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Title	Geographical variations in abundance and body size of the hydromedusa Aglantha digitale in the northern North Pacific and its adjacent seas
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Citation	北海道大学水産科学研究彙報, 62(3), 63-69
Issue Date	2012-12-14
Doc URL	https://hdl.handle.net/2115/51114
Type	departmental bulletin paper
File Information	62(3)p63-69.pdf

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Bull. Fish. Sci. Hokkaido Univ.
62(3), 63–69, 2012.

Geographical variations in abundance and body size of the hydromedusa *Aglantha digitale* in the northern North Pacific and its adjacent seas

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(Received 20 August 2012, Accepted 11 September 2012)

Abstract

Geographical variations in abundance and body size of the hydromedusa *Aglantha digitale* (O.F. Müller, 1766) were evaluated in the northern North Pacific (NP), the water around Aleutian Islands (AL), eastern Bering Sea shelf (BS) and Chukchi Sea (CH) during the summers of 2007 and 2008. Abundances of *A. digitale* ranged between 38 and 221 ind. m^{-2}, and had significant inverse relationships with the proportion of mature individuals. While abundances showed large annual variability, body sizes had a common regional pattern both 2007 and 2008. Body size and minimum size of maturity *A. digitale* were smaller in the BS and CH than those in the NP and AL. The smaller size at maturity in the BS and CH suggests regional variations in the acquired energy budget. The rapid maturity and reproduction in the BS and CH may indicate that they utilize acquired energy to mature and reproduce from smaller body sizes, while slow maturity in the NP and AL may imply that they convert acquired energy to somatic growth first.

Key words : *Aglantha digitale*, jellyfish, abundance, body size, geographical variation

Introduction

Jellyfish, belonging to the phylum Cnidaria, are planktonic taxa distributed throughout the world's oceans. Recently, incidents of massive blooms of large-size jellyfish (e.g. *Nemopilema nomurai* and *Chrysaora melanaster*) have had serious negative impacts on fisheries in various locations around the world (Purcell et al., 2007). Many studies were made on the biology and ecology of these scyphozoan jellyfishes (Kramp, 1959, 1961 ; Russell, 1953, 1970 ; Fraser, 1972 ; Brodeur et al., 2002). However, relatively little information is available on the biology and ecology of small oceanic jellyfish.

The hydromedusa *Aglantha digitale* (O.F. Müller, 1766) is a holoplanktonic jellyfish without a benthic polyp phase and is a cosmopolitan species in oceanic and neritic high latitude seas of the Northern Hemisphere (Kramp, 1965). Large individuals of this species are carnivorous and mainly feed on copepods and chaetognaths, while small juveniles feed on microplankton such as diatoms or ciliates (Smedstad, 1972 ; Williams and Conway, 1981 ; Pagès et al., 1996). *Aglantha digitale* has been reported to be selectively preyed upon by the Atlantic mackerel *Scomber scombrus* in the North Atlantic (Runge et al., 1987). This suggests that *A. digitale* fills a vital role between primary production and fish production.

The life history of *A. digitale* has been studied in various locations of the Northern Hemisphere (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). Because the geographical distribution of *A. digitale* is wide (North Pacific, North Atlantic, Arctic Ocean and their marginal seas), their abundance and body size are expected to have large geographical variations. However, no previous studies address these expected variations based on samples collected from a broad geographical distribution area.

The aim of this study is to reveal geographical changes in abundance and body size of *A. digitale* based on plankton samples collected in the northern North Pacific, the water around Aleutian Islands, the eastern Bering Sea shelf and Chukchi Sea during the summers of 2007 and 2008. The primary causes of geographical differences in abundance and body size are discussed.

