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North-south changes of zooplankton community and copepods population along the 110°E line in the Indian sector of the Southern Ocean during the austral summer

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Abstract

Various zooplankton studies have been conducted in the Indian sector of the Southern Ocean, but studies investigating spatial changes in both meso- and macro-zooplankton populations are limited. To reveal the north-south change of the meso- and macro-zooplankton community structure and the population structure of large copepods, we investigated zooplankton communities collected by the Ocean Research Institute (ORI) net along the 110°E transect in the Indian sector of the Southern Ocean during the austral summer. The zooplankton abundance and biomass were high at the stations north of 60°S and was dominated by large copepods, especially *Calanoides acutus*. A cluster analysis identified four zooplankton community groups. The distribution pattern of the community groups is likely to be related to the frontal system. The population structure of the dominant species of *C. acutus*, *Calanus propinquus* and *Rhincalanus gigas* had a similar tendency ; early copepodite stages were abundant in the northern region, while late copepodite stages dominated in the southern region. The meridional changes in the population structure are explained by different reproduction periods in each region related to sea-ice melt timing.

Key words : Antarctic Ocean, Zooplankton community, Copepoda, Population structure

Introduction

In the Indian sector of the Southern Ocean, physical fronts, which are boundaries of different water masses, tend to develop because strong ocean currents such as the Antarctic Circumpolar Current (ACC) are present (Moore et al., 1999 ; Sokolov and Rintoul, 2002). Four fronts are defined by the potential water temperature and distributed from north to south as follows ; the southern branch of the Polar Front (PF-S), the northern branch of the Southern Antarctic Circumpolar Current Front (SACC-N), the Southern Boundary (SB) and the Antarctic Slope Front (ASF) (Sokolov and Rintoul, 2002 ; Aoki et al., 2006). Around the fronts, high primary production is observed due to the input of nutrients from upwelling (Moore et al., 1999 ; de Baar et al., 1995 ; Laubscher et al., 1993). However, because local eddies repeatedly develop and disappear in this area, ocean currents such as the ACC often meander, and a sporadic water intrusion occurs between different water masses (Chiba et al., 2001). As above, the Indian sector of the Southern Ocean is characterized by fronts related to high primary production and short-term changes in the hydrographic conditions following local-scale current branches.

Zooplankton have a shorter life cycle and higher turnover rate between generations than predators such as marine mammals, sea birds and fish in the Southern Ocean. Because they are close to the base (i.e., primary production) of the food web, their response (e.g., growth) to environmental change is sensitive (Takahashi et al., 1998). The zooplankton community structure also quickly responds to environmental changes in this study region (Chiba et al., 2001). Generally, zooplankton communities have different structures in the north and the south ; in northern areas, salps, small euphausiids, amphipods, copepods and chaetognaths dominate, while in southern areas, large euphausiids and fish larvae dominate (Hosie and Cochran, 1994 ; Hosie et al., 1997). Because of

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the meandering of ocean currents such as the ACC, zooplankton communities also show longitudinal differences (Hosie et al., 2000 ; Chiba et al., 2001 ; Hosie et al., 2014).

Copepods are the most dominant species in the zooplankton community, and *Calanoides acutus, Calanus propinquus, Metridia gerlachei, Metridia lucens, Paraeuchaeta antarctica* and *Rhincalanus gigas* are the dominant copepods (Chiba et al., 2001 ; Pane et al., 2004). Among the copepods, species-specific distributions are observed ; *C. acutus* and *R. gigas* are approximately ten times more abundant than *C. propinquus* in the ACC (Bathman et al., 1993) and the Scotia Sea (Voronina, 1975 ; Voronina et al., 1978 ; Vladimirskaya, 1978 ; Marin, 1987 ; Bondarenko and Polonsky, 1990 ; Atkinson, 1991). However, in this study area (i.e., the Indian sector of the Southern Ocean), although many studies have been conducted using a Continuous Plankton Recorder (CPR) or a North Pacific Standard Net (NORPAC) (Takahashi et al., 1998 ; Chiba et al., 2001 ; Takahashi et al., 2011 ; Takahashi et al., 2017), few studies have investigated the community structure of meso- and macro-zooplankton.

Regarding to population structure of copepods, it is informative parameter to understand life cycle of the copepods and predict the future changes on the species abundance by modelling (e.g., Matsuno et al., 2020). However, in the Indian sector of the Southern Ocean, the information is limited. Because of the problem, it is still unclear how relate the environmental factors including sea ice extent to the population structure.

The purpose of this study was to reveal the north-south changes of the zooplankton community structure, copepod species composition and population structure along the 110°E transect in the Indian sector of the Southern Ocean during the austral summer. To this end, we test two hypotheses : 1) that the zooplankton community will differ by fronts, 2) that the population structure of copepods will associate with sea-ice extent.

Materials and Methods

Field sampling

The sampling was conducted during a UM-17-09 cruise from 31 December 2017 to 22 January 2018 by the training vessel *Umitaka-maru* of the Tokyo University of Marine Science and Technology. Zooplankton were collected at 9 stations from 59.00 to 64.68°S on the 110°E transect by an oblique tow using an Ocean Research Institute (ORI) net (mouth diameter : 1.6 m ; mesh size : 500 µm) from a depth of 200 m to the surface (Fig. 1, Table 1). COMPACT-TD (JFE Advantech Co., Ltd.) was attached to the net opening to measure the maximum depth. A flow meter (General Oceanics, Inc.) was attached to the center of the net ring to measure the volume of filtered sea water. Zooplankton samples were preserved in 5% neutral formaldehyde-seawater and taken back to the laboratory. At each station, CTD (Sea-Bird Electronics Inc., SBE 911plus) cast was conducted to measure the temperature, salinity and fluorescence. The seawater was filtered onto a GF/F filter and chlorophyll *a* (chl. *a*) was extracted with N,N-dimethylformamide and measured with a fluorometer (Turner Designs Inc., 10-AU-005). For converting fluorescence to chl. *a* concentration (mg m^{-3}), we applied the relationship between measured chl. *a* concentration and fluorescence (Appendix 1).

