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Short-term changes in the population structure of hydromedusa *Aglantha digitale* during the spring phytoplankton bloom in the Oyashio region

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Abstract

To evaluate the effects of water mass changes and the spring phytoplankton bloom, we analysed short-term changes in the population structure of the dominant hydromedusa *Aglantha digitale* in the Oyashio region during March–April 2007. Samples were collected with Bongo nets at night via oblique towing from a depth of 200 m to the surface on eight occasions in March and April of 2007. The abundance, biomass and mature individual compositions of *A. digitale* rapidly increased from April onward. During April, the reproduction and growth of *A. digitale* is achieved due to the initiation of the spring phytoplankton bloom and the increase in small copepods. Based on dry mass, the growth rate of *A. digitale* ($1.3\% \text{ day}^{-1}$) was lower than the reported maximum value ($4.9\% \text{ day}^{-1}$) for this species. The rapid exchange of the dominant water masses was also observed during spring in the Oyashio region. Significant effects of water mass exchange were detected in the abundance, biomass and body sizes of *A. digitale*. Thus, the abundance, biomass and population structure of *A. digitale* in the Oyashio region may be altered during spring by two factors: internal growth and external water mass exchange.

Key words: spring bloom, hydromedusae, water mass, growth rate

Introduction

The holoplanktonic hydromedusa *Aglantha digitale* is a cosmopolitan species that dominates in both the oceanic and neritic high-latitude areas of the high latitude of the Northern Hemisphere (Kramp, 1965). *A. digitale* is known to be carnivorous and feeds primarily on copepods and chaetognaths. Small-sized juveniles (<4–5 mm bell height) are known to feed on micro-sized plankton such as diatom or ciliates (Smedstad, 1972; Williams and Conway, 1981; Pagès et al., 1996). In the North Atlantic Ocean, *A. digitale* has been reported to be selectively preyed on by the Atlantic mackerel *Scomber scombrus* (Runge et al., 1987). These findings suggest that *A. digitale* has a vital role that connects the primary producers and pelagic fishes. The life histories of *A. digitale* have been studied in various regions in the Northern Hemisphere from (Russell, 1938; McLaren, 1969; Smedstad, 1972; Arai and Fulton, 1973; Williams and Conway, 1981; Fulton et al., 1982; Ikeda and Imamura, 1996; Takahashi and Ikeda, 2006; Hosia and Båmstedt, 2007) and are known to be altered by water temperature and food concentration.

In the Oyashio region of the western subarctic Pacific, dominant water masses with of different temperatures are switched at the surface layer within a short period during the spring (Kono and Sato, 2010). Simultaneously, a large phytoplankton bloom is known to occur at the surface layer, and nearly half of the annual primary production is concentrated during spring (Saito et al., 2002; Liu et al., 2004; Ikeda et al., 2008). These drastic changes in water temperature and food conditions are expected to strongly affect *A. digitale* population dynamics. Through the “Ocean Ecodynamics Comparison in the Subarctic Pacific” (OECOS) project that was organized by the North Pacific Marine Science Organizations (PICES), short-term changes in the population structure and vertical distribution of epi- and mesopelagic copepods during the spring phytoplankton bloom have been evaluated (Yamaguchi et al., 2010a, 2010b; Abe et al., 2012), but no information is available for the dominant jellyfish *A. digitale* during the same period. During the OECOS project, changes in the water mass were found to alter the amount of phytoplankton (Chl. *a*) (Kono and Sato, 2010). However, the effects of water mass changes and the phytoplankton bloom on *A. digitale* population remain unknown.

