Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific

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Biodiversity of cnidarian and ctenophore forms in Toyama Bay, Japan Sea, was lower than that in Sagami Bay, north-western Pacific, according to all the indices investigated. Highest richness of forms occurred in the 400–600 m depth layer in Sagami Bay, while in Toyama Bay richness was low in most layers. New forms continued to occur with increasing depth in Sagami Bay but not in Toyama Bay and species composition differed remarkably between the two bays. Putative secondary deep-sea gelatinous forms were identified. Horizontal patchiness in normalized abundances was the rule rather than the exception and for accurate calculations of biodiversity indices incorporating evenness or equitability, the necessity for multiple submersible dives in a single area and survey period was noted. Vertical migration and predation were identified as possible factors contributing to the higher diversity in the 400–600 m depth layer in Sagami Bay.

INTRODUCTION

The oceans' midwater is the most extensive habitat on the surface of our planet but remains largely unknown. A modicum of information exists concerning its more robust inhabitants, such as fish, shrimps, copepods and other organisms that are still recognizable after collection in a trawled net, but the gelatinous fauna remains largely unstudied. Cnidarians and ctenophores are two of the most dominant groups in midwater communities. However, few of the species have been described, principally the more robust species that remain recognizable after collection in a trawled net (Youngbluth, 1989). Critical studies of the biodiversity and ecological roles of these fragile fauna require access to the vast mesopelagic environment via submersibles and remotely operated vehicles (ROVs) (Robison, 1983; Hunt & Lindsay, 1999; Armstrong et al., 2004).

Reports of biodiversity patterns in gelatinous macroplankton are limited, with one study using crewed submersibles that recorded medusan species number vs depth and temperature at three sites in the north-western Atlantic (Larson et al., 1991) and the majority of other studies being based on net-caught samples (e.g. Pugh, 1974; Roe et al., 1984). No information is yet available for the Pacific Ocean or the Japan Sea. Diversity maintenance mechanisms in the midwater zone are thought to differ from those in benthic or terrestrial environments (Madin & Madin, 1995; Tsuda, 1995; Armstrong et al., 2004) and a clearer understanding of them will undoubtedly force us to rethink paradigms based on terrestrial and benthic systems.

Species diversity patterns are known to affect both ecosystem stability and function (McCann et al., 1998). Because marine zooplankton are significant mediators of fluxes in carbon, nitrogen, and other critical elements in ocean biogeochemical cycles (see Berger et al., 1989), it is imperative to understand the patterns of species diversity, community structure, their maintenance mechanisms, and their effect on the global system. However, efforts using traditional techniques to describe species and map their distributions in space and time (spatio-temporal niche apportionment) can never hope to yield complete knowledge of plankton biodiversity. This paper describes the biodiversity of cnidarians and ctenophores in two midwater regimes near Japan and discusses the utility of submersibles for future explorations in this realm.

The Japan Sea is a relatively closed marginal sea that is separated from the Deep Sea Proper by shallow sills. It is also the second coldest sea in the world with
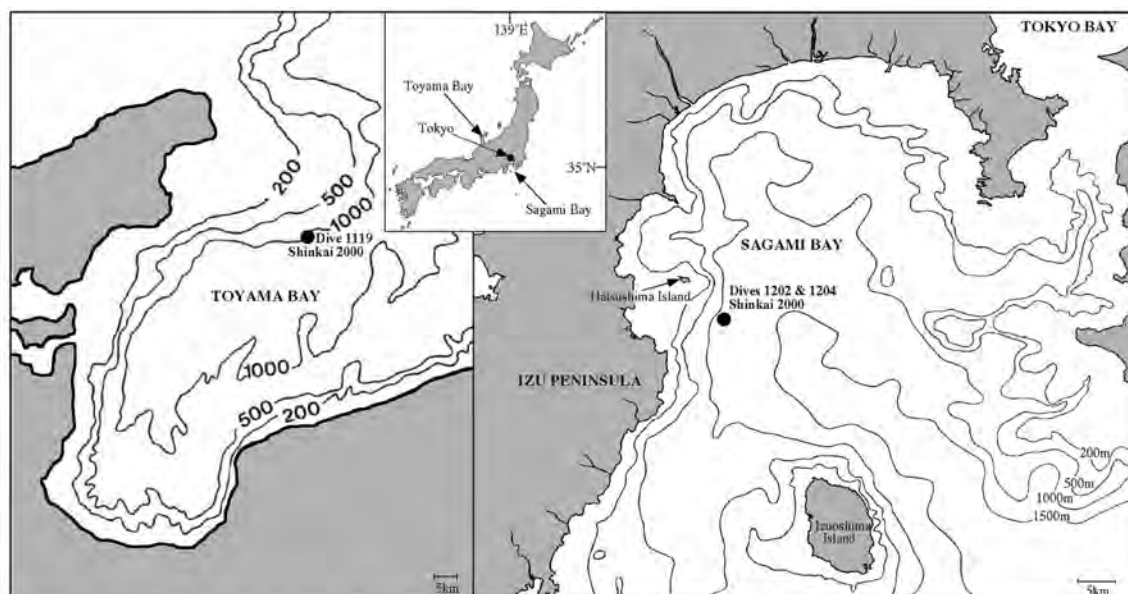
Figure 1. Map of Toyama and Sagami bays.

