Horizontal distribution of *Thetys vagina* Tilesius (Tunicata, Thaliacea) in the Japan Sea during spring 2004

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The occurrence of the salp Thetys vagina was observed in the Japan Sea during spring 2004. Catches up to 187 kg wet weight (WW) per 2.18 × 10^5 m^3 (equal to ~0.9 g WW m^{-3}) were collected with 10-m diameter surface-water otter trawl nets. The horizontal distribution indicated that the high biomass was related to the area with high chlorophyll a (Chl a) concentration, which was located around the subarctic front with the warm Tsushima Current. Five prey taxa were identified from the gut contents of individuals from the high Chl a area. The diatom Coscinodiscus spp. (13–55 μm in diameter) dominated numerically. Another significant prey was the large diatom Coscinodiscus wailesii (219–313 μm) that is an indicator of the spring bloom in this area. The mass occurrence of T. vagina thus appears related to phytoplankton availability, though the mechanisms remain uncertain.

INTRODUCTION

Thetys vagina is the largest of the salps, with a body length (BL) measuring up to 306 mm (Nakamura and Yount, 1958). This species is widely distributed in the warm waters of all oceans and has also been observed in colder zones (McAlice, 1986; Sims, 1996; Van Soest, 1998). Salps have a complex life history with alternation of generations between aggregated sexual blastozooids (aggregate form) and solitary asexual oozooids (solitary form), and they often form vast swarms at various spatial scales (Raymont, 1983). *Thetys vagina*, however, has rarely been caught and typically occurs at fairly low densities in all oceans (Ensal and Daponte, 1999; Hubbard and Pearcy, 1971); little is known about the ecology of this species.

The Japan Sea is a marginal sea. Its only connection with the North Pacific, the Sea of Okhotsk and the East China Sea is through four shallow straits (<130 m deep). Seasonal changes in temperature and salinity in the upper layer of the southern Japan Sea reflect both local meteorological events and the intrusion of the warm Tsushima Current that enters through the Tsushima Straits and is the only major current flowing into the Japan Sea (Fig. 1A). This current strongly influences the species composition of the zooplankton in the Japan Sea (Iguchi, 2004). There has been no official record of *T. vagina* in the Japan Sea, but during spring 2004 fisheries institutes along the Japan Sea coast received extensive information regarding the presence of *T. vagina*. The institutes were informed because of the nuisance impact on fisheries (i.e. the presence of *T. vagina* hampered fishing activities by clogging set-nets and gill-nets), especially along the coast of northern Honsyu and southern Hokkaido, Japan, in April (unpublished results).

The ecological importance of gelatinous zooplankton, including salps, in marine ecosystems has been recognized (Andersen, 1998; Mills, 2001). There is concern that gelatinous zooplankton are becoming more prevalent in the Japan Sea. For example, mass occurrences of the medusa *Nemopilema nomurai* were observed in 1995, 2002 and 2003 (Omori and Kitamura, 2004; Yasuda, 2004) and of both the salp *Salpa fusiformis* and the medusa *Aurelia aurita* in 2000 (Kuroda *et al.*, 2000). However, their large size, fragile bodies and fluctuating abundance have

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hindered studies and rendered systematic and scheduled field research difficult. At present, the processes and mechanisms relating to the prevalence of gelatinous zooplankton have not been explained in detail.

METHODS

The horizontal distribution of *T. vagina* was determined with surface-water trawl nets, and food items were also examined. This series of collections was made during fisheries research program activities, and *T. vagina* was caught incidentally. The results are analysed from the viewpoint of the relationship between the occurrence of *T. vagina* and the prevailing environmental conditions in the Japan Sea.

Collections of pelagic animals, including salps, were made from April 11 to 22, 2004, at 38 stations located in the southeastern part of the Japan Sea (Fig. 1A). At each station, surface-water otter trawl nets were towed at night down to 30-m depth for 30 min (5.6 km h^{-1}). The nets were 10 m in diameter with a 4-mm nylon mesh tail bag (total 21 m long). The anterior portions of the trawl nets have a large mesh size (15 cm) that becomes progressively smaller with distance from the opening. The volume of water filtered is calculated as 2.18×10^5 m^3 on the assumption of 100% filtration efficiency. CTD (SBE-911plus) casts were made at each station to determine the vertical temperature and salinity profiles.