Materials and Methods

Field sampling

Oceanographic observations and zooplankton sampling were conducted at 211 stations (104 stations in 2007 and 107 stations in 2008) in the northern North Pacific, the water around the Aleutian Islands, the eastern Bering Sea shelf and

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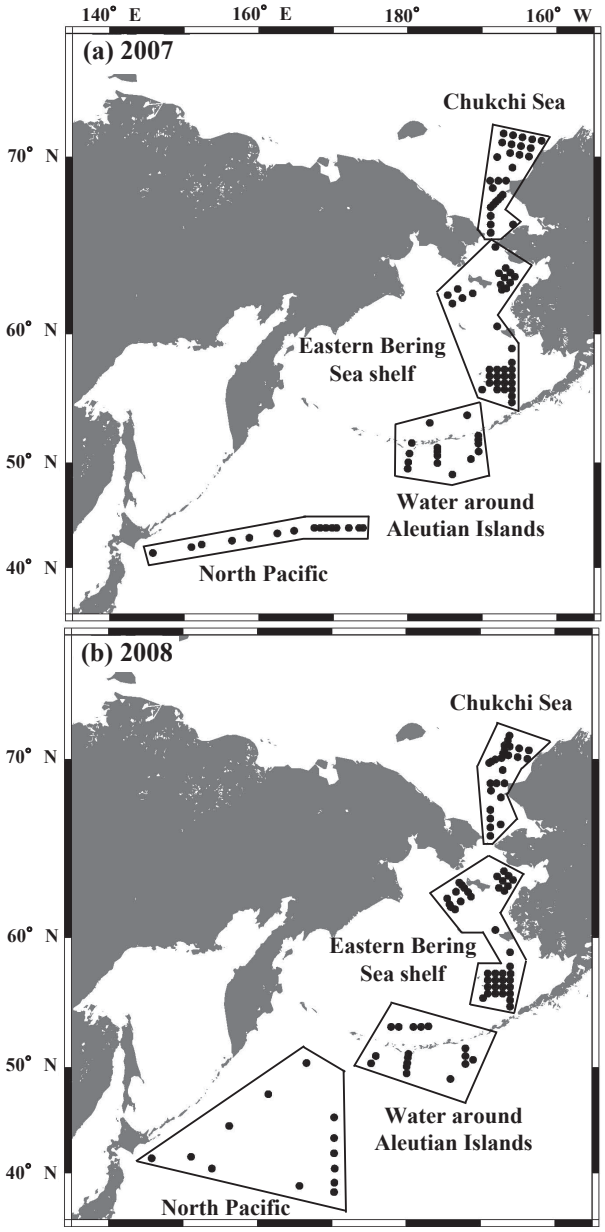

Fig. 1. Location of sampling stations during July to August 2007 (a) and June to July 2008 (b).
Four groups of sampling stations are indicated for regional comparison : North Pacific (NP), the water around Aleutian Islands (AL), eastern Bering Sea shelf (BS) and Chukchi Sea (CH).

Chukchi Sea during 2 July to 13 August 2007 and 3 June to 13 July 2008 (Fig. 1). The sampling period was one month earlier in 2008 than in 2007. Zooplankton samples were collected by vertical hauls of a 0.10-mm-mesh size NORPAC net (Motoda, 1957) from 150 m, or 5 m above bottom at stations where the depth was less than 150 m. The volume of water filtered was calculated from counts of a flowmeter (Rigosha Co., Ltd.) mounted on the net ring. Samples were immediately preserved with 5% borax-buffered formalin sea water. At each station, vertical profiles of temperature and salinity were measured with a CTD (Sea-Bird Electronics, Inc., CTD-SBE9plus).

Enumeration and measurement

In the land laboratory, zooplankton samples were examined under magnification of a dissecting microscope. *Aglantha digitale* was sorted, counted, and abundances quantified as number of individuals per m^2. For all individuals, bell height (BH) and gonad length (GL) were measured with the precision of 0.025-1 mm. Based on the ratio of GL to BH, gonad development of *A. digitale* was assigned as immature (GL/BH < 10%) or mature (GL/BH >10%) (McLaren, 1969). Maturity composition was calculated the proportion of mature individuals to the total number of *A. digitale*. For specimens damaged during net collection or formalin preservation (< 4% of the total number), only size measurements were made and the jellyfish were not included maturity composition calculation.

For regional comparison, sampling stations were divided into four regions : North Pacific (NP), the water around Aleutian Islands (AL), eastern Bering Sea shelf (BS) and Chukchi Sea (CH) (Fig. 1). For each region, body size data were converted to histograms, which were separated into one to several normal curve cohorts using Microsoft Excel Solver (Aizawa and Takiguchi, 1999).