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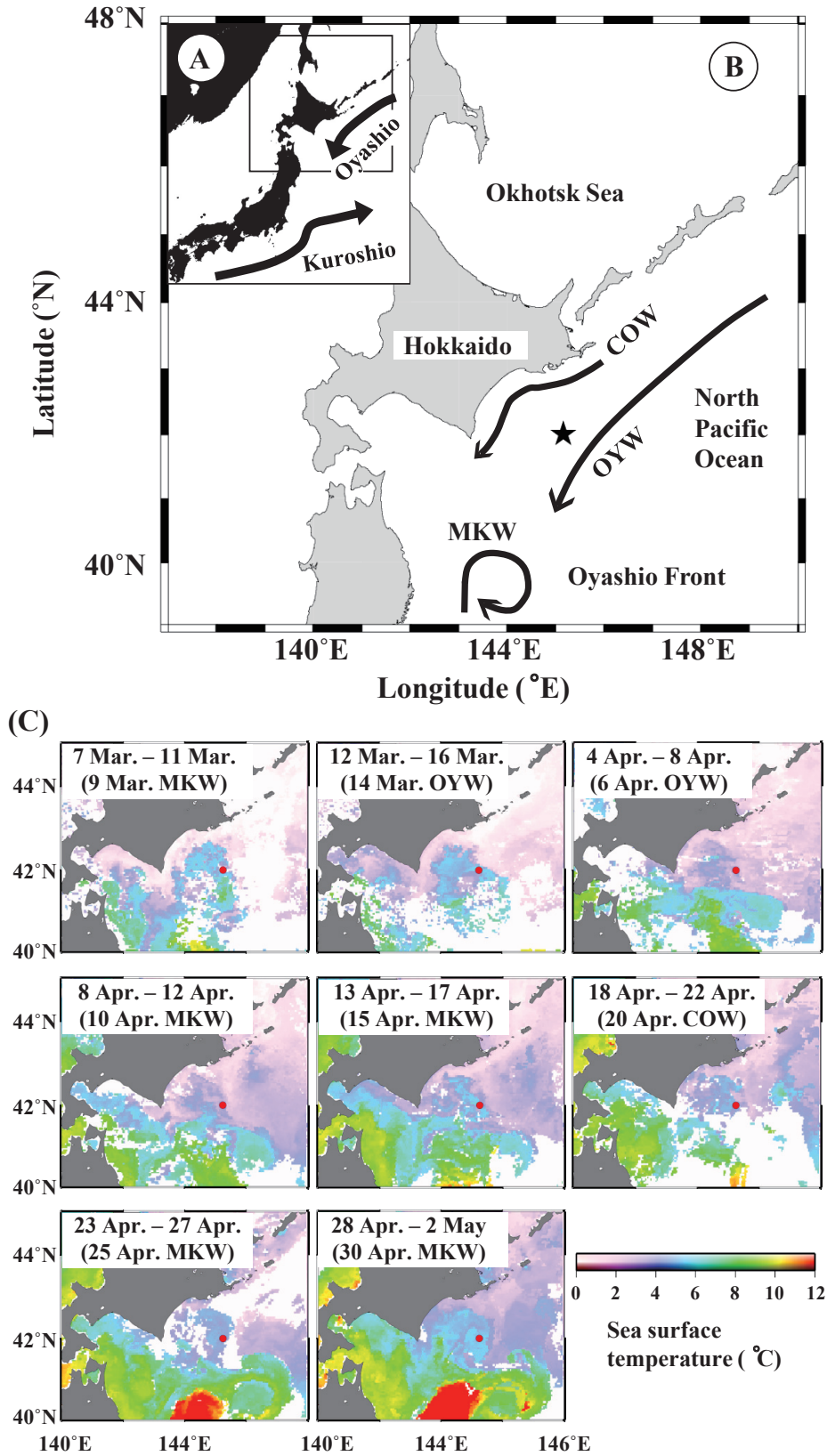


Fig. 1. Locations of the Oyashio region (A) and the sampling station (star) in the Oyashio region (B). For A and B, the approximate positions of the water masses are shown. Sea surface temperature at eight sampling dates as detected by satellite images (C). The temperature data are the means of five days around the sampling dates. The dominant water masses at each sampling date are shown with the following abbreviations : COW ; coastal Oyashio water, MKW ; mixed Kuroshio water, OYW ; Oyashio water.

As a part of the OECOS project, this study aimed to evaluate the short-term changes in the population structure of the dominant hydromedusa *A. digitale* in the Oyashio region during March and April of 2007. We analysed *A. digitale* from Bongo net samples that were collected from 0–200 m with 4- to 5-day intervals and evaluated the effects of water mass changes and the phytoplankton bloom on the *A. digitale* population.

Material and Methods

Field sampling

Samples were collected at a single station (42°00'N, 145°15'E, depth 4,000 m) in the Oyashio region of the western subarctic Pacific at night time (20 : 00–21 : 00 local time) on the 9th and 14th of March and the 6th, 10th, 15th, 20th, 25th and 30th of April 2007 (Fig. 1). Bongo nets (70 cm mouth diameter, 335 µm mesh size) were obliquely towed from a depth of 200 m to the surface (400 m wire out with 60° wire angle) at a speed of 2 knots. After collection, the zooplankton samples were preserved immediately in 5% borax-buffered formalin-seawater. The filtered water volumes were estimated from the readings of a flow-meter (Rigosha Co. Ltd.) mounted on net ring.

As environmental parameters, temperature, salinity and chlorophyll *a* (Chl. *a*) fluorescence were measured with CTDs (Sea Bird Electronics SBE-9 plus) cast at each sampling. Based on the temperature and salinity data, the mixing ratio of the three water masses (Coastal Oyashio Water : COW, Oyashio Water : OYW, modified Kuroshio Water : MKW) in 0–50 m water columns were calculated using the procedures of Kono and Sato (2010). Regarding the food conditioned, mesozooplankton wet mass (g WM m⁻²) data collected with NORPAC nets (0.335 mm mesh size, 45 cm diameter) from 0–150 m during the nights of the 9th–14th of March and the 6th of April to the 1st of May were analysed (Yamaguchi et al., 2010a).

Enumeration and measurement

The whole samples were examined in our land laboratory. *Aglantha digitale* were sorted and counted, and the results are expressed as abundance per m². Size measurements of the following three parts were made : bell height (BH), bell diameter (BD), and gonad length (GL). For all individuals, the sizes of the BH and BD parts were measured with an eyepiece micrometer with a precision of 0.5 mm, and the gonad lengths were measured with a precision of 0.05 mm. Based on the ratio of the GL to the BH, the *A. digitale* were separated into immature (GL/BH was <10%) and mature (GL/BH was ≥10%) groups according to gonad length (McLaren, 1969). Biomass (dry mass : DM, mg) was estimated from the BH (mm) using the following equation (Takahashi and Ikeda, 2006) :

$$\log_{10}DM = 0.454(\log_{10}BH)^2 + 1.883\log_{10}BH - 2.402 \quad (1)$$

From the biomass data, growth rates (G, % day⁻¹) were estimated using the following equation :

$$G = 100 \times (\ln [DM_{t_2} / DM_{t_1}]) / t \quad (2)$$

where DM_{t₂} and DM_{t₁} are the average biomasses (mg DM ind.⁻¹) on the 30th of April and the 14th of March, respectively, and t is the number of days (46 days) between the two sampling dates (Hosia and Båmstedt, 2007).