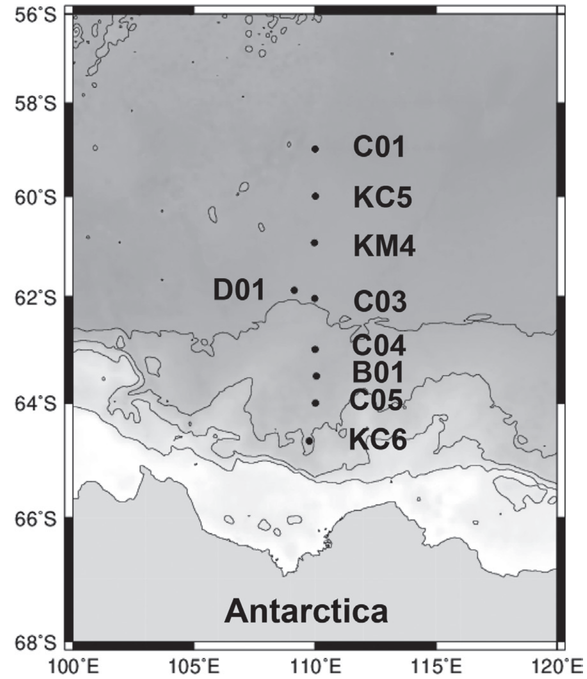

Fig. 1. Location of the sampling stations along the 110°E in the Indian sector of the Southern Ocean during January 2018.

Identification and enumeration

In the laboratory, each sample was divided from 1/16 to 1/256 using a Motoda plankton splitter (Motoda, 1959). Number of the enumerated individuals were ranged from 176 to 642 (mean 356) per sample. All animals were enumerated at the taxa level under a stereo microscope and weighed with a precision of 0.01 g using an electron microbalance (AT261, METTLER TOLEDO). Copepods were identified to the species level and copepodid stage level according to Bradford-Grieve et al. (1999). The mean copepodid stage (*MCS*) of dominant large-sized copepods (*C. acutus*, *C. propinquus* and *R. gigas*) was calculated using the following equation :

$$MCS = \frac{\sum_{i=1}^{6} i \times Ai}{\sum_{i=1}^{6} Ai}$$

where i (1-6 indicates C1-C6) is the copepodid stage, and Ai (ind. m^{-3}) is the abundance of the ith copepodid stage.

Table 1. Summary of ORI net sampling and time since sea-ice melt (days) derived by AMSR2 at each station along the 110°E in the Indian sector of the Southern Ocean during January 2018.

Station	Posotion		Date & Time (UTC)		Towing depth (m)	Filtered water (m^3)	Time since sea-ice melt (days)
	start	finish	start	finish			
C01	59.00 °S 110.00 °E	58.98 °S 110.01 °E	2018/1/7 14 : 30	2018/1/7 14 : 59	128	2,775	-
KC5	59.99 °S 110.01 °E	59.97 °S 110.03 °E	2018/1/8 3 : 00	2018/1/8 3 : 28	167	3,907	100
KM4	60.93 °S 109.97 °E	60.95 °S 109.99 °E	2018/1/8 21 : 10	2018/1/8 21 : 40	169	4,486	68
D01	61.88 °S 109.15 °E	61.90 °S 109.16 °E	2018/1/9 10 : 24	2018/1/9 10 : 52	187	4,026	59
C03	62.04 °S 109.99 °E	62.06 °S 109.98 °E	2018/1/9 17 : 09	2018/1/9 17 : 40	139	3,141	59
C04	63.01 °S 110.00 °E	63.03 °S 109.99 °E	2018/1/10 6 : 25	2018/1/10 6 : 55	167	2,815	51
B01	63.50 °S 110.06 °E	63.51 °S 110.09 °E	2018/1/10 13 : 10	2018/1/10 13 : 38	177	3,345	42
C05	64.00 °S 110.02 °E	64.01 °S 110.04 °E	2018/1/10 19 : 57	2018/1/10 20 : 25	168	3,568	31
KC6	64.68 °S 109.77 °E	64.68 °S 109.73 °E	2018/1/11 11 : 11	2018/1/11 11 : 38	142	3,888	25

- : not available (no sea ice coverage).

Satellite observation

To evaluate the timing of sea-ice retreat at each station, the AMSR2 (Advanced Microwave Scanning Radiometer 2) standard sea-ice concentration (SIC) product was obtained from the Arctic Data archive System (ADS, https://ads.nipr.ac.jp/). The AMSR2 data were supplied by the Japan Aerospace Exploration Agency through the ADS, under a partnership between the National Institute of Polar Research and JAXA. Using the data, we calculated the time since sea-ice melt (TSM). The TSM was defined as the number of the open-water days from the last date when the SIC fell below 20%, prior to the observed annual sea-ice minimum across the study region, to the sampling date.

To investigate the spatial and temporal variability of chlorophyll *a* concentration around the sampling region, ocean color data from November 2017 to January 2018 were downloaded from the GlobColour project (https://hermes.acri.fr/index.php). The merged products, calculated with a weighted averaging merging (AVW) method, had a spatial resolution of 4 km and a temporal resolution of 8 days.

Statistical analysis

The data on the number of individuals (X; ind. m^{-3}) per taxon (in the case of copepods, per species) were logarithm transformed ($\text{Log}_{10}\,[X+1]$) in order to reduce the bias of abundant species, and then the Bray-Curtis index was used to construct the matrix of Bray-Curtis similarity. This similarity was subjected to cluster analysis using the Unweighted Pair Group Method using Arithmetic mean (UPGMA). This analysis was produced using Primer7. One-way ANOVA and the Turkey-Kramer test were performed in StatView to assess the difference of the abundance among clusters. To clarify the relationship between the zooplankton community and the environmental parameters (latitude, temperature, salinity and chl. *a* concentration), BEST-BIOENV was performed using PRIMER v7 software (PRIMER-E Ltd.).

To reveal the relationship between MCS and TSM or chl. *a* concentration, we tested linear regressions. However, the comparison between MCS and chl. *a* concentration could not be made because there were many lacks on chl. *a* data.