Results

Abundance

Mean abundance of *A. digitale* during July to August 2007 ranged between 38 and 221 ind. m^{-2}, and was greater in the BS (mean : 220 ind. m^{-2}) and CH (mean : 126 ind. m^{-2}) than in the NP (38 ind. m^{-2}) and AL (64 ind. m^{-2}) ($p < 0.05$, one-way ANOVA, Fisher's PLSD, Table 1). Common to the all regions examined, *A. digitale* occurred at approximately two-thirds of the stations. Mature individuals composed 34-47% of all individuals and there was little regional difference in 2007.

During June to July 2008, mean abundance was greater in the NP and AL (161-167 ind. m^{-2}) than in the BS and CH (33-46 ind. m^{-2}) ($p < 0.0001$, one-way ANOVA, Fisher's PLSD, Table 1). This regional pattern of abundance in 2008 was opposite to that in 2007. A smaller proportion of mature individuals was collected in the NP and AL (27-46%), while this proportion was substantially larger in the BS and CH (67-84%) (Table 1).

During July to August 2007, the relative frequency of abundance showed several stations over 200 ind. m^{-2} in the BS and CH, while almost all stations had < 100 ind. m^{-2} in the NP and AL (Fig. 2a). Regional trends in abundance during June to July 2008 were opposite to those observed in 2007. Thus in 2008, > 200 ind. m^{-2} were observed at several stations in the NP and AL and almost all stations had < 100

Table 1. Regional comparison of mean abundance (mean ± sd.), number of stations (occurred/total) and cumulative maturity composition of *Aglantha digitale* in the North Pacific (NP), Aleutian Islands (AL), Bering Sea shelf (BS) and Chukchi Sea (CH) during July to August 2007 and June to July 2008. Differences in abundance were tested by oneway ANOVA followed by a post-hoc test by Fisher's PLSD, and the results were shown by letters in parentheses. The same letter indicates no significant differences between regions.

	NP	AL	BS	CH
2007				
Mean abundance (ind. m^{-2})	$38.4 \pm 44.0^{(a)}$	$64.4 \pm 79.4^{(a)}$	$220.5 \pm 230.9^{(b)}$	$126.4 \pm 154.9^{(a,b)}$
Station number (occurred/total)	12/21	10/16	27/36	21/31
Maturity composition (%)	46.8	40.0	33.8	42.6
2008				
Mean abundance (ind. m^{-2})	$167.1 \pm 112.4^{(a)}$	$160.6 \pm 178.0^{(a)}$	$32.7 \pm 15.2^{(b)}$	$45.9 \pm 37.7^{(b)}$
Station number (occurred/total)	12/19	15/18	22/41	22/29
Maturity composition (%)	26.5	45.9	67.4	83.8