Statistical analyses

From the BH and BD data at each sampling date, cohort analyses were performed with the aid of the free software “R” and the add-on package “mclust”.

The *A. digitale* population parameters (i.e., abundance, biomass, composition of mature individuals and average BH of each cohort) were calculated for each sampling date, and correlation analyses between each parameter were conducted. The correlation analyses between the population parameters and the environmental parameters (i.e., the Julian day from the 1st of March, integrated mean temperatures and salinities, water mass mixing ratios in 0–50 m water columns, Chl. *a* and zooplankton biomass at 0–150 m water column) were also performed.

Results

Hydrography

The changes in temperature, salinity, Chl. *a*, water mass conditions in 0–50 m water columns and mesozooplankton biomass in 0–150 m water columns from the 8th of March to the 1st of May 2007 are shown in Fig. 2. During this period, the temperature and salinity varied between 2 and 6°C and 33.2 and 34.2, respectively (Fig. 2A, B). Chl. *a* had three peaks (1–6 mg m⁻³) that occurred on the 7th, 11th and 23rd of April (Fig. 2C). During March, the OYW and MKW each composed nearly half of the 0–50 m water column. Cold COW occurred beginning in April, and the timings of these occurrences were consistent with the Chl. *a* peaks mentioned above. For the eight Bongo net samplings, the dominant water masses were COW on the 20th of April, OYW on the 14th of March and the 4th of April and MKW on the 9th of March and the 10th, 15th, 25th and 30th of April (Fig. 2D). Occurrences of clockwise warm water eddies were detected from satellite images (Fig. 1C). The dominant warm water eddy was found to be MKW during the OECOS project. Mesozooplankton biomass varied from 13.2 to 93.9 g WM m⁻², was lower during March, and increased from the 10th of April onward (Fig. 2E).