an average water temperature of 0.9°C, compared to that of the Arctic Ocean at 0.7°C. The water in the meso- and bathypelagic depths of the Japan Sea Basin is restricted to the Japan Sea and is unlike water found in any of the other deep oceans of the world. Only one or two of the 'ancient' tropical–subtropical primary deep-sea species characteristic of the Pacific deep water fauna are known to have been able to penetrate into the Japan Sea and reproduce there (Nishimura, 1965–1969). Most of the deep-sea fauna are boreal or sub-boreal species that are only now evolving into a deep-sea mode of life. The non-gelatinous midwater fauna of the Japan Sea is known to be species poor with virtually no primary deep-sea forms of hard-bodied organisms such as fish or shrimps able to colonize the extremely cold meso- and bathypelagic waters since the Sea opened following the Pleistocene (Tyler, 2002 and references therein). Only secondary deep-sea forms that evolved in polar regions before colonizing the deep sea have been reported to overwinter in the Japan Sea. The ability of gelatinous deep-sea species to colonize waters with such extreme physical parameters is undetermined, as is whether or not both primary and secondary deep-sea species of gelatinous organisms exist. The only deep-water bay on the western side of Japan is Toyama Bay in the Japan Sea. Toyama Bay is located north of Toyama City and is partly circumscribed to the west by the Noto Peninsula (Figure 1). In contrast Sagami Bay, one of only two deep-water bays on the eastern side of Japan in the Pacific Ocean, the other being Suruga Bay, harbours a rich mesopelagic fauna of both gelatinous (Toyokawa et al., 1998; Hunt & Lindsay, 1999;

Lindsay et al., 2001) and non-gelatinous forms. The pelagic community in the Sea of Japan (Toyama Bay) is relatively species-poor (Zenkevitch, 1963). The number of species recorded from the Sea of Japan includes 95 copepods (390 in the western North Pacific; Morioka, 1980), 10 euphausiids (39 in Sagami Bay; Hirota et al., 1982), 2 hyperiid amphipods (53 in Sagami Bay; Lindsay et al., unpublished data), 17 chaetognaths (21 in the western North Pacific; Kitou, 1974), micronektonic crustaceans (none in Toyama Bay and 49 in the north-west Pacific; Hayashi, 1991) and fish (one in Toyama Bay and 75 in the north-west Pacific; Okiyama, 1971; Kawaguchi, 1974). Sagami Bay is located south of Tokyo Bay, being circumscribed by the Izu Peninsula to the west and the Miura Peninsula to the east (Figure 1). These two bays were the focus of the present study.

MATERIALS AND METHODS

Submersible data collection

Data were collected using the crewed submersible 'Shinkai 2000' during one dive in Toyama Bay, Japan Sea (37°16.5'N 137°33.5'E), on 28 July 1999 and two dives in Sagami Bay, north-western Pacific (35°00.0'N 139°13.7'E), on 9 and 11 July 2000. Dives started at 0937, 1026 and 0919, respectively. The 'Shinkai 2000' was equipped with a Victor GF-S1000 HU three chip CCD camera specially modified for the vehicle. There were eight lights: five 250-W SeaLine SL-120/250 halogen lamps and three 400-W SeaArc HMI/MSR metal halide lamps. Video footage was recorded simultaneously on both ST-120PRO S-VHS and

BCT-D124L Digital Betacam tapes. Specimens were collected for positive identification using a suction sampler. A gate valve sampler was attached to this suction sampler (see Hunt et al., 1997, figure 1) to allow collection of the larger and more fragile organisms. The 'Shinkai 2000' submersible observation and sampling system has been described in detail elsewhere (Lindsay, 2003). Animals were transferred to shipboard aquaria or planktonkreisels (Hamner, 1990) for behavioural observation, positive identification, and photographic recording with a Nikon D1^H digital still camera with a macro lens (AF Micro Nikkor 105mm 1:2.8 D) and recorded in TIFF-RGB format at an image size of 2000×1312 pixels. Observations of the live animals were also made in the ship's laboratory under a Nikon SMZ-U dissecting microscope and recorded on DV tape. Sketches were made in cases where the still image and video equipment were unable to resolve or record internal or fine structures to our satisfaction. Specimens were fixed in buffered 5% formalin–seawater after detailed morphological analysis and recording.

Physico-chemical data were collected using a SeaBird SBE19 CTD attached to the vehicle on all dives and also with an SBE13 oxygen sensor during the dives in Sagami Bay. The CTD and dissolved oxygen can be correlated to the presence of a given animal by matching the timecode on the CTD series to the timecode on video.

Two training dives in Sagami Bay using the ROV 'HyperDolphin' were carried out within the same survey period. The ROV 'HyperDolphin' was equipped with a high-definition camera integrating an ultra sensitive super HARP (High gain Avalanche Rushing Photo-conductor) tube. Camera sensitivity was F1.8 at 2 lux, gain was variable at 4 to 200 times, the signal to noise ratio was 43 dB and resolution was 800 TV lines. The zoom lens has a minimum focal length of 5.5 mm and a 5-times zooming ratio. There were five 400-W SeaArc HMI/MSR metal halide lamps. Two were situated on the port swinging boom arm and one on the starboard swinging boom arm. These arms were usually opened such that the lights optimized the field of view of the high-definition camera, but were sometimes moved to optimize lighting during observations of individual organisms *in situ*. The remaining two lights were forward-pointing and fixed to the frame of the vehicle. Video footage was recorded continuously and simultaneously on both ST-120PRO S-VHS and BCT-124HDL (60i) HDCAM tapes.