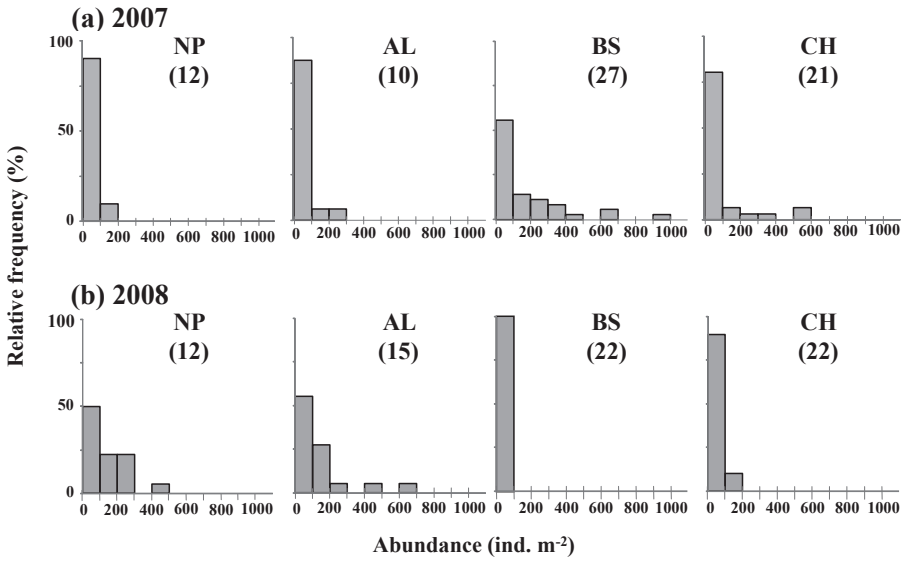

Fig. 2. Relative frequency in standing stock of *Aglantha digitale* in the North Pacific (NP), the water around Aleutian islands (AL), eastern Bering Sea shelf (BS) and Chukchi Sea (CH) during July to August 2007 (a) and June to July 2008 (b). Numbers in parentheses indicate numbers of stations.

ind. m^{-2} in the BS and CH (Fig. 2b).

Body size

Bell height of *A. digitale* ranged between 0.6 and 17.0 mm and showed two small cohorts in the NP and AL but only one small cohort in the BS and CH (Fig. 3). These regional differences in bell height were common in both 2007 and 2008. Mean bell heights of immature and mature individuals ranged between 2.5–7.7 mm and 4.2–13.0 mm, respectively. Mean bell heights of both immature and mature individuals were larger in the NP and AL than in BS and CH.

Gonad lengths ranged between 0.1–7.4 mm (Fig. 3). The gonad length showed mostly one cohort, except for the NP and AL in 2007. Mean gonad length of immature and mature individuals was larger in the NP and AL than in the BS and CH in 2007. In contrast, the mean size of mature individuals in 2008 was larger in the BS and CH than in the NP and AL.

Discussion

Geographic trends in abundance of *A. digitale* varied with year : abundance was greater in the BS and CH during July and August 2007 while greater in the NP and AL during June and July 2008 (Table 1). A significant inverse relationship was observed between years in total abundance of *A. digitale* (ind. m^{-2}) and maturity composition (%) ($p < 0.001$, Fig. 4). This relationship shows that while the abundance was high, the maturity composition was relatively low, i.e. dominated by immature individuals. If higher abundance means greater reproduction, then the peak of reproduction would be expected between 24 July and 13 August in the BS and CH during sampling in 2007, and between 3and 20 June in the NP and AL during sampling in 2008 (Table 1). Throughout the