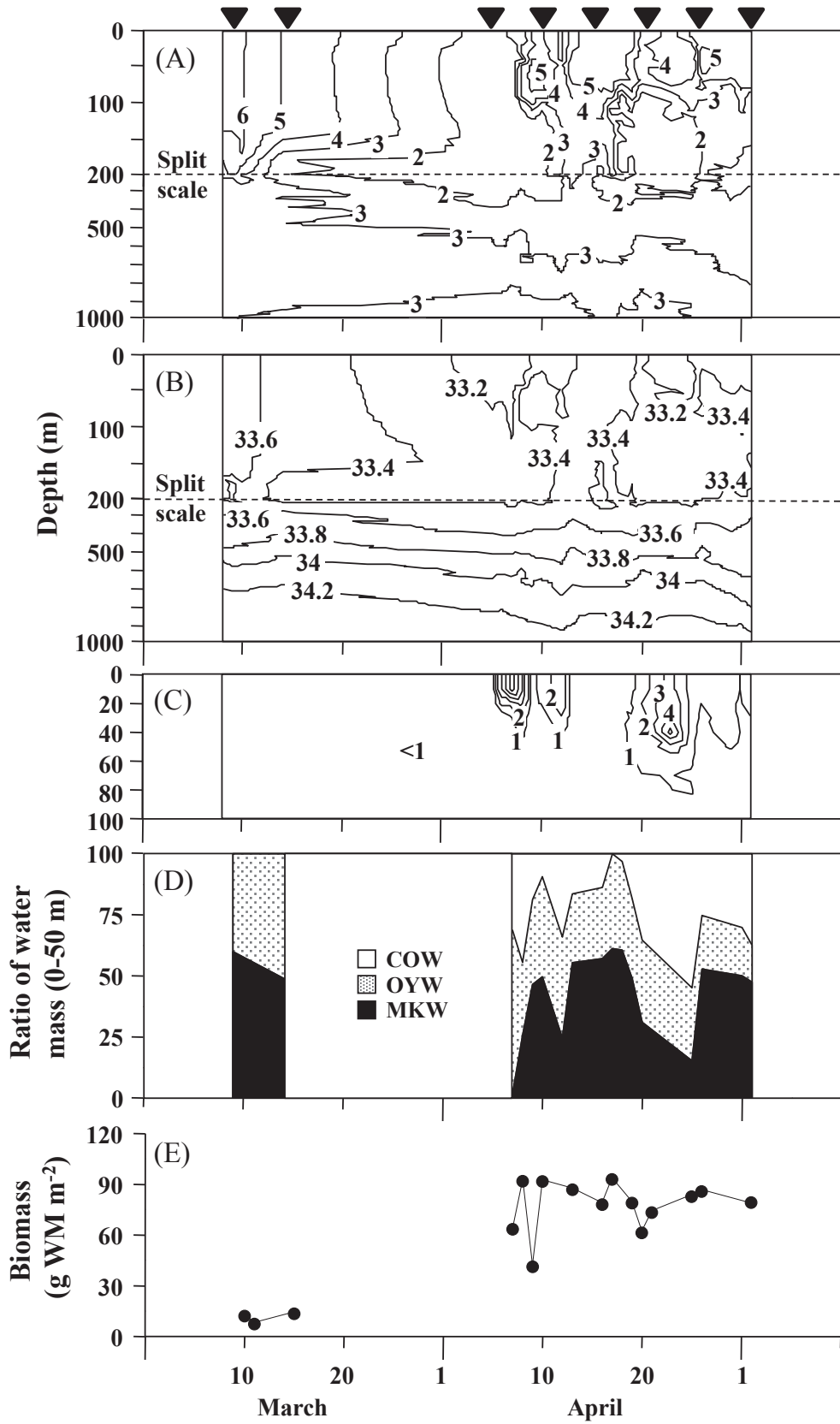


Fig. 2. Temporal changes in temperature (A, °C), salinity (B), chlorophyll *a* (C, mg m⁻³), the ratio of water mass at 0-50 m (D, %) and mesozooplankton wet mass at 0-150 m (E, mg WM m⁻²) in the Oyashio region between the 9th of March to the 1st of May 2007. Data in D and E are from Kono and Sato (2010) and Yamaguchi et al. (2010a), respectively. COW ; coastal Oyashio water, MKW ; mixed Kuroshio water, OYW ; Oyashio water.

Abundance and biomass

The abundance of *A. digitale* varied between 16 and 316 ind. m⁻² (mean : 115 ind. m⁻²) during the sampling period (Fig. 3). The biomass varied between 0.02 and 0.39 g DM m⁻² (mean : 0.12 g DM m⁻²). Both abundance and biomass were low during March but rapidly increased from April onward. Mature individuals composed 8 to 49% of the total abundance. The composition of mature individuals was low (<8.3%) from the 9th of March to the 10th of April and increased rapidly (>30%) after the 15th of April.

Body size and growth rate

The BHs of the *A. digitale* varied from 4–18 mm (Fig. 4). Cohort analysis revealed two cohorts (large and small BH cohorts) that were present throughout the sampling period. The mean BH of the small- and large-sized cohorts varied between 6.2–9.1 mm and 10.5–13.1 mm, respectively. The small- and large-sized cohorts composed 24–52% and 48–76% of the total abundance, respectively. For most of the sampling date, the abundance of the large-sized cohort was greater than that of the small-sized cohort. Interestingly, the temporal patterns of changes in the mean BHs of the small- and large-sized cohort were synchronized (Fig. 5). The temporal changes in the mean BHs corresponded to the changes in the water masses. The large BH was predominant in the periods dominated by MKW (Fig. 5). Individual dry masses were estimated from the mean BHs of each

cohort, and the small- and large-sized cohorts were 0.42–0.53 mg DM ind.⁻¹ and 1.42–1.87 mg DM ind.⁻¹, respectively. From these DM data, the growth rate was estimated as 1.33% day⁻¹ during the study period.

Correlations between each parameter

The correlation analyses of the population parameters of *A. digitale* (i.e., abundance, biomass, mature individual composition and mean BHs of the small- and large-sized cohorts) revealed three significant positive correlations among the parameters : abundance and biomass, mean BH of the large-sized cohort and mature individual composition, and the mean BH of the small-sized cohort and the mean BH of the large-sized cohort (Fig. 6).

The correlation analyses of the population parameters of *A. digitale* and the environmental parameters revealed six significant correlations (Table 1). Positive correlations were observed between Julian day and biomass, between Julian day and mature individual composition, between COW ratio and abundance, and between COW ratio and biomass. Negative correlations were observed between OYW ratio and the mature individual composition and between the OYW ratio and the mean BH of the large-sized cohort.

Discussion

Abundance and biomass

The abundance of *A. digitale* observed in this study

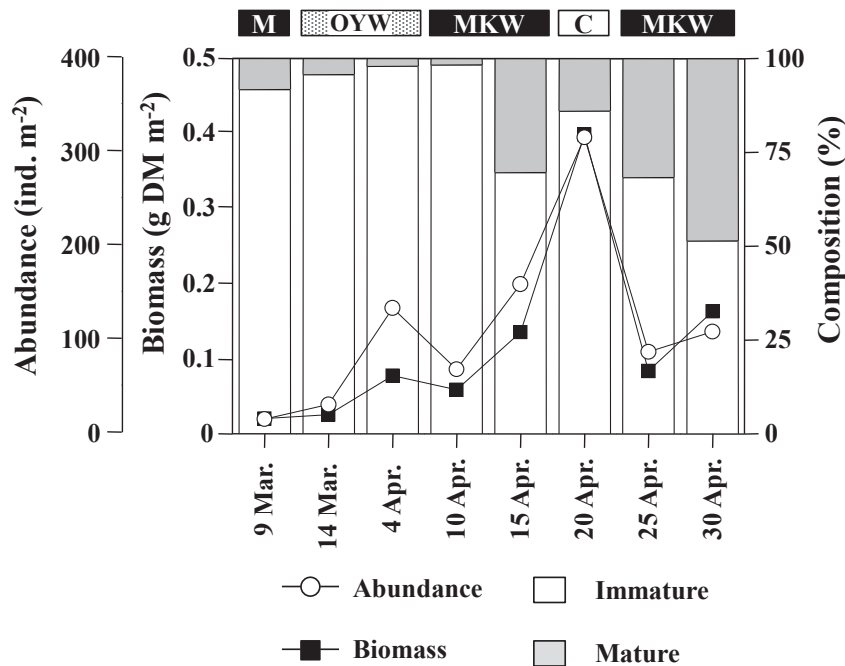


Fig. 3. Temporal changes in the abundance, biomass and population structure (immature/mature composition in abundance) of *Aglantha digitale* in the Oyashio region from the 9th of March to the 1st of May 2007. The dominant water masses at each sampling date are shown by the upper bars. C ; coastal Oyashio water, MKW ; mixed Kuroshio water, OYW ; Oyashio water.

