et al., 1991; Keister et al., 2011; Pepin et al., 2011; Pepin et al., 2015). In our study, the response of zooplankton to temperature was focused after VIF selection, but the horizontal advection of zooplankton by the CBTWC is also relevant; the importance of the original zooplankton community structure has been demonstrated in a study of eddies associated with the Leeuwin Current off Australia (Strzelecki et al., 2007). When the other db-RDA was done with max S and SST as the explanatory parameters instead of mean T and SSS, the coefficients of SST and maximum salinity were 0.0392 and 0.0192, respectively. The SST variation was considered as the results of the CBTWC, water temperature in winter and Qnet, while the maximum salinity was one of the index of CBTWC transport, because the maximum of salinity of the TWC is increased from spring to summer at the Tsushima Strait (Morimoto et al., 2009). Therefore, we considered that the contributions of CBTWC was at least one-third of RD1 variation. Hence, as it was difficult to completely separate the effects of temperature and zooplankton transportation, the CBTWC can be assumed to be an important control on zooplankton community structure. The spatial variation in Toyama Bay and other areas has been discussed, but differences were also observed between the northern and western parts of the Noto Peninsula, which are downstream and upstream of the CBTWC, respectively (Fig. 4).

This difference may result from differences in the original water masses and zooplankton communities. Since the velocity of the CBTWC is ~10 cm s^{-1} and rarely > 30 cm s^{-1} (Hase et al., 1999; Igeta et al., 2011; Fukudome et al., 2016), it takes ~10 days for a water mass to travel 100 km. Wakasa Bay is ~500 km from the Tsushima Strait, so it is possible for water that is present in the Tsushima Strait in March to reach Wakasa Bay and the western part of Noto Peninsula in May; however, it would not yet reach the northern part of Noto Peninsula, which is ~700 km from the Tsushima Strait. Near the Tsushima Strait, dominant copepods in the upstream CBTWC include the warm-water species *C. sinicus*, *P. parvus,* and *C. vanus*, even in March (Hirakawa et al., 1995); cold-water species are present and dominant in the Sea of Japan during winter (Chiba and Saino, 2003).

The dominance of warm-water zooplankton can be treated as the key indicator of the CBTWC. Zooplankton communities have been treated as water mass indicators in other areas (Russell, 1935). Rapid changes in zooplankton community in response to oceanic currents have been identified in areas such as the Kuroshio coast and Mediterranean (Raybaud et al., 2008; Sogawa et al., 2017), but in our study site, the zooplankton community was reporoducible. In addition, the dominance of the herbivorous *O. atlantica* in Toyama Bay suggests its food web structure differs from the other areas, which are dominated by the carnivorous *C. affinis* (Ohtsuka and Nishida, 1997); the effect of bottom topography on the path of the CBTWC creates a heterogenic ecosystem along the Japanese coast in the Japan Sea. Previously, it was known that submarine canyons have impacts on the pelagic ecosystem via local upwelling (Fernandez-Arcaya et al., 2017). In Toyama Bay, there is cyclonic circulation when the CBTWC intrudes (Igeta et al., 2017), which produces downwelling. Therefore, our results show that changes in the path of the current induced by the submarine canyon promote ecosystem heterogeneity and the rich spatial biodiversity along the coast of Japan.

5. Conclusion

We investigated zooplankton community structure over a 15-year period along the Japanese coast of the Japan Sea, with continental shelf and a submarine canyon. Distance-based RDA indicated that zooplankton community structure is largely influenced by water temperature of the CBTWC. Warm-water zooplankton were dominant in the path of the CBTWC and along the Japanese coast, and cold-water zooplankton were dominant in Toyama Bay where intrusion of the CBTWC is prevented by a submarine canyon. Therefore, dominance of warm-water species can be used as an index of the CBTWC along the Japanese coast of the Japan Sea. Even though our study area was close to the coast, the effect of land is not dominant, and biological productivity is mainly controlled by the ocean. Surface waters in the Japan Sea have been affected by global warming and East Asian industrial development for half a century (Belkin, 2009; Kodama et al., 2016). Our study indicates that water temperature largely determines the zooplankton community; therefore, an elevation in sea surface temperature is likely to change zooplankton community structure. Continuous monitoring in our study site helps the effects of global warming on biological productivity to be better understood.

Acknowledgement

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Table 1 Environmental parameters and associated VIF values.