Observational analysis

Although training dives using the ROV 'HyperDolphin' were also undertaken during the study period, only observations during the surveys by the crewed submersible 'Shinkai 2000' were used in the biodiversity analysis. Identifications by observers on the 'Shinkai 2000' were checked through referral to the video records of both the 'Shinkai 2000' and the ROV 'HyperDolphin' as well as through referral to physical specimens and accompanying *in situ* video footage captured both during these dives and during other dives in the bays. Direct visual observation by the researcher allows more accurate estimation of the size as well as better morphological and behavioural observations of each organism. Furthermore, a greater volume of water can be investigated due to the superior 3-D resolution and focusing speed of a pair of human eyes as compared to the 2-D in-focus frames from video cameras mounted on ROVs. Regardless, only cnidarians and ctenophores of minimum body dimension equal to or exceeding one centimetre were recorded, in order to increase confidence in each identification.

A matrix of cascading taxonomic levels was constructed and the first observation at each taxonomic level recorded during each dive (Table 1). Accurate classification at the lower levels such as genus and species was not always possible. However, where we were confident that an organism represented a discrete form, it was identified and recorded. Post-dive analysis of comments on the audio track of the video record allowed us to determine the time of first and subsequent observations for each form for entry into a second data table that contained the associated physico-chemical parameters and other data. Each form was given a unique name upon first observation and oral description, and this name was used thereafter during the remainder of the dive. Part of the identification table is shown in Table 1. Form rather than species was considered the more appropriate lowest taxonomic level for assessing biological/ecological diversity (Livingston, 1988).

Statistical analyses

Biodiversity indices are biased as to which aspects of diversity they stress depending on the way in which each index is calculated. Two indices were chosen for each aspect of biodiversity that was investigated to complement each other's strengths and weaknesses. The following indices of biological diversity were calculated:

number of species observed (S_{obs});
Margalef's richness index: $D_{Mg}=(S-1)/\ln(N)$, where S is the number of taxa, and N is the number of individuals (Margalef, 1958);

Table 1. *An example of the matrix of cascading taxonomic levels used in this study with times of first occurrence during 'Shinkai 2000' Dive 1202 marked for each taxonomic level.*

Phylum	Class	Order	Family	Genus	Species	Form	New Phyla	New Class	New Order	New Family	New Genus	New Species	New Form
Cnidaria							9:37:51						
	Hydrozoa							9:37:51					
		Physonectae							10:31:00				
			Apolemiidae							15:47:45			
						brown fuzzy one (same morphotype as *Tottonia contorta* - siphosome caught on 2K#945)							15:47:45
			Agalmidae							10:31:00			
						small orange w/ spotted siphosome							10:45:48
						hinoobi hinoobi (*Marrus* aff. *antarcticus pacificus*)						15:07:42	15:07:42
				Bargmannia							10:31:00		
					elongata							10:31:00	10:31:00
				Halistemma							15:05:09		
					aff. *amphytridis*							15:09:10	15:09:10
				Nanomia							11:46:53		
					bijuga							11:46:53	11:46:53
			Forskaliidae							10:51:12			
				Forskalia							10:51:12		
					tapering nectosome 'non-kawamuraiensis type'							10:51:12	10:51:12
		Narcomedusae							9:56:30				
			Aeginidae							12:00:20			
						the 6-tentacled one with elbows and secondary tentacles							13:10:20
				Solmundella							12:00:20		
					bitentaculata							12:00:20	12:00:20
				Aegina							14:00:13		
					citrea							14:00:13	
						adult							14:00:13
				Aeginura									
					grimaldii							15:09:11	15:09:11
			Solmarsidae							9:56:30			
				Solmissus							11:00:52		
					aff. *marshalli*							11:00:52	
						juvenile?							9:56:30
						adult							11:00:52
					incisa								13:35:08
		Trachymedusae							11:12:15				
			Halicreatidae							11:19:26			
				Halicreas							11:19:26		
					minimum							11:19:26	11:19:26
			Rhopalonematidae							11:12:15			
				'Lace Curtain' Rhopalonematid									
						Orange 'Lace Curtain' Rhopalonematid						15:40:40	15:40:40
				Arctapodema							14:15:18		
					sp. A.							14:15:18	14:15:18
				Colobonema							11:12:15		
					sericeum							11:12:15	11:12:15
				Crossota							11:47:50		
					rufobrunnea							11:47:50	11:47:50
				Pantachogon							15:32:48		
					sp. A							15:32:48	15:32:48

Menhinick's richness index: $D_{Mn}=S/\sqrt{N}$ – the ratio of the number of taxa to the square root of sample size (Menhinick, 1964);

Shannon–Wiener diversity statistic: H', where $H'=-\Sigma p_i \ln p_i$, where p_i, is the proportion of individuals found in the ith species (Shannon & Weaver, 1949);

Fisher's alpha diversity index: defined implicitly by the formula $S=a*\ln(1+N/a)$ where S is number of taxa, N is number of individuals and a is the Fisher's alpha (Fisher et al., 1943);