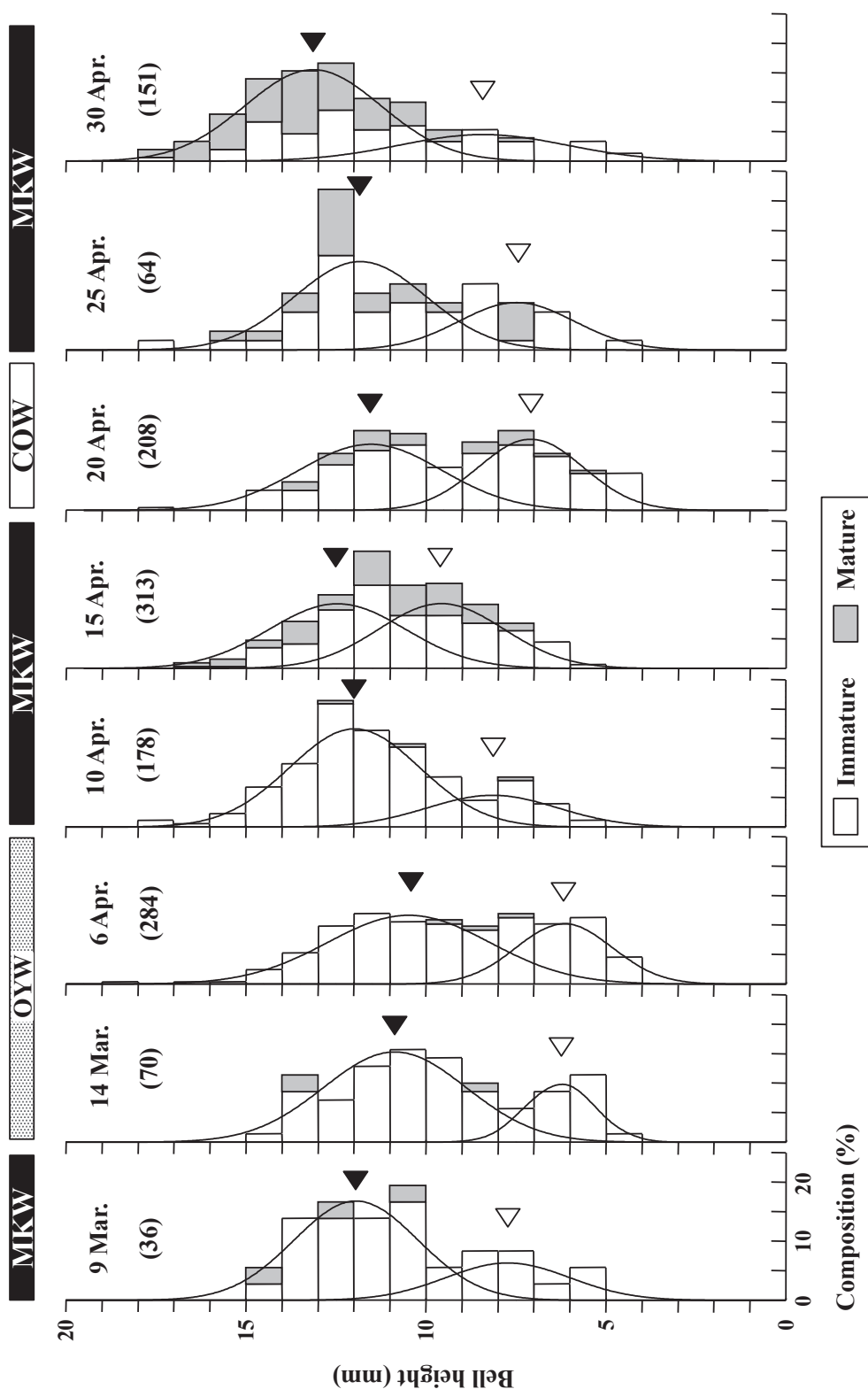


Fig. 4. Temporal changes in the bell heights compositions of *Aglantha digitale* in the Oyashio region from the 9th of March to the 1st of May 2007. Cohort analysis identified two cohorts for each date, and the means of these cohorts are shown with open (small cohort) and solid (large cohort) triangles. The numbers in the parentheses are individual measurements. The dominant water masses at each sampling date are shown by the upper bars. COW ; coastal Oyashio water, MKW ; mixed Kuroshio water, OYW ; Oyashio water.