Parameter	Abbreviation	VIF before selection	VIF after selection
Temperature at 5 m depth	SST	7.6	removed
Mean temperature in water column	Mean T	24.9	1.8
Minimum temperature in water column	Mini T	10.9	removed
Salinity at 5 m depth	SSS	2.4	1.5
Mean salinity in water column	Mean S	6.9	removed
Maximum salinity in water column	Max S	5.2	removed
Mixed layer depth	Z_m	1.6	1.1
Sea surface chlorophyll a concentration	SSChl a	1.1	1.0
Bottom depth of station	Bottom depth	1.9	1.4
Observed vertical haul depth of Norpac net	Haul depth	3.0	removed
Time of day of sampling	Time	1.8	1.0

Table 2 Coefficients for environmental parameters calculated using db-RDA.

	RD1	RD2	RD3
Mean T	0.0525	-0.0240	-0.0387
SSS	0.0079	0.0517	-0.0068
SSChl a	-0.0031	-0.0069	-0.0253
Z_m	-0.0011	0.0261	0.0390
Bottom depth	-0.0009	0.0224	-0.0461
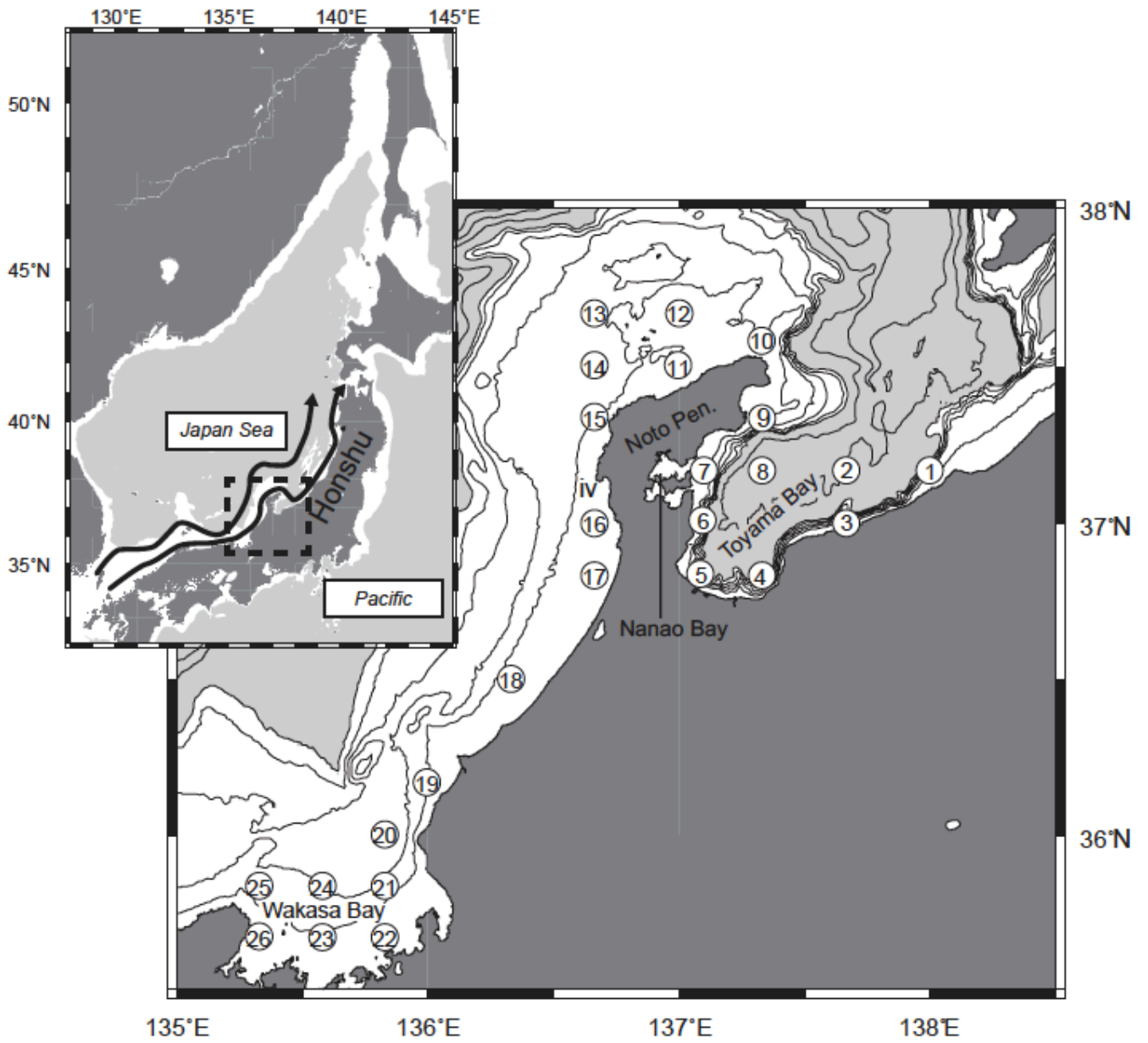