Results

Sea-ice extent and surface chlorophyll a

From satellite observation, TSM was calculated from 25 to 100 days except st. C01 because of no ice-coverage though a year. The TSM showed the longest at st. KC5 and the shortest at st. KC6 (Table 1). For phytoplankton bloom, it is onset from early December around 60°S (i.e., sts. KC5 and KM4) (Fig. 2). Then, the phytoplankton bloom shifted gradually to southward over time, but the bloom area was not observed sts. C05 and KC6 during the sampling period (Fig. 2).

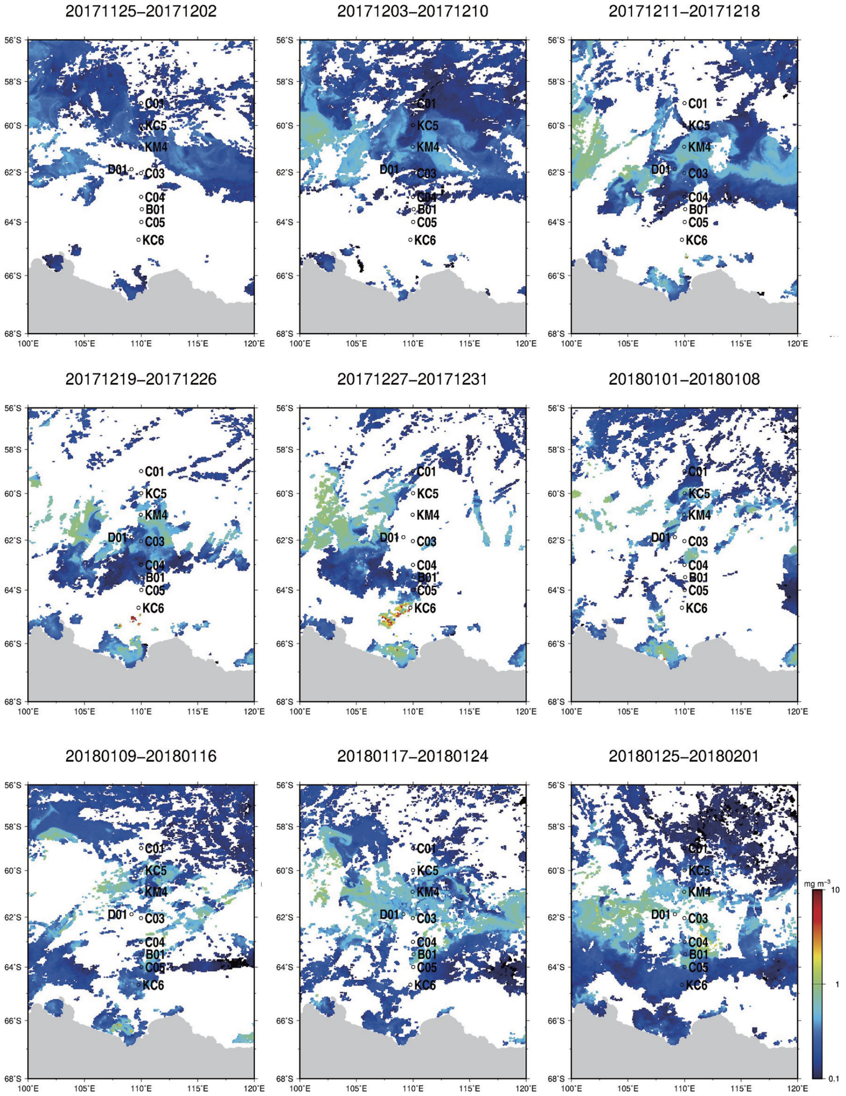

Fig 2. Satellite-derived surface chlorophyll *a* concentration around the 110°E transect in the Indian sector of the Southern Ocean from November 2017 to January 2018.

Hydrography

The water temperature varied from -1.8 to 3.0°C and was high at the surface layer and at 200 m, while it was low ($\leq$ 0°C) between 50 and 150 m (Fig. 3A). The salinity ranged from 33.2 to 35.0 and was low at the surface (Fig. 3B). For north-south changes, lower temperature and salinity values were observed in the southern stations (Fig. 3A and B). Because physical fronts can be defined according to the potential temperature (cf. Sokolov and Rintoul, 2002; Aoki et al., 2006), four fronts were observed as follows; PF-S was between st. KC5 and KM4, SACC-N was between st. KM4 and D01, SB was between st. B01 and C05 and ASF was between st. C05 and KC6. A high chl. *a* concentration was seen at 40 m, and a massive phytoplankton bloom was observed around 62-63°S (Fig. 3C).

Abundance, biomass and species composition

In the sampling region, the zooplankton abundance ranged from 12.99 to 247.90 ind. m^{-3}, and the biomass varied from 21.26 to 346.87 mg m^{-3} (Fig. 4A and B). Both of these measures were high at the stations north of 60°S (i.e., st. C01 and KC5), while the biomass was high north of 60°S and at st. KC6, the most southern station. Copepods were the most dominant taxon, contributing to 68-93% of the total abundance of each zooplankton community (Fig. 4A). Copepods, chaetognaths and amphipods occupied 29-90%, 1-16% and 1-23% of the total zooplankton biomass, respectively (Fig. 4B).

Copepod abundance was high at st. C01 (126 ind. m^{-3}) and KC5 (92 ind. m^{-3}), and less than 70 ind. m^{-3} at the southern stations (Fig. 5). At all stations, *C. acutus* and *R. gigas* comprised 21-68% and 13-52% of the total copepods