Simpson's dominance index: $D_{Si} =\Sigma(p_i(p_i-1))/(N(N-1))$, where p_i, is the proportion of individuals found in the ith species, and N is the number of individuals (Ludwig & Reynolds, 1988);

Berger–Parker's dominance index: the number of individuals in the dominant taxon relative to N (Berger & Parker, 1970);

Pielou's evenness index: $\mathcal{J}$, where $\mathcal{J}=H'/H_{max}$, where $H_{max} =H'/\ln S$, i.e. when all forms are equally abundant (Pielou, 1966);
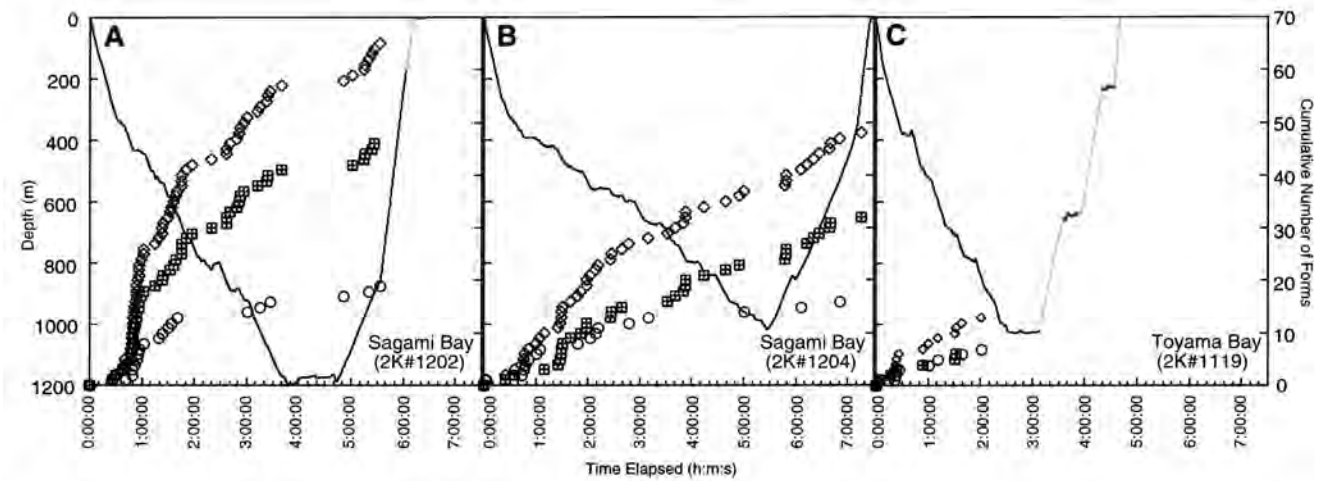

Figure 2. Profiles of depth vs time for (A) 'Shinkai 2000' Dive 1202; (B) 'Shinkai 2000' Dive 1204 in Sagami Bay; and (C) 'Shinkai 2000' Dive 1119 in Toyama Bay. Lines denote dive profiles of the submersible with portions in grey signifying that the lights were turned off at those depth-time co-ordinates. The first observations of discrete forms are denoted by open circles for Ctenophores, hatched squares for Cnidarians, and open diamonds for combined Ctenophores+Cnidarians.
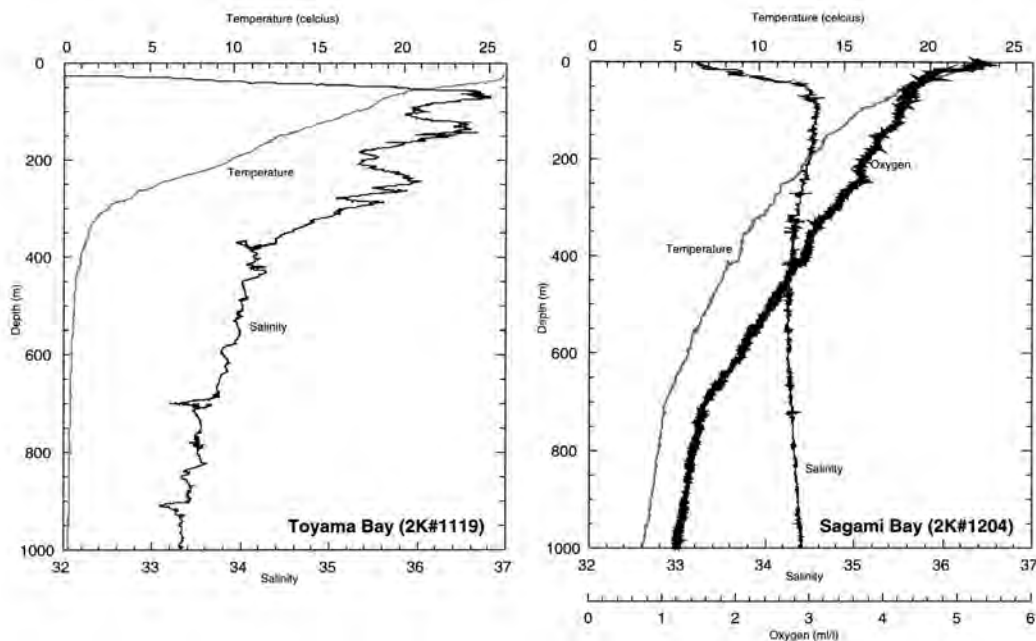

Figure 3. Profiles of water column physical parameters for Toyama Bay (CTD) and Sagami Bay (CTD-DO) during the study period.