The contents of each trawl were sorted, and a batch of all *T. vagina* individuals was weighed (wet weight, WW) to the nearest 100 g. At 10 of the 38 stations, no weights were recorded and only the presence or absence of *T. vagina* was confirmed. At two stations (A and B, Fig. 1A), a subsample of *T. vagina* individuals was frozen. In the laboratory, the samples were thawed, measured (BL, from the oral opening to the atrial opening) and weighed (WW).

Among the specimens mentioned, seven individuals were preserved in 5% buffered formalin–seawater. The stomach contents, which were fractionated, were later examined under microscopes and food organisms identified and enumerated arbitrarily, and the maximum length of randomly selected organisms was then measured. The remaining salps were rinsed with isotonic ammonium formate (6% W/V) to remove seawater from the surface and the internal cavity, and the dry weights (DW) were determined following freeze-drying.

Sea surface temperature data for April 21, 2004, in the Japan Sea were extracted from SIDaB (Satellite Image Database System in Computer Center for Agriculture, Forestry and Fisheries Research, Japan). Chlorophyll *a* (Chl *a*) images for April 20–21, 2004, from the AQUA MODIS sensor were provided by JAXA/Tokai University, Japan.

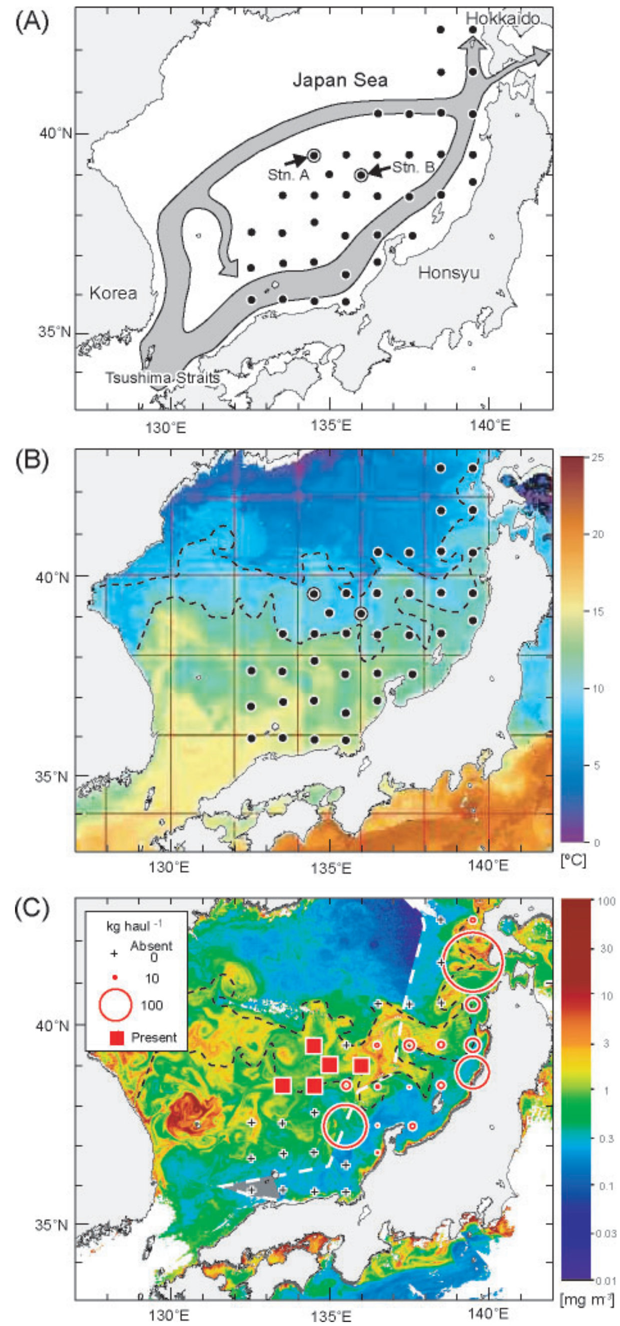

Fig. 1. (**A**) Location of sampling stations and schematic view of the warm Tsushima Current (arrows) from Senjyu (Senjyu, 1999). (**B**) Sea surface temperature image from NOAA MCSST in the Japan Sea on April 21, 2004. Area between dashed lines indicates the approximate location of the subarctic front (7–10°C). (**C**) Chlorophyll *a* image from AQUA MODIS sensors, which is a composite of images obtained on April 20 (western area) and April 21 (eastern area), separated by a white dashed line. Horizontal distribution of the biomass (kg $haul^{-1}$) of *Thetys vagina* in April 2004 is superimposed.

RESULTS AND DISCUSSION

Oceanographic data show that the warm Tsushima Current flows from the East China Sea branches after passing the Tsushima Straits (Fig. 1B). The westernmost current flows northward along the east coast of Korea. After coming into contact with the subarctic water, it then flows eastward along the subarctic front at ~40°N (here defined as the area between 7 and 10°C; Fig. 1B). The Chl *a* image shows that the surface waters of the subarctic front have a high Chl *a* concentration (>1.2 mg m^{-3}), which indicates that the spring bloom occurred in this area (Fig. 1C).