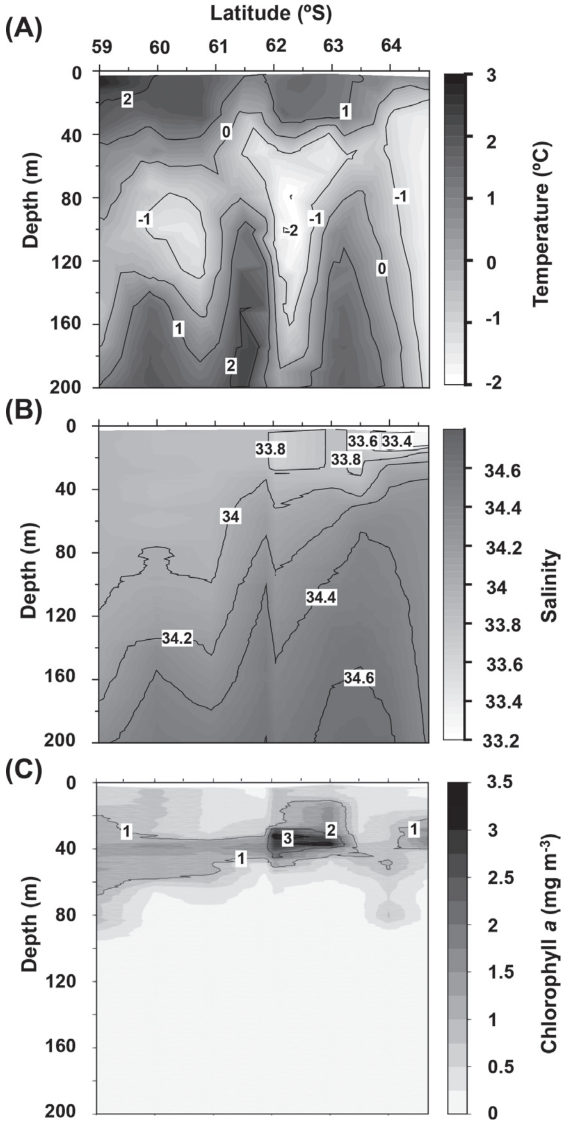

Fig. 3. Meridional changes in temperature (A), salinity (B) and chlorophyll *a* concentration (C) along the 110°E in the Indian sector of the Southern Ocean during January 2018.

abundance, respectively (Fig. 5). *M. gerlachei* was increased at southern stations near Antarctica.

Cluster analysis

From the results of the cluster analysis based on abundance, four zooplankton community groups were identified at a 61% similarity level (Fig. 6A). Each group was called A (two stations), B (one station), C (three stations) and D (three stations) from the north to the south (Fig. 6C). The BEST-BIOENV results showed that latitude and salinity were selected as the most contributing parameters to the zooplankton clustering (Table 2).

Comparing the abundances between the clustering groups, the total zooplankton abundances in group A was significantly higher (about ten times) than those of the other groups (Table 3 and Fig. 6B). Group A was characterized by a high abundance of copepods *C. acutus*, *C. propinquus*, *Calanus simillimus* and *R. gigas* compared to the other groups. Chaetognaths and euphausiids had significant differences between group A and D and between group A and B, respectively (Table 3).

Copepod population structure

The north-south changes of the population structure for the dominant species (*C. acutus*, *C. propinquus*, *M. gerlachei* and *R. gigas*) varied with the species. For *C. acutus* and *C. propinquus*, early copepodid stages (from one (C1) to four (C4)) dominated at the northern stations, while late copepodid stages (from five (C5) to adults (C6)) dominated at the southern stations (Fig. 7A and B). In the case of *M. gerlachei*, only C4 and older stages occurred, but early copepodid stages (C1-C3) were absent at the all stations (Fig. 7C). C5-C6 of *R. gigas* occurred frequently at the most northern station (st. C01), and early stages (C1-C4) were increased at the other stations (Fig. 7D). Comparing the MCS of the dominant species and the TSM, a significant negative relationship was found for only *C. acutus* (Fig. 8). However for *C. propinquus* and *R. gigas*, the relationships were not significant (p = 0.082 and 0.893, respectively).

Discussion

Zooplankton community structure and hydrography

Many studies about zooplankton communities have been reported using CPR and NORPAC in this research area (Takahashi et al., 1998 ; Chiba et al., 2001 ; Takahashi et al., 2011 ; Takahashi et al., 2017). CPR is a sampling device that is towed from a ship to continuously collect surface (6-8 m depth) zooplankton (Takahashi et al., 2011 ; Hosie et al., 2014 ; Takahashi et al., 2017). The NORPAC net can quantitatively collect meso-zooplakton by vertical hauls from 150 m to the surface (Takahashi et al., 1998 ; Chiba et al., 2001). The ORI net is often used to collect fish larvae ; however, in addition to meso-zooplankton, macro-zooplankton with a high swimming capability can be caught quantitively because of the high towing speed and the large net mouth (Cuzin-Roudy and Labat, 1992). In a previous study on zooplankton abundance based on NORPAC (Chiba et al., 2001), Chiba et al. (2001) showed that the abundance, biomass and biomass/abundance ratio were 286 ± 615 ind. m^{-3}, 214 ± 509 mg m^{-3} and 0.75, respectively. The current study showed that they were 79.90 ± 106.79 ind. m^{-3}, 122.37 ± 107.09 mg m^{-3} and 1.53, respectively. In short, this study found a lower abundance and biomass and a higher biomass/abundance ratio than the previous research. This suggests that the ORI net could collect large and heavy meso- and macro-zooplankton individuals quantitively while miss-