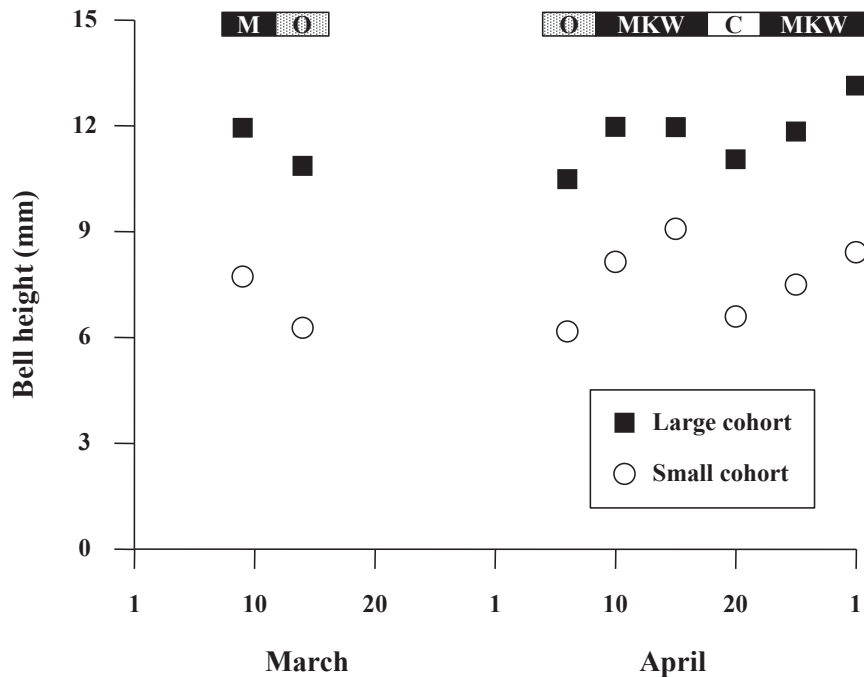


Fig. 5. Temporal changes in the mean bell heights of the small and large cohorts of *Aglantha digitale* identified from Fig. 4. The individual dry masses (mg DM ind.⁻¹) were estimated from the bell heights of each cohort. The dominant water masses at each sampling date are shown by the upper bars. C ; coastal Oyashio water, MKW ; mixed Kuroshio water, O ; Oyashio water.

(mean : 115 ind. m⁻², 0-200 m) corresponds well to that of a previous report in this region (100-150 ind. m⁻², 0-250 m, March-April 1997, Takahashi and Ikeda, 2006). However, the biomass of *A. digitale* observed in this study (mean : 0.12 g DM m⁻²) is greater than that of the previous study (<0.1 g DM m⁻², Takahashi and Ikeda, 2006). Differences in sampling methods between the two studies may be responsible for this discrepancy in the observed biomasses. For example, this study collected samples via the oblique towing of Bongo nets with large mouth areas, while Takahashi and Ikeda (2006) collected samples via vertical towing of Gama-guchi nets with small mouth areas. Because of the large filtered volumes (435-773 m³ for the former technique and 14-283 m³ for the latter), the previous study may not have obtained accurate population structures. Consequently, the mean BH of this study (9.0-11.8 mm) was greater than that of the previous study (8-10 mm, Takahashi and Ikeda, 2006), and the bimodal distribution of BHs found in this study was not detected in the study of Takahashi and Ikeda (2006) (only a small BH cohort was examined in this study). Bimodal distributions of *A. digitale* BHs have been reported in various region (Hosia and Båmstedt, 2007 ; Saito et al., 2012 ; Shio-ta et al., 2013).

In the Oyashio region, *A. digitale* has been reported to have a one-year generation length with a reproductive peak during June and August (Takahashi and Ikeda, 2006). Based on this information, the recruitments of the large- and small-sized BH populations of this study likely occurred during

spring to summer and late summer to autumn of the previous year, respectively. Population recruitments of *A. digitale* in the Nordic fjord and North Sea have been to occur during spring, and these populations mature and reproduce at small sizes during the summer when temperatures and food concentrations are high ; the remaining population overwinter with at large sizes (Pertsova et al., 2006 ; Hosia and Båmstedt, 2007). To evaluate the life cycle of *A. digitale* in the Oyashio region in detail, seasonal samples collected with large mouth nets similar to those used in this study (i.e., Bongo nets) over years are needed in the future.

Growth of *A. digitale*

Positive correlations were observed between Julian day and biomass, and between Julian day and mature individual composition (Table 1). These findings may reflect of the growth of *A. digitale* during the study period of March to April. The food items of *A. digitale* have been reported to be copepod nauplii (66%), copepodids (15%), adult (11%) and eggs (5%) (Costello and Colin, 2002). Another study also reported that 71% of the gut contents of *A. digitale* were composed of copepod nauplii (Mills, 1981). In the present study, the biomass of mesozooplankton, a major food item of *A. digitale*, increased rapidly from April onward (Fig. 2E). The high levels of mesozooplankton biomass that occur during April may provide favourable food condition for *A. digitale* and may induce rapid growth rates at this time. The BH of the large-sized cohort and the mature individual composition