Table 2. *Species diversity indices as observed from the 'Shinkai 2000' for different depth layers in the water column in Sagami Bay (Dives 1202 & 1204) and, in parentheses, Toyama Bay (Dive 1119).*

Depth (m)	S (Species No.)	Richness (Margalef)	Richness (Mehinick)	Diversity (Shannon-Weiner)	Diversity (Fisher's Alpha)	Dominance (Simpson)	Dominance (Berger-Parker)	Evenness (Pielou)	Eveness (Molinari)	ES (Chao 2)	ES (2nd-order Jackknife)	ES (Bootstrap)	No. ind (N)
0–100	1 (1)	0.00 (-)	0.18 (1.00)	0.00 (0.00)	0.19 (-)	1.00 (-)	1.00 (-)	- (-)	- (-)	1.5 (-)	2.9 (-)	1.4 (-)	30 (1)
101–200	3 (4)	1.44 (0.76)	1.50 (0.56)	1.04 (0.60)	5.45 (1.01)	0.17 (0.71)	0.5 (0.84)	0.95 (0.44)	0.67 (0.10)	7.5 (12)	6.8 (11.8)	3.9 (5.5)	4 (51)
201–300	3 (5)	0.76 (1.82)	0.80 (1.67)	0.99 (1.30)	1.20 (4.63)	0.35 (0.28)	0.5 (0.56)	0.90 (0.81)	0.62 (0.30)	7.5 (17.5)	8.4 (13.3)	4.1 (6.7)	14 (9)
301–400	13 (3)	2.89 (0.67)	1.63 (0.67)	1.43 (0.74)	4.92 (0.97)	0.44 (0.53)	0.66 (0.70)	0.56 (0.54)	0.06 (0.37)	98 (7.5)	38.4 (8.6)	17.7 (4.1)	64 (20)
401–500	33 (5)	6.49 (1.52)	2.81 (1.34)	2.86 (1.39)	13.70 (2.78)	0.09 (0.23)	0.20 (0.36)	0.82 (0.86)	0.22 (0.52)	578 (17.5)	98.3 (13.9)	45.1 (6.8)	138 (14)
501–600	28 (6)	6.13 (1.62)	3.09 (1.28)	2.87 (1.38)	15.00 (2.71)	0.08 (0.29)	0.23 (0.50)	0.86 (0.77)	0.22 (0.34)	420 (24)	83 (17.2)	38.2 (8.2)	82 (22)
601–700	21 (8)	4.34 (1.77)	2.10 (1.11)	2.05 (1.59)	8.10 (2.64)	0.22 (0.25)	0.34 (0.42)	0.67 (0.77)	0.13 (0.38)	242 (40)	62.4 (23.5)	28.7 (10.9)	100 (52)
701–800	24 (5)	4.46 (1.74)	1.82 (1.58)	1.63 (1.36)	7.52 (3.97)	0.39 (0.24)	0.61 (0.50)	0.50 (0.84)	0.05 (0.39)	312 (17.5)	71.6 (13.5)	32.8 (6.7)	174 (10)
801–900	24 (5)	4.68 (1.34)	2.06 (1.12)	1.89 (1.45)	8.45 (2.13)	0.26 (0.22)	0.37 (0.35)	0.59 (0.90)	0.12 (0.59)	312 (17.5)	71.5 (14.3)	32.8 (6.8)	136 (20)
901–1000	21 (4)	3.70 (0.86)	1.40 (0.70)	1.66 (1.12)	5.67 (1.19)	0.29 (0.38)	0.46 (0.58)	0.54 (0.81)	0.17 (0.38)	242 (12)	62.7 (11.6)	28.7 (5.4)	224 (33)

Molinari's calibrated version of Alatalo's evenness index: $G = (\arcsin F\{\text{in degrees}\}/90)*F$, when $F < \sqrt{0.5}$; $G = F^3$, when $F \leq \sqrt{0.5}$ ($F = ((1/S(p_i^2)-1)/(e^{H'}-1))$ (Molinari, 1989);

Chao 2 non-parametric species richness estimator: least biased estimator of species richness for small numbers of samples (Colwell & Coddington, 1994);

Jackknife 2 non-parametric species richness estimator: an estimator of species richness for small numbers of samples (Colwell & Coddington, 1994);

Bootstrap estimator: another estimator of species richness (Colwell & Coddington, 1994).