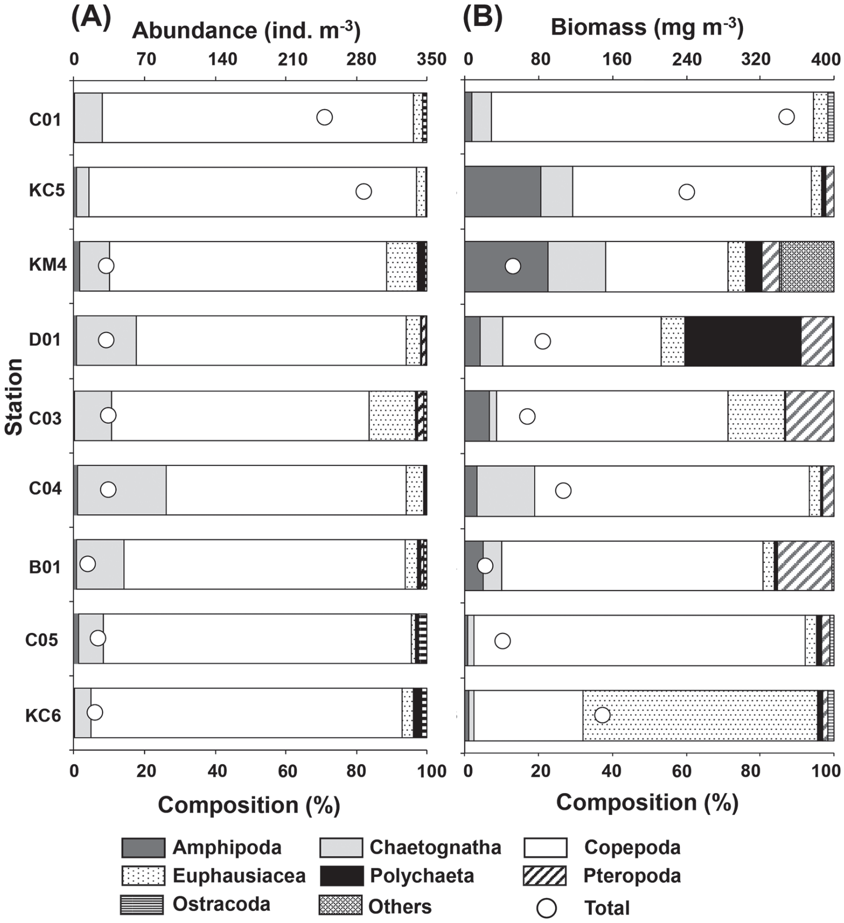

Fig. 4. Meridional changes in zooplankton community on abundance (A) and biomass (B) along the 110°E in the Indian sector of the Southern Ocean during January 2018.

ing small meso-zooplankton that could avoid the mesh due to the large mesh size (500 μm).

In the Indian sector of the Southern Ocean, physical environments such as fronts, divergence and convergence generally divide the zooplankton community structure (Errhif et al., 1997 ; Tanimura et al., 2008). In this study, the community structure was distinctly classified by PF-S and SACC-N, but similar communities were observed in the area beyond SB and ASF. This mismatch of distributions between fronts and the zooplankton community was presumably caused by the high similarity between groups C and D (ANOSIM, Global R=0.593) compared to the low similarity between groups A and B.

According to Hosie et al. (2000) and Wallis et al. (2016), zooplankton communities are affected by fronts as well as sea ice, water temperature and chl. *a* concentration. However, the BEST-BIOENV analysis showed that salinity was the parameter most related to community classification, and the relationship with chl. *a* concentration was low. In general, biological production (i.e., chl. *a* concentration) is known to be enhanced around the fronts in the Southern Ocean (Laubscher et al., 1993 ; de Baar et al., 1995 ; Moore et al., 1999). In contrast, Sokolov and Rintoul (2007) reported that the distribution of chl. *a* concentration is affected by upwelling of high-nutrient deep water due to the seafloor topography and water currents and is not associated with fronts. Chiba et al. (2001) revealed that the environmental factors influencing the zooplankton community structure were highly related in the order of latitude, water temperature, and chl. *a* concentration. Thus, in this study, the zooplankton community structure was divided with the water mass and had a low relationship with chl. *a* concentration in the Indian sector of the Southern Ocean during the austral summer. The findings are consistent with previous studies.

North-south change of copepods

In this study area, large copepods have species-specific distributions related with the complicated current and their life cycle. On abundance, *C. acutus* and *R. gigas* occurred ten times more than *C. propinquus* in the ACC north of SB (Bathmann et al., 1993) and the Scotia Sea (Voronina, 1975 ; Voronina et al., 1978 ; Vladimirskaya, 1978 ; Marin, 1987 ; Bondarenko and Polonsky, 1990 ; Atkinson, 1991). The results of the copepod community structure in this study

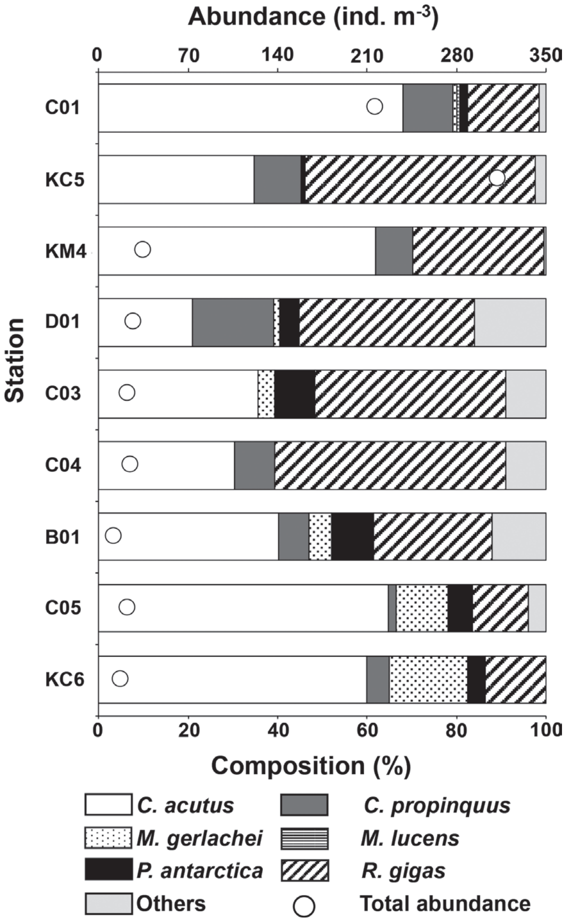

Fig. 5. Meridional changes in copepods community on abundance along the 110°E in the Indian sector of the Southern Ocean during January 2018.

almost corresponded with the results of previous studies.

The subantarctic species *C. simillimus* is abundant in the ACC (Takahashi et al., 2011). However, the copepods were hardly observed in this study, *C. simillimus* occurred only in the PFZ. Because *C. simillimus* was most abundant at the northern station in the PFZ, corresponding with previous studies, *C. simillimus* seems to be distributed in the northern PFZ despite the lack of quantitative net sampling.