Figure 1: Distribution of sampling stations (numbers in open circles) along the Japanese coast of the Japan Sea. Contours indicate bottom depth at 100 m intervals to 500 m depth (white areas), and 500 m intervals thereafter (gray areas). The superimposed map shows location of the study area in the Japan Sea, and Tsushima Warm Current according to Hase et al. (1999).
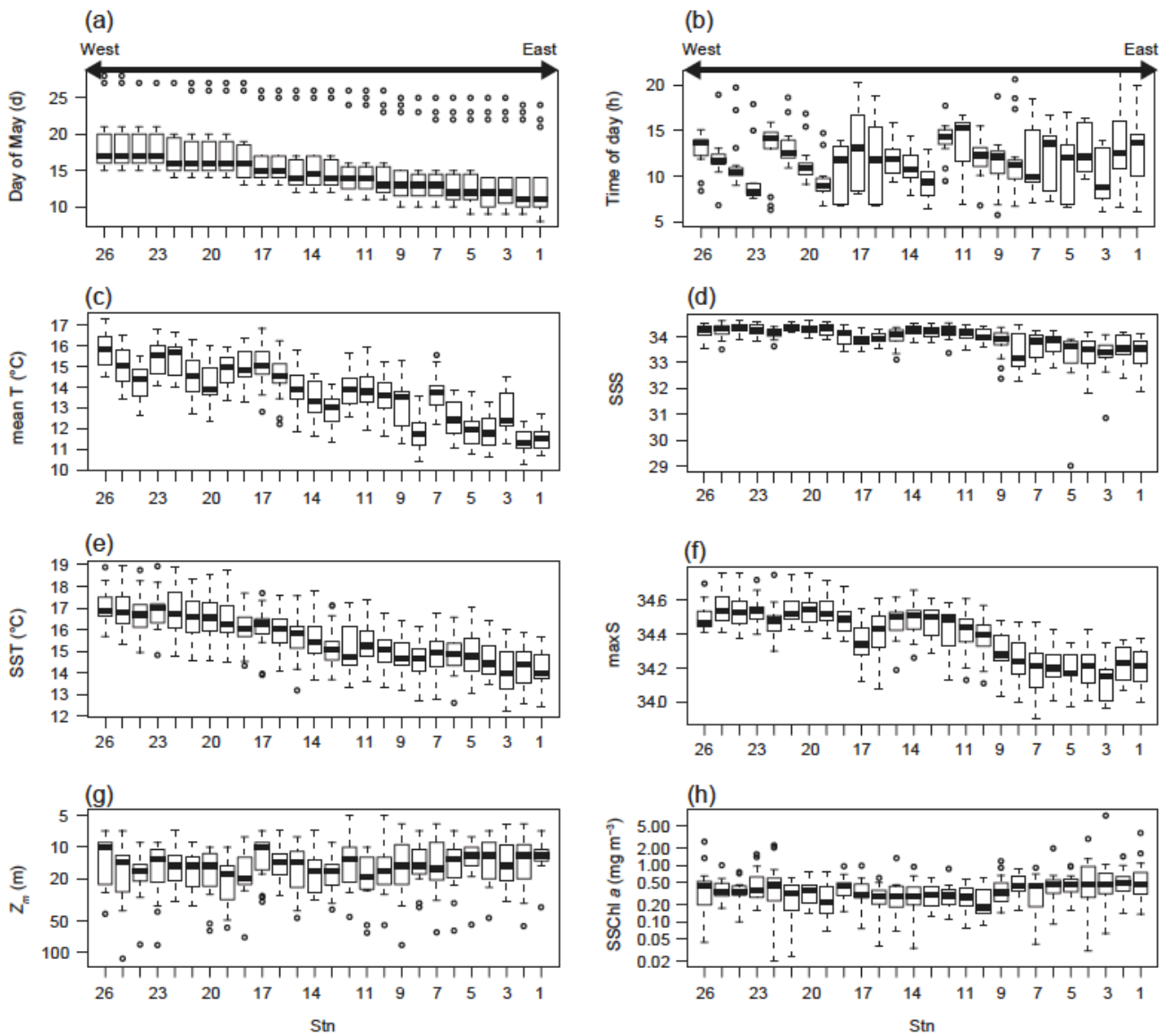
Figure 2: Spatial variations of: (a) day of May; (b) time of day; (c) mean temperature of the water column (mean T); (d) salinity at 5 m depth (SSS); (e) temperature at 5 m depth (SST); (f) maximum salinity of the water column (max S); (g) mixed layer depth (Z_m); and (h) sea surface chlorophyll a concentration in May (SSChl a). The X-axis indicates the station number. The plots show the median (horizontal lines within boxes), upper and lower quartiles (boxes), quartile deviation (bars), and outliners (circles).
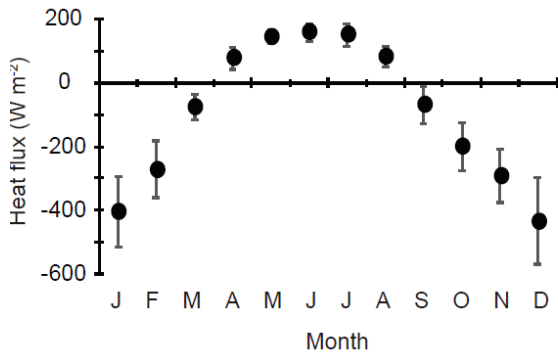
Figure 3: Horizontal distribution of mean absolute sea surface height (counters) and mean current velocity (arrows) in May estimated by AVISO.