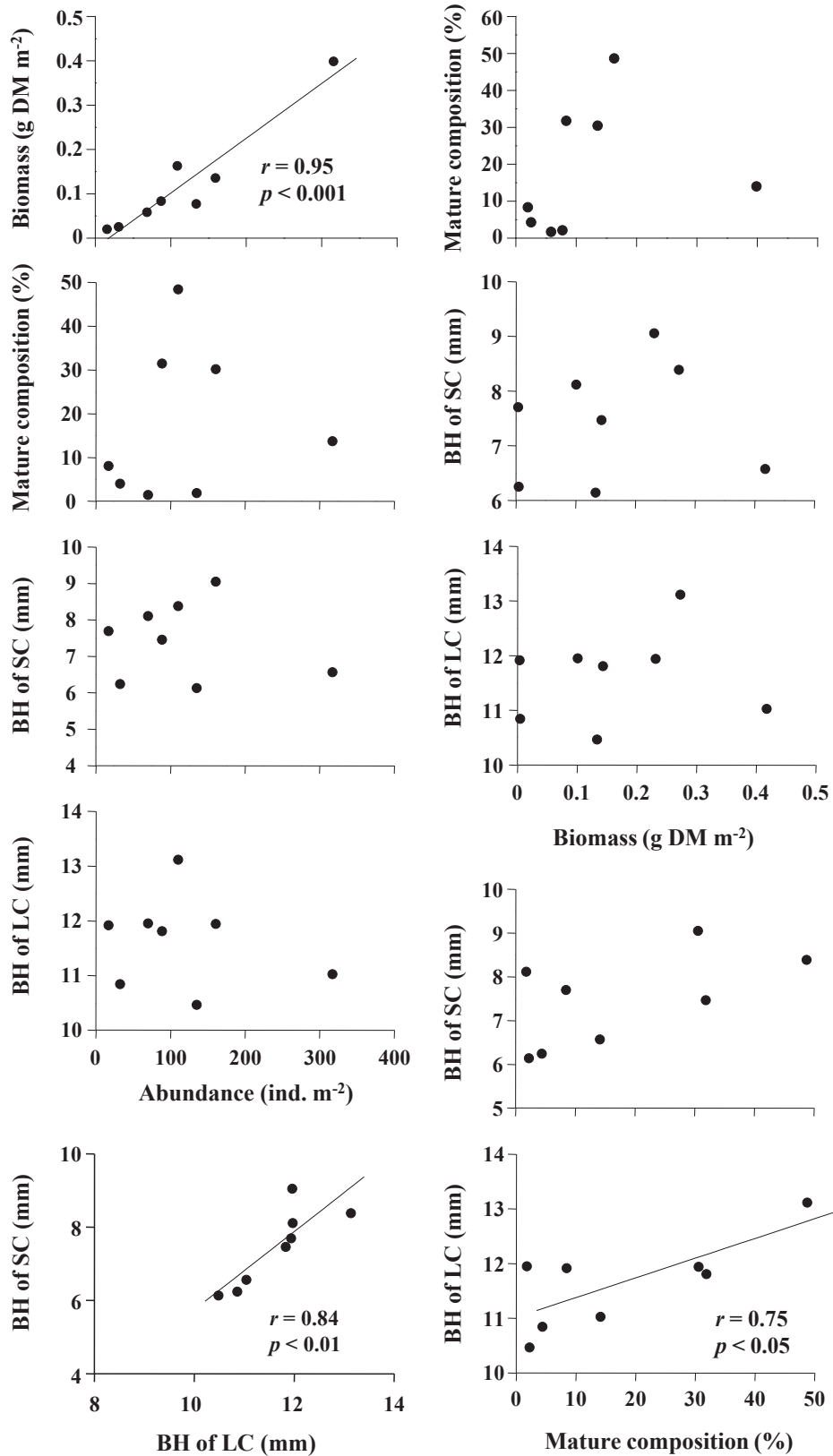


Fig. 6. Correlation analysis of the population parameters (abundance, biomass, mature composition, and bell heights [BH] of the small [SC] and large cohorts [LC] of *Aglantha digitale* in the Oyashio region between the 9th of March and the 1st of May 2007. Significant correlations are indicated by the regression lines.

Table 1. Correlation coefficient (r) between environmental parameters (Julian day, integrated mean temperature, salinity, mixture ratio of water mass, chlorophyll a and mesozooplankton wet mass) and population parameters of *Aglantha digitale* (abundance, biomass, composition of mature specimen, modal bell height [BH] of each cohort) in the Oyashio region during March–April 2007. COW : coastal Oyashio water, OYW : Oyashio water, MKW : modified Kuroshio Water. For details of mixture ratio of water mass, see Kono and Sato (2010). * : $p < 0.05$, ** : $p < 0.01$.

Environmental parameter	<i>Aglantha digitale</i> (0–200 m)				
	Abundance	Biomass	Mature composition	BH of small cohort	BH of large cohort
Julian day	0.563	0.734*	0.696*	0.409	0.343
Temperature (0–50 m)	–0.352	–0.188	0.098	0.567	0.521
Salinity (0–50 m)	–0.446	–0.401	–0.139	0.398	0.521
COW ratio of water mass (0–50 m)	0.735*	0.742*	0.4134	–0.094	–0.009
OYW ratio of water mass (0–50 m)	–0.236	–0.653	–0.854*	–0.667	–0.767*
MKW ratio of water mass (0–50 m)	–0.472	–0.083	0.316	0.623	0.627
Chlorophyll a (0–150 m)	0.524	0.387	–0.038	–0.326	–0.360
Mesozooplankton wet mass (0–150 m)	0.438	0.588	0.211	0.113	0.022

were correlated (Fig. 6). These findings suggest that both growth and maturation may primarily be supported by the same factor (i.e., food concentration). The favourable food conditions produced by the massive reproduction of epipelagic large grazing copepods (i.e., *Eucalanus bungii*, *Metridia pacifica*, and *M. okhotensis*) that occurs in mid-April and is initiated by the spring phytoplankton bloom (Yamaguchi et al., 2010a) may support the maturation of *A. digitale* in this period (Fig. 3).