Thetys vagina was present at 21 stations. The mean biomass was 40 kg WW $haul^{-1}$, ranging from 1 to 187 kg WW (n = 16). The maximum biomass was observed at a station off Hokkaido (Fig. 1C) and was equivalent to ~0.9 g WW m^{-3}. The large mesh size in the anterior portions of the trawl nets enables *T. vagina* to pass through, and thus the biomass is underestimated. At five stations among 10 no-weighing stations *T. vagina* was present (Fig. 1C), and at each station a minimum of 20-L basket containers of *T. vagina* were caught. The biomass was abundant within the subarctic front, which has a high Chl *a* concentration, and also within the southern area adjacent to the subarctic front (Fig. 1C). The relationship between *T. vagina* occurrences and temperatures and salinities at 20-m depth revealed that *T. vagina* was confined within a temperature range of 7–12°C and a salinity range of 33.9–34.4 (Fig. 2). Because the water mass with the high salinity (~34.2–34.7) is strongly influenced by the warm Tsushima Current (Yasui *et al.*, 1967), *T. vagina* was not always abundant in the warmer waters and core Tsushima Current waters.

To compare the biomass of *T. vagina* with that of other salps, we converted the biomass expressed by WW in this study to carbon using the regression equation established for *Salpa thompsoni* (Iguchi and Ikeda, 2004). The resulting maximum biomass off Hokkaido is 44 mg C m^{-2} (1.46 mg C m^{-3} × 30 m), which is comparable with the mass occurrence of *S. fusiformis* off Ireland (31 mg C m^{-2}; Bathmann, 1988). The large size of *T. vagina* makes it difficult to correctly evaluate their abundance with small-diameter nets, and mass occurrences of *T. vagina* may exist undetected in the world's oceans.

All specimens examined were of the aggregate form, and the BL range was 39–159 mm (n = 40). The relationships between BL and WW and BL and DW were calculated (Fig. 3). The results of a covariance test revealed that the regression lines between BL and WW differed significantly for station A and station B data (for slope, F = 0.752, df = 1,36, P > 0.35; for intercept, F = 47.58, df = 1,37, P < 0.01), whereas the data for DW were essentially the same (for slope, F = 2.094, df = 1,33, P > 0.15; for intercept, F = 3.167, df = 1,34, P > 0.05). Thus, the regression lines from stations A and B for the relationship between BL and WW were expressed