(a) Temporal variation of sea surface heat flux

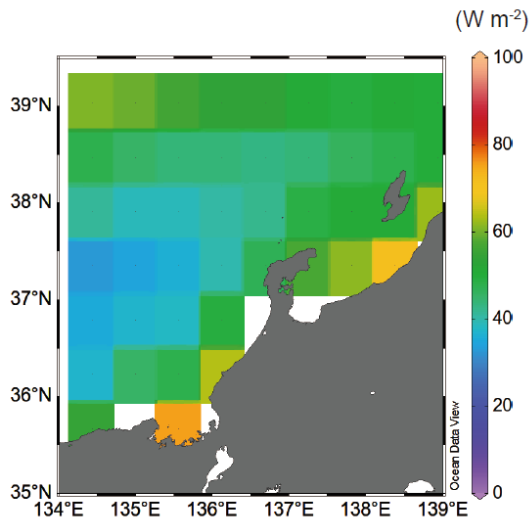## (b) Spatial variation of sea surface heat flux in spring

Figure 4: Temporal and spatial variations in sea surface heat flux. (a) Annual variations in sea surface heat flux (W m^{-2}) between 2000–2013 in the area of 134–139° E and 35–39°30' N. Vertical bars denote one standard deviation. (b) Spatial variation of sea surface heat flux (W m^{-2}) during spring (March–May) from 2000–2013. Blank areas were excluded because they were ascribed as landmass in JRA55.