Considering the horizontal change of the copepod community structure, remarkable east-west changes in abundance have been observed compared to north-south changes (Hosie et al., 2000 ; Chiba et al., 2001). Hosie et al. (2014) reported that the copepod abundance was ten times higher in the north area (PFZ) than in the south area (ACC). In this study, three dominant copepods (*C. acutus*, *C. propinquus* and *R. gigas*) except *M. gerlachei* were abundant in the PFZ, similar to the results in Hosie et al. (2014). This is because the distribution of the most dominant species *C. acutus* was similar in this study and the previous study. According to Hosie et al. (2014), the abundance of *C. acutus* at the stations in the PFZ was approximately three times higher than those at the southern stations. Similarly, the species abundance in the PFZ was approximately 12.93 times greater than those at the southern stations of this study. Because the sampling methods (CPR vs. ORI) and the research area (entire Southern Ocean vs. the Indian sector) were different between this study and the previous study, these differences may have affected the change of abundance. Because the results were similar despite the differences in the sampling methods and the region, the dominance and high abundance for *C. acutus* in the PFZ are interpreted as a general trend in the Indian sector of the Southern Ocean during the austral summer.

North-south change of the population structure for dominant large copepods

The dominant large copepod *C. acutus* grow to C5 until the summer in the north of SB and then descend to the deep layer and diapause using wax ester as an energy source in the winter (Bathmann et al., 1993). After overwintering, an adult female is fertilized in the deep layer and spawns in the surface layer. Hatched nauplius grow to late stages and descend to the deep layer for diapause and reproduction (Voronina, 1978). They reproduce from the spring to the summer, and the reproductive period is delayed gradually southwards (Voronina, 1978 ; Hagen and Schnack-Schiel, 1996). An adult male stays in the deep layer even in the spring (Marin, 1988).

In this study, early stages (C1-C3) were often observed at the north stations (from st. KC5 to st. D01), and late stages (C4-C6) dominated at the southern stations. Because of this population change between the north and the south, it is thought that this species reproduced earlier in the north region than in the south region (Voronina, 1978 ; Hagen and Schnack-Schiel, 1996). From st. C01 to D01, since no adult and many early copepodite stages were observed, they had finished reproduction there. Between st. C03 and st. B01, both adults and early copepodite stages were occurred, inducing they had started reproduction. This species starts to reproduce with grazing in the surface layer when a phytoplankton bloom occurs (Marin, 1988). In this study period, because pre-matured adult females were observed south of st. C03 (data not shown) with the phytoplankton bloom, this species presumably continue to reproduce using the sufficient food. At st. C05 and KC6, only adults and late copepodite stages were observed with no phytoplankton bloom. That is, the population structure of this species is thought to be linked to the timing of phytoplankton bloom.

During the spring, small-scale phytoplankton blooms regionally occur around 60°S, and these blooms shift from the north to the south in association with sea-ice melt timing (Sokolov and Rintoul, 2007 ; Iida and Odate, 2014). The similar trend was found in this study by satellite observation. According to Sedwick and DiTullio (1997), melting sea-ice stimulates phytoplankton production due to the availability of

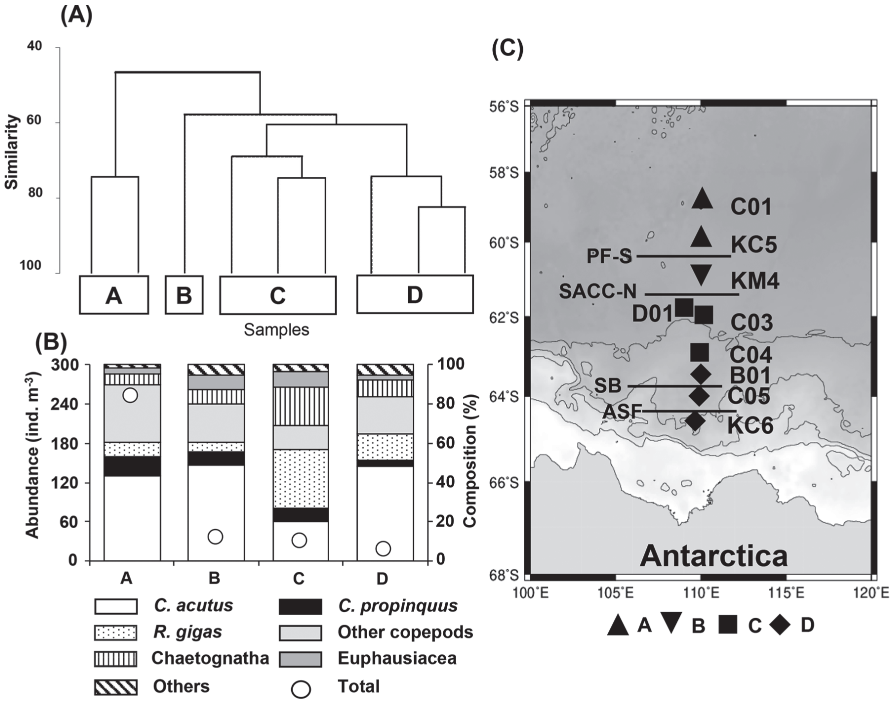

Fig. 6. Results of cluster analysis based on zooplankton abundance along the 110°E in the Indian sector of the Southern Ocean during January 2018 (A). Four groups (A-D) were identified from Bray-Curtis similarity connected with UPGMA. Mean abundance and species/taxon composition of each group (B). Spatial distribution of the group in the Indian sector of the Southern Ocean during January 2018 (C).

Table 2. Results of BEST-BIOENV for zooplankton community with environmental parameters (latitude (Lat), temperature (Tem), salinity (Sal), chlorophyll *a* concentration (Chl)) in the Indian sector of the Southern Ocean during January 2018.

Number of variables	Best variables combinations using 0-200 m layer data (Spearman Rank Correlation Coefficient)				
1	Lat (0.67)	Sal (0.53)			
2	Lat, Sal (0.67)	Lat, Chl (0.46)	Tem, Sal (0.39)	Sal, Chl (0.38)	Lat, Tem (0.38)
3	Lat, Sal, Chl (0.59)	Lat, Tem, Sal (0.50)			
4	Lat, Tem, Sal, Chl (0.47)				

iron from the ice. Thus, the timing of sea-ice melt determines the phytoplankton bloom and causes the north-south change of the population structure of *C. acutus* during the summer. The strong negative relationship between MCS and TSM supports this finding.