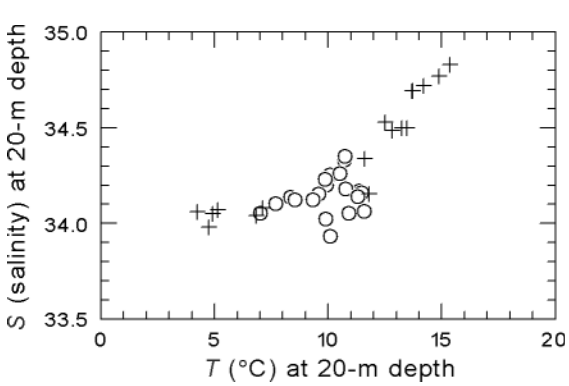

Fig. 2. Scatter plots of salinity versus temperature (°C) at 20-m depth from each sampling station. Open circles indicate the presence of *Thetys vagina* and crosses their absence.

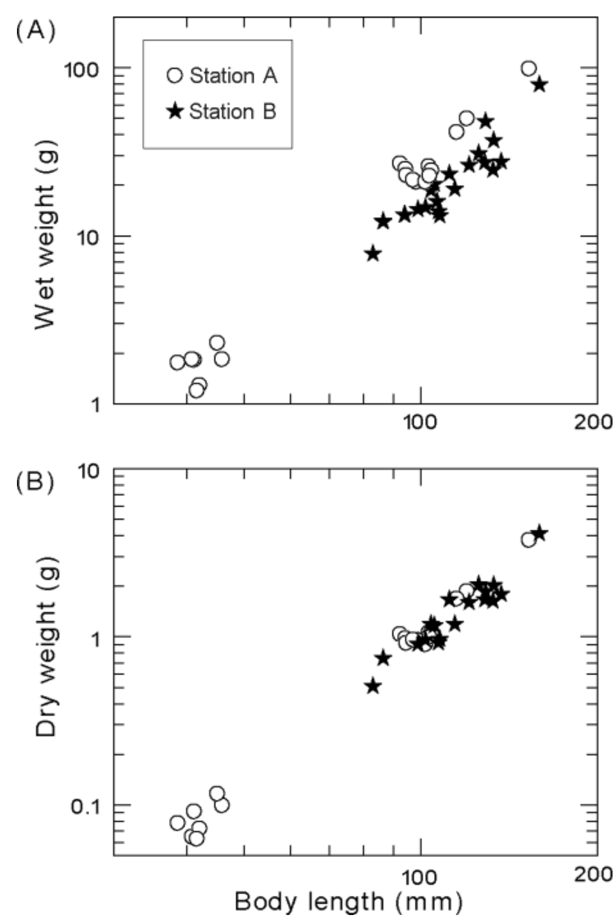

Fig. 3. The relationship between body length (BL) and wet weight (**A**) and BL and dry weight (**B**) at stations A and B, respectively.

separately: log(WW) = [3.099 (log(BL)] − 4.805 (r = 0.991, n = 19) station A; log(WW) = [2.732 (log(BL)] − 4.292 (r = 0.929, n = 21) station B; log(DW) = [2.831 (log(BL)] − 5.679 (r = 0.991, n = 37). The thawing process is likely to have caused the difference between the equations for WW, but differences in food condition may be another cause, as the small salps were found only at station A, which indicates the possibility of ongoing regeneration (Fig. 3).

Identifiable food items found in the stomach contents of *T. vagina* (n = 7; BL, 45–107 mm) were classified into five groups: dinoflagellates, silicoflagellates, diatoms, tintinnids and copepods (Table I). Food particles consisted predominantly of the diatom *Coscinodiscus* spp. that was 13–55 µm in diameter and accounted numerically for 62% of all identifiable items. The largest object was the prosome of a Calanoida copepod (1725 µm). The diatom *Coscinodiscus wailesii* was present in small numbers, but due to their large size (219–313 µm) their contribution to the volume was comparable to that of *Coscinodiscus* spp. (Table I).