Some of these calculations (Chao 2, Jackknife 2 and Bootstrap) were done using the software application EstimateS (Colwell, 1997).
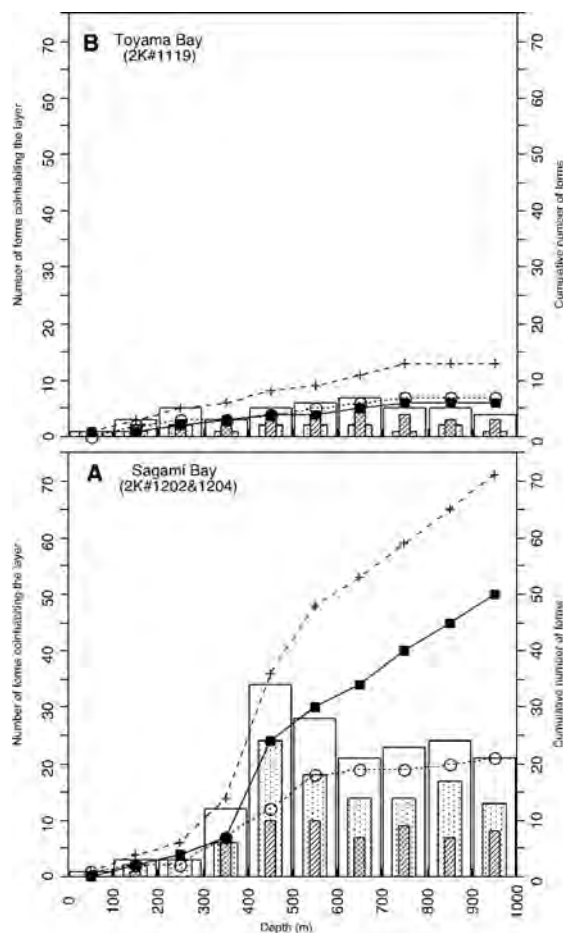

Figure 4. Profiles of number of Ctenophore forms (striped bar), Cnidarian forms (dotted bar), and combined Ctenophore+Cnidarian forms (open bar) coinhabiting each depth layer, and the cumulative number of Ctenophore forms (open circle), Cnidarian forms (closed square), and combined Ctenophore+Cnidarian forms (cross) vs depth for (A) Sagami and (B) Toyama Bays.
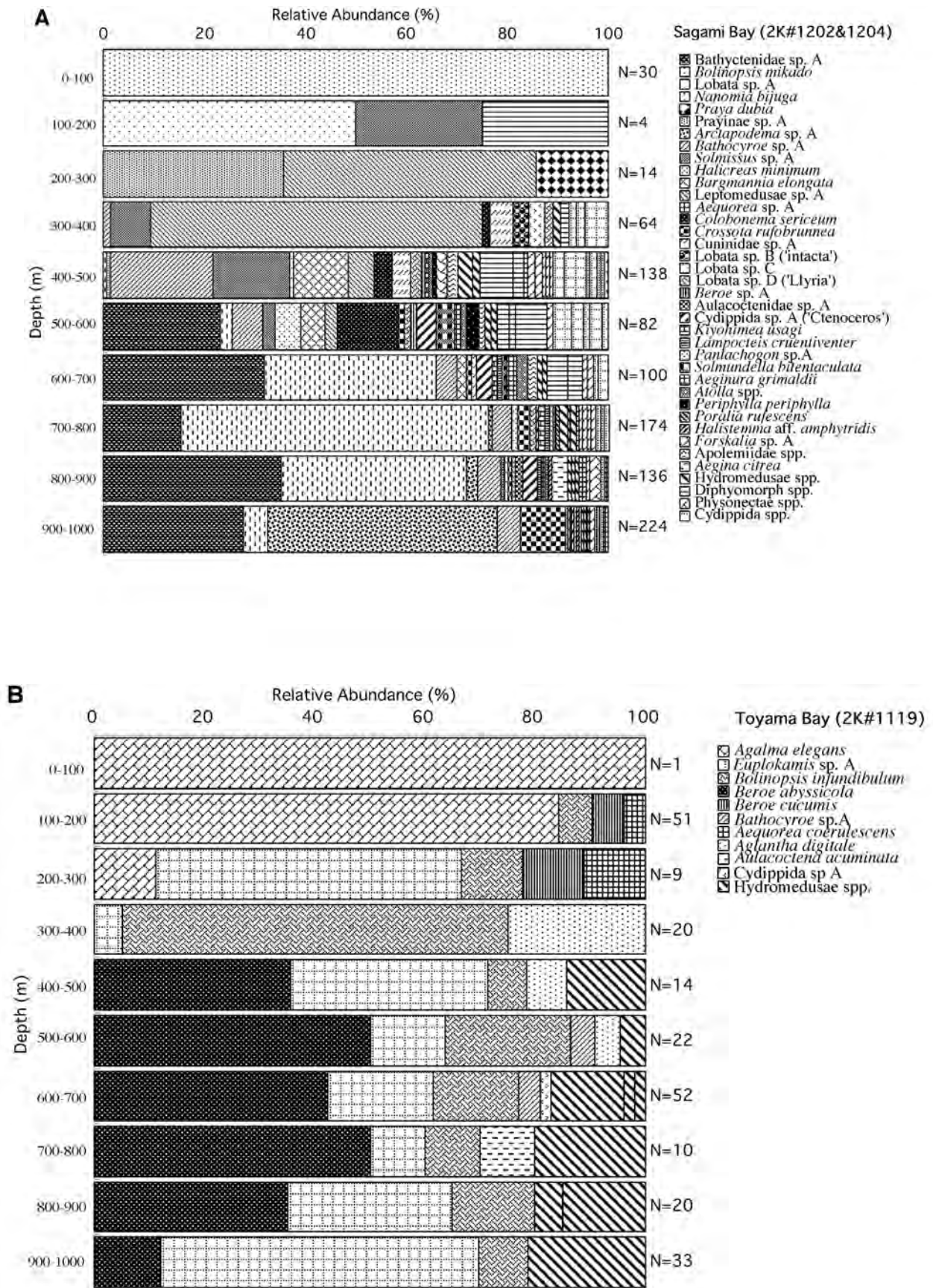
Figure 5. Relative abundances of Ctenophore and Cnidarian forms inhabiting each depth layer for (A) Sagami and (B) Toyama Bays.