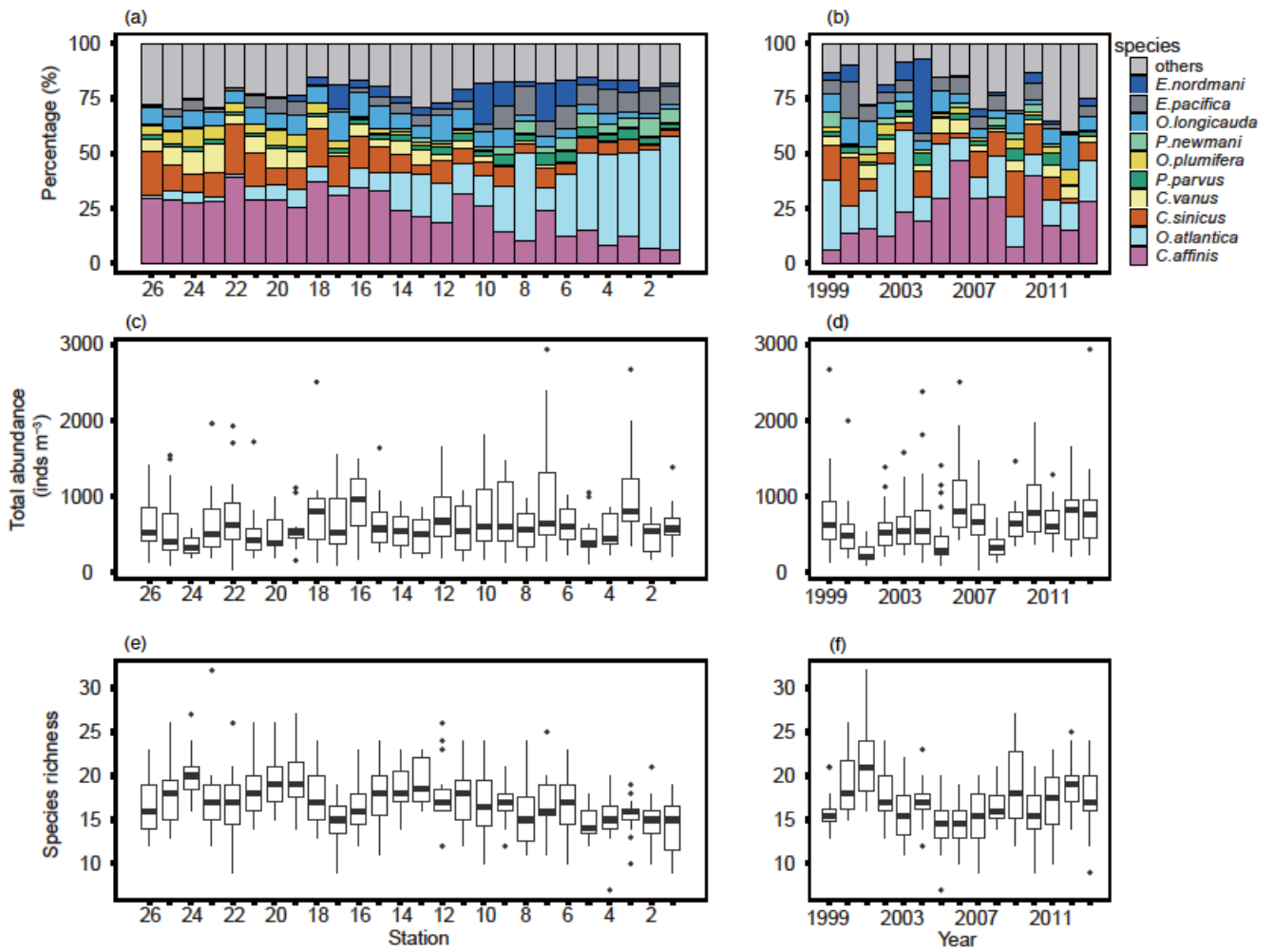
Figure 5: Spatial and yearly variations of contributions of top 10 most abundant species (a, b), total zooplankton abundance (c, d), and species richness (e, f) The total zooplankton abundance plots show the median (horizontal lines within boxes), upper and lower quartiles (boxes), quartile deviation (bars), and outliners (circles).
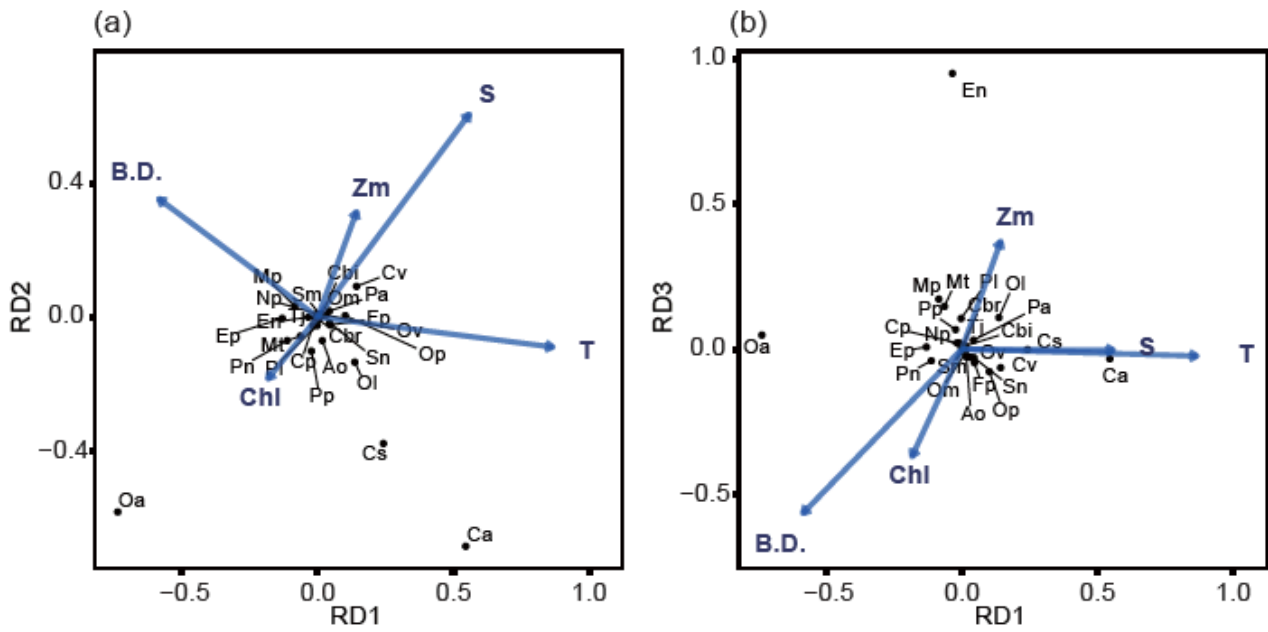
5