C. propinquus has a similar life cycle to *C. acutus* ; they grow to C5-C6 until the austral summer north of SB and reproduce from the spring to the summer (Bathmann et al., 1993). However, they do not have a diapause phase in the winter, and all copepodite stages are distributed in the surface layer (Voronina, 1978 ; Hagen and Schnack-Schiel, 1996).

In this study, it is assumed that *C. propinquus* reproduces in this study period or after this research because adult females occurred at the same dominance as matured individuals at only two southern stations (st. C05 and KC6). In addition, given that early copepodite stages dominated the population at the northern stations, the north-south change in the population structure of *C. propinquus* induced the variation of their reproduction period similar to *C. acutus*.

The north-south changes had thought to be mostly induced by the timing of sea-ice melt, as mentioned above. However, the relationship between MCS and TSM was not significant for *C. propinquus*. This was caused by the high MCS (> 5) for *C. propinquus* observed at st. C05 and KC6 where phytoplankton bloom was not occurred yet. In other words, they did not reproduce at the southern stations. Considering

Table 3. Comparison of the zooplankton abundance between the groups identified by cluster analysis (cf. Fig. 6A) in the Indian sector of the Southern Ocean during January 2018. Differences between the groups were tested by one-way ANOVA and post hoc test by Tukey-Kramer. Any groups not connected by the underlines are significantly different ($p < 0.05$). Values are mean. Numbers in parenthesis are the number of stations belonging to each group.

Species	Abundance (ind m^{-3})				One-way ANOVA	Tukey-Kramer
	A (2)	B (1)	C (3)	D (3)		
Aetideus sp.	0	0	0.11	0	NS	
Calanoides acutus	108.86	17.58	5.8	7.87	***	C D B A
Calanus propinquus	24.49	2.4	1.96	0.52	***	D C B A
Calanus simillimus	1.27	0.11	0.23	0	**	D B C A
Ctenocalanus citer	1.05	0	0	0	NS	
Euchirella rostomagna	0.52	0	0	0	NS	
Haloptilus oxycephalus	0.52	0	0.45	0.18	NS	
Heterorhabdus sp.	0.52	0	0.27	0.03	NS	
Metridia gerlachei	0.74	0	0.3	1.66	NS	
Metridia lucens	0.74	0	0	0	NS	
Oithona frigida	0	0	0	0.03	NS	
Oithona similis	0	0.28	0	0	NS	
Oncaea antarctica	0.74	0	0	0	NS	
Paraeuchaeta antarctica	2.52	0	0.88	0.79	NS	
Racovitzanus antarctica	0	0	0.76	0.27	NS	
Rhincalanus gigas	18.51	1.83	8.71	2.17	***	B D C A
Rhincalanus gigas nauplius	64.92	6.51	0.34	0	NS	
Scaphocalanus sp.	0	0	0.24	0.1	NS	
Amphipoda	1.64	0.54	0.22	0.17	NS	
Chaetognatha	14.42	2.6	5.67	1.41	*	D B C A
Cnidaria	0	0.46	0	0	NS	
Decapoda	0.14	0	0	0	NS	
Euphausiacea	7.03	2.74	2.4	0.47	**	D C B A
Ostracoda	1.66	0.23	0.15	0.33	NS	
Polychaeta	0.2	0.54	0.2	0.24	NS	
Pteropoda	0.2	0.06	0.35	0.07	NS	
Total	250.67	35.58	29.32	16.29	***	D C B A

* : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$.

above the results, life cycle of *C. propinquus* may be related to the timing of sea-ice melt as well as *C. acutus*.

R. gigas has one- or two-year generation lengths in each area, and it has been reported to be one-year in the ACC (Arashkevich, 1978). In the Weddell Sea, the species has a two-year generation length because all copepodite stages occur during the summer (Marin, 1988). In this study area, a nauplius was observed at the northern stations (st. C01-D01), and late copepodite stages dominated the population at st. C01, KM4 and D01. Therefore, it is thought that *R. gigas* reproduced actively at the northern stations in this study period.

The chl. *a* concentration derived by satellite observation could not compare with the MCS of the dominant copepods. Instead of the comparison, TSM showed a significant relationship with MCS, and the relationship (i.e., significant or not) varied with the species. This was caused by differences of life cycle of the species. In other words, *C acutus* seems to have the strongest relationship to sea ice on their life cycle. In future, if the TSM change, population structure of the species will be the most strongly affected.

Conclusion

This study revealed the structures of the meso- and macrozooplankton community and the population of the dominant copepods in the Indian sector of the Southern Ocean during the austral summer of 2018. The zooplankton community structure had meridional differences associated with oceanic fronts but a low relationship with chl. *a* concentration. In terms of the species composition of copepods, this study