The gut contents of *T. vagina* showed that this species utilizes rather large phytoplankton such as *C. wailesii* (Table I). In the central Japan Sea, *C. wailesii* is thought to be an indicator of the spring bloom (Nishimura, 1969). Salps filter food using their pharyngeal mucous nets, and no qualitative differences between gut contents and available particulate matter have been found (Madin and Purcell, 1992). Thus, the gut contents in this study would reflect the ambient phytoplankton species composition, especially that of testaceous phytoplankton. A relationship between the mass occurrence of *S. fusiformis* and the spring phytoplankton bloom has been observed off Ireland and in the western Mediterranean (Bathmann, 1988; Ménard *et al.*, 1994). By considering those results, it appears that the diatoms in the spring bloom most likely enhanced the growth and reproduction of *T. vagina* in the Japan Sea, although a study of the relative contribution of small and nontestaceous objects as food items is needed in the future.

An understanding of the mechanisms controlling the prevalence of *T. vagina* in the Japan Sea requires research into the conditions that existed when the species was rare, that is, seed population (Paffenhöfer *et al.*, 1995). In this study, abundant biomass was observed offshore along the subarctic front and in the southern area adjacent to the front, which is influenced by the warm Tsushima Current. Thus, a certain quantity of *T. vagina* would have been brought by the westernmost branch of the warm Tsushima Current into the Japan Sea in 2004, as has been observed in the course of salp incursions into colder zones in other areas (McAlice, 1986; Sims, 1996). The seed population would encounter high phytoplankton concentrations at the subarctic front area and rapidly multiply and grow. We found no information regarding the occurrence of this species within the upstream area of the warm Tsushima Current (East China Sea and Yellow Sea) in 2004, which probably indicates that *T. vagina*

Table I: Summary of Thetys vagina gut contents (n = 7 salps)

Prey taxa		Maximum length (µm)	Number	% of total
Phytoplankton				
Dinoflagellates	*Prorocentrum balticum*	13–15	21 400	<1
Silicoflagellates	*Distephanus speculum*	25–28	358 000	6
Diatoms	*Bacteriastrum spp.*	10–15	126 000	2
	Chaetoceros spp.	33–418	319 200	5
	Coscinodiscus wailesii	219–313	18 980	<1
	Coscinodiscus spp.	13–55	4 037 420	62
	Eucampia zodiacus	30–63	162 000	3
	Rhizosolenia alata	30–213[a]	372 600	7
	Rhizosolenia hebetata f. hiemalis	50–375[a]	568 600	9
	Pennales	45–163	187 800	3
Zooplankton				
Tintinnids	*Codonellopsis pusilla*	65	400	<1
	Parafavella denticulata	100–245	3400	<1
	Tintinnina	35–45	225 800	3
Copepods	*Oncaea conifera*	625	1	<1
	Calanoida	700–1725[a]	14	<1

[a]Broken part of cell or body.

multiplied rapidly within the Japan Sea. The eastward flowing branch of the warm Tsushima Current would then have transported *T. vagina*. Strong monsoonal winds that blow from the northwest in winter and spring would have enhanced the entrainment of *T. vagina* onto the coast of Honshu and Hokkaido (e.g. Nishimura, 1968), causing the nuisance impact on fisheries. This entrainment and convergence would result in the mismatch at some stations between the distribution of the species and areas with high Chl *a* concentrations (Fig. 1C).

In the Japan Sea, the mass occurrence of gelatinous zooplankton has occurred since 1995. The outbreak of the salp *T. vagina* examined in this study is a similar phenomenon to that observed in other species, although the periods of occurrence do differ. The horizontal distribution and biomass of *T. vagina* are apparently related to high phytoplankton concentrations. The timing of the spring phytoplankton bloom was not unusual compared with other years (Yamada *et al.*, 2004), and the triggering mechanism of the salp outbreak remains unknown. Off the Oregon coast (USA), *T. vagina* was collected only during unusually warm years, primarily with an Isaacs–Kidd midwater trawl (Hubbard and Pearcy, 1971). Thus, high water temperature appears to be a causal triggering mechanism for abundance of this species and for other gelatinous organisms in the Japan Sea. A long-term monitoring scheme for both gelatinous organisms and environmental variables is needed; however, information is also needed regarding the origin areas of the warm Tsushima Current (East China Sea and Yellow Sea).

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