Figure 6: Relationship between environmental parameters (arrows) and zooplankton species (crosses) in db-RDA diagram: (a) combination of RD1 and RD2, and (b) combination of RD1 and RD2. The abbreviations T, S, Chl, Zm and B.D. adjacent to arrows represent mean temperature of water column (mean T), salinity at 5 m depth (SSS), sea surface chlorophyll *a* (SSChl *a*), mixed layer depth (Z_m) and bottom depth of station, respectively. The 25 zooplankton spices were represented by their initials.
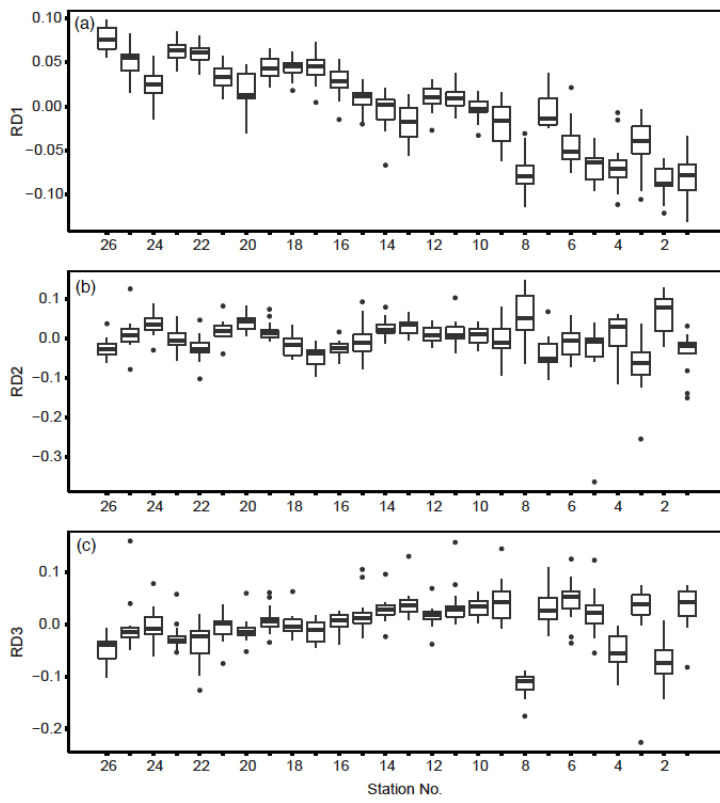
Figure 7: Spatial variation of station db-RDA scores: (a) RD1, (b) RD2, and (c) RD3. Plots show the median (horizontal lines within boxes), upper and lower quartiles (boxes), quartile deviation (bars), and outliers (circles).