Based on the DMs, the growth rate of *A. digitale* in this study ($1.3\% \text{ day}^{-1}$) was lower than the value that has been reported for the Nordic fjord ($4.9\% \text{ day}^{-1}$) (Hosia and Båmstedt, 2007). Across various regions, the growth of *A. digitale* has been reported to be faster when temperatures are high (i.e., during the summer) (Takahashi and Ikeda, 2006 ; Hosia and Båmstedt, 2007 ; Prudkovsky, 2013). Because the temperatures observed in this study were fairly low ($2\text{--}6^\circ\text{C}$) (Fig. 2B), the growth rate of *A. digitale* was expected to be low due to these low temperatures.

The ingestion rates of *A. digitale* have been reported to be $1.0\text{--}4.5$ copepods $\text{ind.}^{-1} \text{ day}^{-1}$ in the Nordic fjord and 5.9 ± 3.6 copepods $\text{ind.}^{-1} \text{ day}^{-1}$ in the North Sea (Pagès et al., 1996 ; Prudkovsky, 2013). Assuming that *A. digitale* in the Oyashio region has the same ingestion rate, we estimate that they consumed 0.15 (9 March)– 1.08% (20 April) of the small-sized copepods during the study period. Thus, *A. digitale* may have moderate effects on the copepod community structure in the Oyashio region during spring.

Effect of water mass exchange

During spring in the Oyashio region the exchange of dominant water masses at the surface layer over short periods is a common phenomenon, and a high Chl. a was observed during the COW-dominated period during the OECOS project

(Kono and Sato, 2010). If *A. digitale* also have such water-mass specific differences in abundance and body size, their characteristics may be maintained longer and more clearly than those of Chl. a because of generation length of *A. digitale* is longer than that of the phytoplankton. Indeed, the abundance and biomass of *A. digitale* were high in the COW, and the mature individual composition and BH of the large-sized cohort were low in the OYW (Table 1). The BHs of both the large-sized and small-sized cohorts were large during the MKW-dominated period (Fig. 5). Regarding the BHs, the close correlation between the BH of the small-sized cohort and the BH of the large-sized cohort (Fig. 6) suggests that the environmental parameters regulating the growth of each cohort are the same. Large BHs were observed in both cohorts under MKW conditions (Fig. 5), and two factor may have caused this observation : (1) faster growth in high temperatures in the MKW, and (2) the phenology at the MKW was faster than that of the other area because of the high temperatures. While quantitative evaluations of each factor are difficult, these two factors may have occurred for the *A. digitale* in the MKW condition. Due to their combined effect, the BH of *A. digitale* in the MKW may larger than that in other water masses.

The observations of high *A. digitale* abundance and biomass in the low-temperature COW are interesting (Table 1). Abundance and biomass were highly correlated (Fig. 6). Two factors should be considered as possible causes of the high abundance of *A. digitale* in the low-temperature COW : (1) because reproduction occurred near the sampling date, a high abundance was observed (bottom-up) or (2) low predation pressure from the fish in the COW resulted in the high abundance (top-down). In the present study, differences in the temperature conditions of the water masses ranged from $<2^\circ\text{C}$ to 6°C (Fig. 2A). These large differences in tempera-

ture may have been sufficient to alter the timing of reproduction, which known to vary with water masses (Takahashi and Ikeda, 2006). As mentioned above, large BHs were observed in the high-temperature MKW (Fig. 5). These large BHs indicate that reproduction occurred much earlier for the population in the MKW. However, in the COW, reproduction may have occurred just prior to the sampling dates, and this late reproduction in the COW may have induced the high abundance and biomass of *A. digitale* in this water mass during the spring.

Alternatively, differences in fish predation across the water masses should also be considered. Epipelagic fish (i.e., mackerel, sardines, and Pacific saury) are important zooplankton predators in the neighbouring waters of Japan and are known to reproduce in subtropical areas (Kuroshio water) during winter-spring (Watanabe et al., 2003; Watanabe, 2009, 2010). *A. digitale* has been reported to be an important food item for Atlantic mackerel (Runge et al., 1987). These findings suggest that the fish predation pressure on the *A. digitale* population during winter-spring was high in the warm MKW. Due to the low fish predation pressure in the low-temperature COW during winter-spring, the abundance and biomass of *A. digitale* are expected to be high at this time in these waters.

Conclusion

During spring in the Oyashio region, rapid exchanges of the dominant water occurred. Due to the intrusion of the COW, the spring phytoplankton bloom began and stimulated increases in zooplankton biomass. Due to the favourable food conditions, the reproduction and growth of *A. digitale* occurred at this time. High food abundance may accelerate the growth of *A. digitale* during spring, and due to the low-temperature conditions, their growth rate was moderate, and the predation pressure on the copepod population was likely modest. The effects of water mass exchanges on the *A. digitale* population include water-mass specific reproduction timing and fish predation pressure. These two factors are related to phenology, which was altered by the water-mass specific temperature conditions. The abundance, biomass and population structure of *A. digitale* in the Oyashio region during the spring may be affected by two factors: internal growth and the external water mass exchange effect.

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