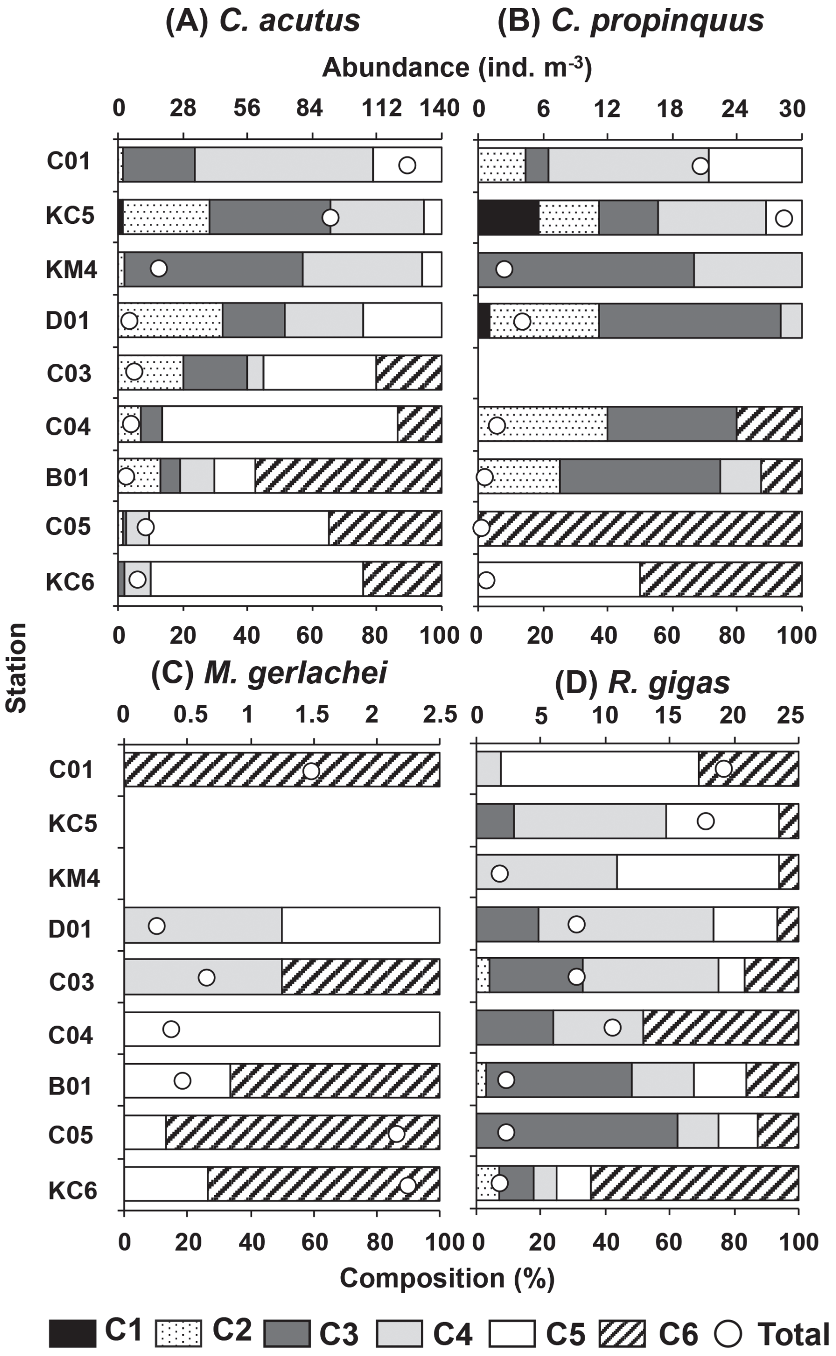

Fig. 7. Meridional changes in stage composition for the dominant four copepods on abundance along the 110°E in the Indian sector of the Southern Ocean during January 2018.

showed the same results as those found in previous reports (e.g., Hosie et al., 2014) ; the most dominant species *C. acutus* changes to total zooplankton on abundance.

Regarding the population structures of the dominant copepods (*C. acutus*, *C. propinnquus* and *R. gigas*), early copepodite stages were often observed in the northern stations, and late stages dominated in the southern stations. This meridional change was caused by the north–south temporal variation of phytoplankton blooms associated with sea–ice melt timing. This variation affected the reproduction period of these copepods, resulting in different population structures between the north and the south.

In conclusion, the front is the most important factor restricting on the zooplankton community. While, sea–ice extent is a significant driver to changing the population structure for copepods in the Indian sector of the Southern Ocean during the austral summer.

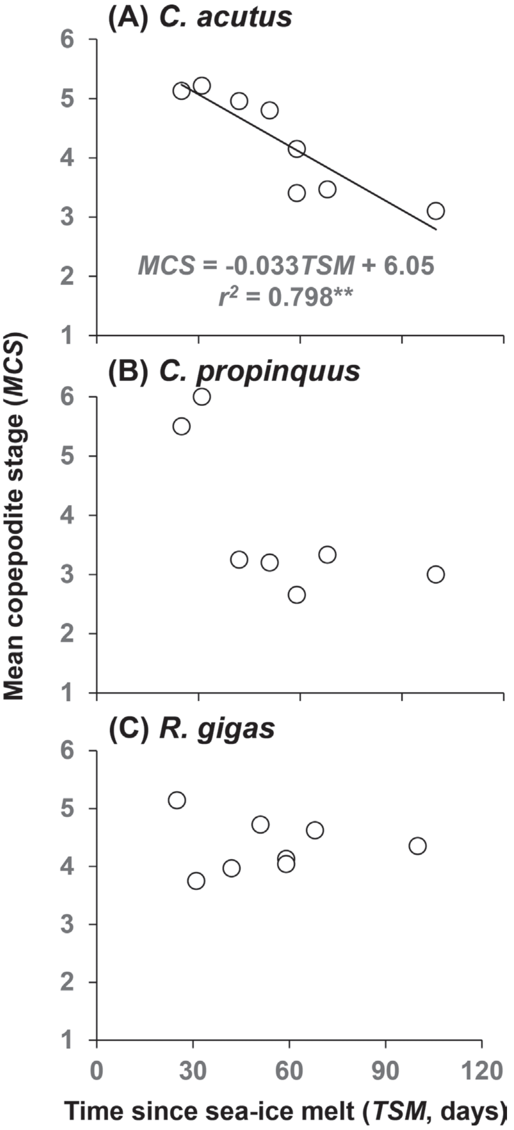

Fig. 8. The relationships between mean copepodite stage (MCS) for dominant copepods and time since sea-ice melt (TSM) along the 110°E in the Indian sector of the Southern Ocean during January 2018. ** : $p < 0.01$

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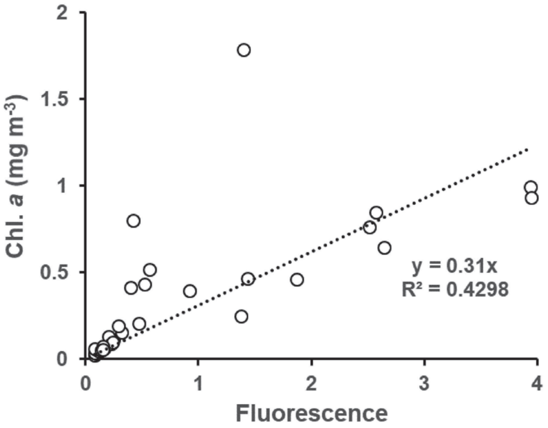

Appendix 1. The relationship between measured chlorophyll *a* concentration and *in-situ* fluorescence.