RESULTS

Biodiversity of cnidarian and ctenophore forms in Toyama Bay, Japan Sea, was lower than that in Sagami Bay, north-western Pacific, according to all the indices investigated (Table 2). The richness of cnidarian and ctenophore forms (the total number of such forms a given area might contain) in the upper 1000 m was over five times greater in Sagami Bay than in Toyama Bay (Figure 2). It is evident from Figure 2A,B that a single dive in an area of moderate to high species diversity is not enough to accurately assess the richness of forms, as 65 were recognized during Dive 1202 while only 48 forms were recognized during Dive 1204. The total number of forms observed for both dives combined was 72. Even after seven hours of dive time in Sagami Bay, an asymptote was not reached and new cnidarian and ctenophore forms were still being recorded (Figure 2A,B). Several species that have been observed in Sagami Bay previously, such as the medusae *Deepstaria enigmatica* Russell, 1967 (Lindsay et al., 2001) and *Tiburonia granrojo* (Matsumoto et al., 2002), were not observed on either Dive 1202 or Dive 1204 (Table 3). In Toyama Bay, however, an asymptote was reached and no new forms were recorded after the first two hours of observation time (Figure 2C). Physico-chemical parameter profiles of the water column at these two areas are outlined in Figure 3. Below 400 m depth in Toyama Bay the water temperature became almost stable at less than one degree Celcius and the salinity–depth gradient also became gentler while still decreasing. These characteristics identify the water mass as Japan Sea Proper Water, which is is formed by melting ice in the northernmost regions of the Sea and is characterized by high dissolved oxygen concentration, low salinity and low temperature. Within this water mass the community was dominated by the beroid ctenophore *Beroe abyssicola* Mortensen, 1927, a euplokamid cydippid species, *Bolinopsis infundibulum* F.O. Müller, 1776, and up to three small hydromedusan forms.

The highest richness of forms (combined data for Dives 1202 and 1204) occurred in the 400–600 m depth layer in Sagami Bay (Figure 4A), while in Toyama Bay richness was low in all layers (Figure 4B). New forms continued to occur with increasing depth in Sagami Bay (Figure 4A) but not in Toyama Bay (Figure 4B). Equitability (the distribution of individuals between those member forms) was investigated visually by graphing the relative abundances of all cnidarian and ctenophore forms according to depth layer (Figure 5A,B). Again, this was greatest in the 400–600 m depth layer. Species composition differed remarkably between Toyama and Sagami Bays. A

subsequent dive in the northern Japan Sea (43°39'N 139°33'E; 24 July 2001), also using the 'Shinkai 2000' submersible system, determined that the species composition of the midwater fauna in the Japan Sea does not vary appreciably below 400 m depth to depths of up to 1890 m (D.J.L., personal observation). This is contrary to the changing species composition of the midwater fauna over a similar depth range in the north-western Pacific Ocean (Toyokawa et al., 1998; Hunt & Lindsay, 1999; Vinogradov & Shushkina, 2002; Lindsay et al., 2004). Furthermore, subsequent dives in the Japan Sea outside Toyama Bay and around the Shiribeshi Seamount off western Hokkaido at 43°36'N 139°34'E (42 hours observation time) have identified only three more midwater cnidarian forms (*Ptychogena lactea* Agassiz, 1865; *Euphysa japonica* (Maas, 1909); *Koellikerina fasciculata* (Péron & Lesueur, 1810)) and one ctenophore form (Mertensiid sp.) (Miyake et al., 2004; D.J.L. & J.C.H., personal observation).

The relative abundances of forms in Sagami Bay differed between Dives 1202 and 1204 due to horizontal patchiness in distributions. For example, the normalized abundance (with respect to both time and horizontal distance travelled) of a species of Leptomedusa (also see Hunt & Lindsay, 1999, figure 5J) in the 300–400 m layer, the layer of maximum abundance, in Sagami Bay was 40-fold higher during 'Shinkai 2000' Dive 1202 than during Dive 1204, even though these dives were held only two days apart and at the same location (Figure 6A–C). A similar although less pronounced trend was observed for the rhopalonematid medusa *Arctapodema* sp. A (10-fold lower) (Figure 6D–F) and the cydippid ctenophore Bathyctenid sp. A (6-fold higher) (Figure 6G–I; also see Hunt & Lindsay, 1999, figure 5F) in the 900–1000 m layer, for the lobate ctenophore *Bathocyroe* sp. A (over 4-fold higher) (Figure 6J–L) in the 400-500 m layer, and for the lobate ctenophore *Bolinopsis mikado* Moser, 1907 (none observed on Dive 1202) in the surface layer. Such between-dive patchiness in normalized abundances was the rule rather than the exception.