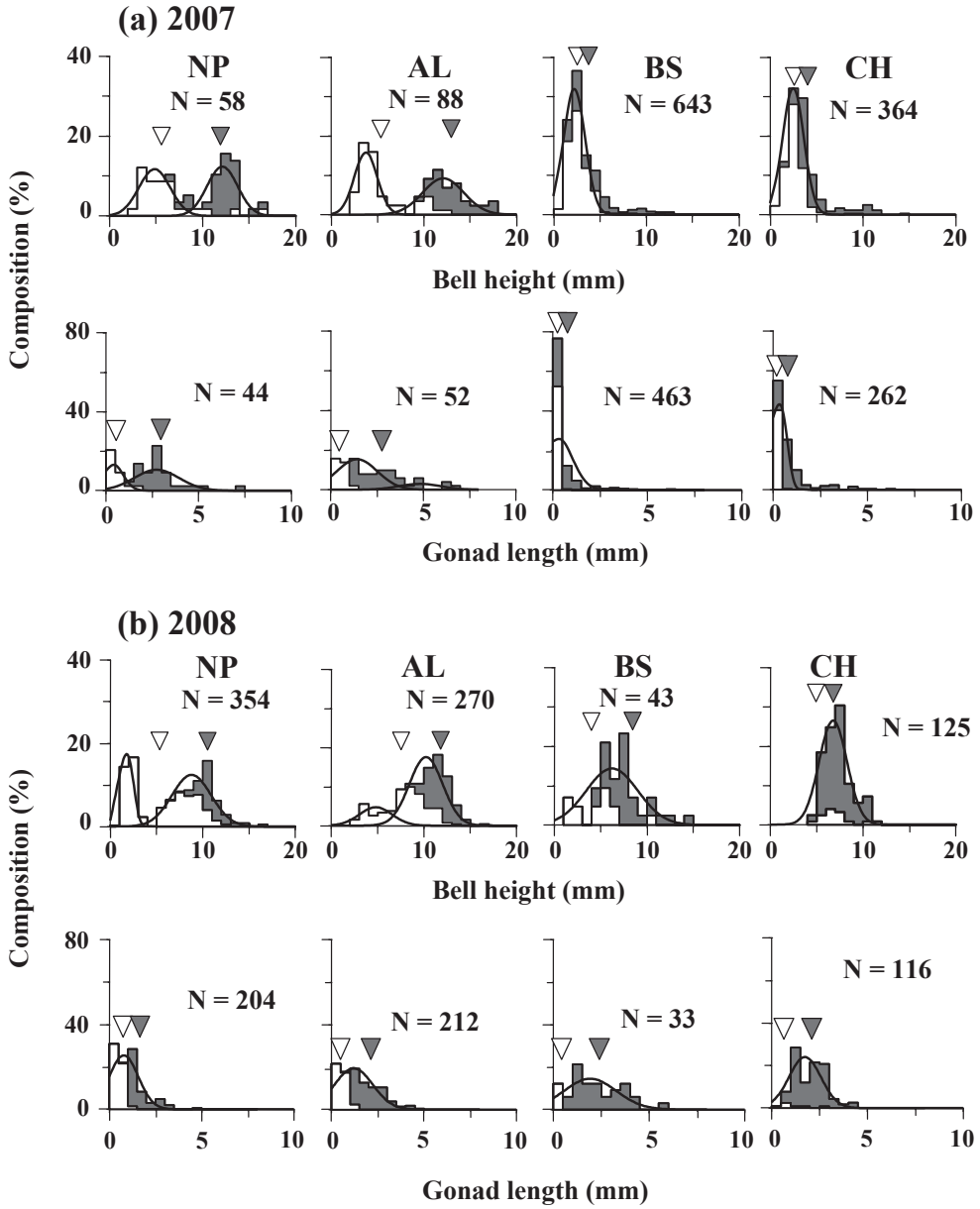

Fig. 3. Body size composition : bell height (upper) and gonad length (lower) of *Aglantha digitale* in the North Pacific (NP), the water around Aleutian islands (AL), eastern Bering Sea shelf (BS) and Chukchi Sea (CH) during July to August 2007 (a) and during June to July 2008 (b). Size frequency was separated into normal curves. Open and solid histogram/symbols indicate mean values of immature and mature individuals, respectively.

region, abundance of *A. digitale* was usually < 100 ind. m^{-2}, but abundance exceeded 200 ind. m^{-2} during the peaks of reproduction (Fig. 2).

Timing of the phytoplankton bloom in the subarctic region is known to vary by latitude. It starts earlier at lower latitudes, and begins close to summer at higher latitudes (Lalli and Parsons, 1997). The latitudinal trends in reproduction peaks of *A. digitale* (July in lower latitudes of the NP and AL, and August in higher latitudes of the BS and CH) (Table 1, Fig. 2) may be related to this latitudinal difference in the timing of phytoplankton bloom. Periods of the phytoplankton bloom and the peak of *A. digitale* reproduction reported around the world are summarized in Fig. 5. In most regions, reproduction of *A. digitale* occurs during February to September and is centered during spring to summer. Reproduction of *A. digitale* occurred after the phytoplankton bloom in the most of the regions (Fig. 5). These facts indicate that the reproduction of *A. digitale* is related to the phytoplankton bloom and to higher temperature at each location. Reproduction after the phytoplankton bloom corresponds to the period when pico- or nano-phytoplankton dominates due to nutrient limitation (Lalli and Parsons, 1997). This phenomenon mostly agrees with Parsons and Lalli (2002), who reported that jellyfish tend to be abundant when the primary

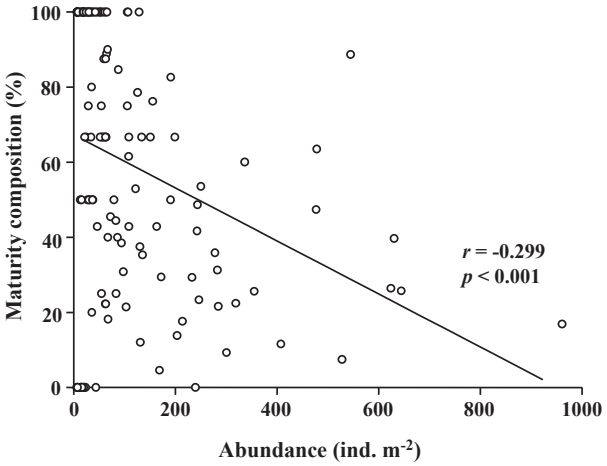

Fig. 4. Relationship between proportion of mature individuals versus abundance of *Aglantha digitale*. For this comparison, all data in 2007 and 2008 are applied.

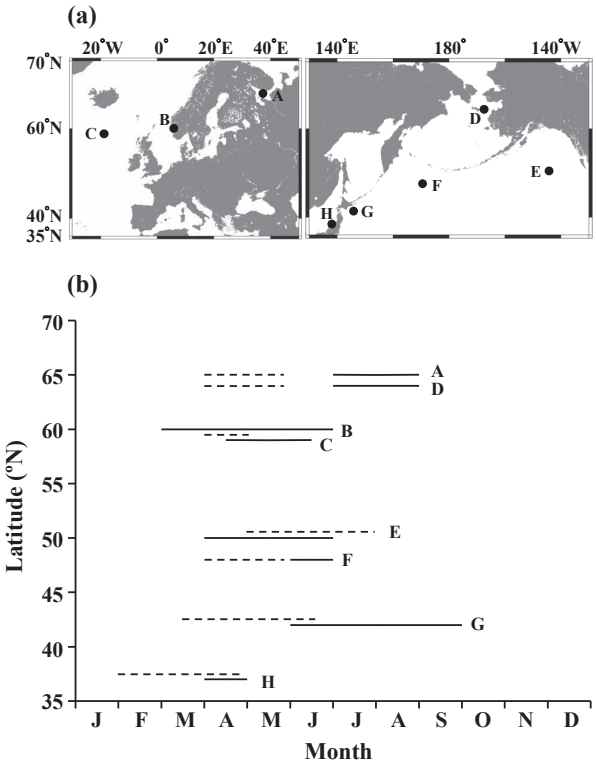

Fig. 5. Comparison of the reproductive season of *Aglantha digitale* from the world's oceans. Location of life cycle studied (a) and period of reproduction (b) ; dashed and solid lines indicate periods of phytoplankton bloom and reproduction of *A. digitale*, respectively. A : White Sea (Pertsova et al., 2006), B : Fanafjord and Korsfjord (Hosia and Båmstedt, 2007), C : Ocean Weather Station India (Williams and Conway, 1981), D : Bering Sea/ Chukchi Sea (this study), E : Station P (Arai and Fulton, 1973), F : North Pacific/Aleutian Islands (this study), G : Site H (Takahashi and Ikeda, 2006), H : Toyama Bay (Ikeda and Imamura, 1996).

production is mainly composed by small-sized phytoplankton.

Maximum jellyfish abundance observed in this study ranged between 408 and 961 ind. m^{-2}. These values are typical of oceanic regions, but are lower than those in neritic waters or embayments (1,350-9,450 ind. m^{-2}, Table 2). Because the abundance of *A. digitale* may depend on the magnitude of reproduction (Fig. 4), high abundance in these regions is thought to be due to the high reproductive success caused by the high primary production. In addition, ontogenetic vertical migration of *A. digitale*, where larger individuals tend to distribute in deeper layers is reported from various locations (McLaren, 1969 ; Williams and Conway, 1981 ; Ikeda and Imamura, 1996). These facts suggest that large individuals may range deeper than 150 m in the oceanic NP and AL. In this case, lower abundance in the oceanic region may be attributed to ontogenetic vertical migration. To confirm this theory, quantitative observation below 150 m is needed in future studies.

Because *A. digitale* is known to perform multiple reproductions within one generation (Williams and Conway, 1981), gonad length is expected to vary before and after of spawning, and thus may have great variability within the generation. This is why there were large regional and annual changes in gonad length (Fig. 3). As the specialized characteristics in body length, minimum maturity sizes of *A. digitale* were smaller in the BS and CH than those in the NP and AL (Fig. 3). This was also supported by the regional comparison, thus bell height of maturity starts at substantially smaller sizes (1.1-1.5 mm) in the BS and CH than in the other region (> 4 mm) (Table 2). The regional differences in body size at maturity (smaller in the BS and CH) suggest that the energy budget may vary among regions. Slow maturation in the NP and AL indicates that *A. digitale* use the energy obtained for rapid somatic growth. On the other hand, rapid maturation and reproduction in the BS and CH suggest that they utilize acquired energy to mature and reproduce at smaller body sizes.

Water depth is different between the two pairs of regions (NP and AL vs. BS and CH). Water depth was ca. 3,000 m in the NP and AL (oceanic region), and mostly < 100 m in the BS and CH (neritic region). Primary production is expected to be greater for the neritic BS and CH than the oceanic NP and AL. With high primary production in the neritic BS and CH, the energy budget of *A. digitale* may increase the proportion of maturation and reproduction, and individuals may mature at small body sizes. The reported body size at maturity of *A. digitale* was 4-25 mm bell height (Table 2). These values are similar to those in the oceanic NP and AL. However, they matured at much smaller sizes (1.1-1.5 mm bell height) in the BS and CH (Table 2). The smaller body size at maturity of *A. digitale* is considered a special characteristic in the neritic and embayment region. However, it is difficult to confirm this theory because of the scarce information in

Table 2. Regional comparison in abundance, range of bell height and maturity bell height of *Aglantha digitale* from various locations in the Northern Hemisphere.

Region	Depth (m)	Period of source data	Abundance (ind. m^{-2})	Range of bell height (mm)	Bell height for maturity (mm)	Source
Toyama Bay (The Sea of Japan)	0–900	June–August	75–450	1–17	6–16	Ikeda and Imamura (1996)
Site H (Oyashio region)	0–2,000	June–August	6–67	1–23	11–23	Takahashi and Ikeda (2006)
The western subarctic Pacific	0–150	June–July	0–368	4–18	7–18	Saito et al. (2012)
North Pacific	0–150	June–August	0–408	0.8–16	6.3–16	This study
The eastern subarctic Pacific	0–150	July–August	0–768	4.5–17	8–17	Saito et al. (2012)
Station P (The eastern subarctic Pacific)	0–110	June–August	10–250	5–20	15–20	Arai and Fulton (1973)
Aleutian Islands	0–150	June–August	0–645	2.3–17	8.6–17	This study
Bering Sea shelf	0–140	June–August	0–961	0.6–14.2	1.1–14.2	This study
Chukchi Sea	0–49	June–August	0–545	0.6–14.2	1.5–14.2	This study
Hardengerfjord, Norway	0–100	April–May	1,350–9,450	0.5–10	—	Pagès et al. (1996)
Fanafjord and Korsfjord, Norway	0–700	June–August	0–420	1–17	4–17	Hosia and Båmstedt (2007)
The White Sea	0–250	June–August	1,350–6,750	1–22	8–22	Pertsova et al. (2006)
The northeast Atlantic Ocean	0–500	June–August	0–2,227	1–25	8–25	Williams and Conway (1981)

neritic and embayment regions. More study is needed to clarify regional differences, especially on body size at maturity of *A. digitale*.

Acknowledgements

We thank Dr. Brenda Holladay (University of Alaska Fairbanks) and Prof. Jennifer E. Purcell (Western Washington University) for kindly review and comments on the manuscript. We are grateful to the captain and crew of the T/S *Oshoro-Maru* for their help in field sampling. This study was supported by Grant-in-Aid for Scientific Research (A) 24248032 and Grant-in-Aid for Scientific Research on Innovative Areas 24110005 from the Japan Society for the Promotion of Science (JSPS).

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