The aforementioned gelatinous macrozooplankters *Arctapodema* sp. A, Bathyctenid sp. A, and *Bathocyroe* sp. A, although patchy in distribution were nevertheless some of the most abundant midwater forms in Sagami Bay. However, all of these species are as-yet undescribed. That three of the most abundant gelatinous macroplankton species in the mesopelagic zone of Sagami Bay are undescribed species attests to the current paucity of information on the biodiversity of this historically undersampled fauna.
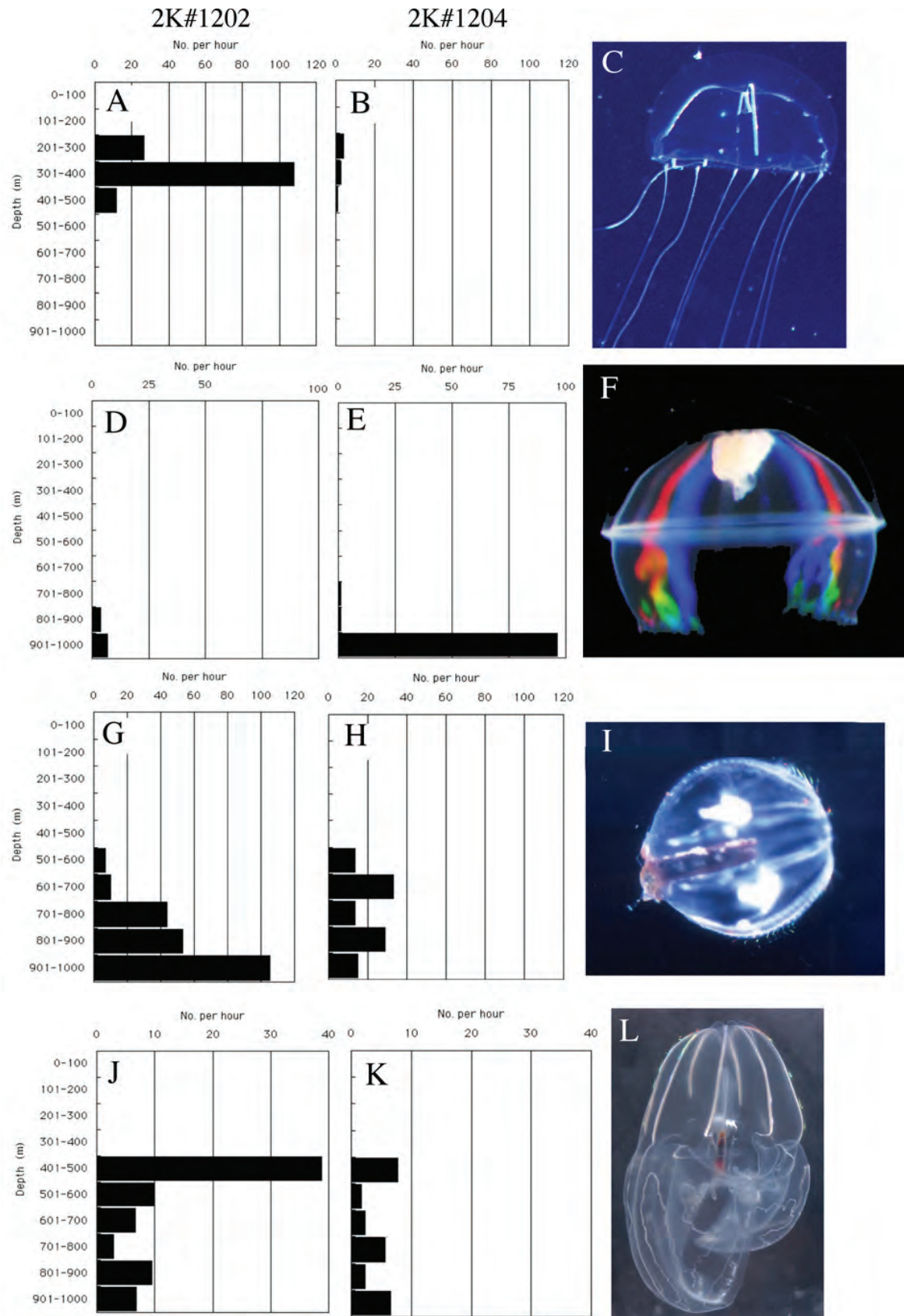
Figure 6. Vertical distribution and abundances on (A) 9 July and (B) 11 July 2000 of *Leptomedusa* sp. A in Sagami Bay; (C) external morphology of *Leptomedusa* sp. A (*in situ*); vertical distribution and abundances on (D) 9 July and (E) 11 July 2000 of the rhopalonematid medusa *Arctapodema* sp. A in Sagami Bay; (F) external morphology of the rhopalonematid medusa *Arctapodema* sp. A (in aquarium); vertical distribution and abundances on (G) 9 July and (H) 11 July 2000 of the cydippid ctenophore Bathyctenid sp. A in Sagami Bay; (I) external morphology of the cydippid ctenophore Bathyctenid sp. A (in aquarium); vertical distribution and abundances on (J) 9 July and (K) 11 July 2000 of the lobate ctenophore *Bathocyroe* sp. A in Sagami Bay; (L) external morphology of the lobate ctenophore *Bathocyroe* sp. A (in aquarium).

Table 3. *List of taxa recorded from Sagami Bay, Japan, using the submersibles 'Shinkai 2000' the ROV 'Dolphin-3K' and the ROV 'HyperDolphin' during the period 1993–2004. Taxa marked '*' were identified from collected specimens. Taxa marked '†' are new records for Japanese waters.*

Phylum Cnidaria Verrill, 1865
Class Hydrozoa Owen, 1843
Subclass Siphonophora Eschscholtz, 1829
Order Physonectae Haeckel, 1888
Family Apolemiidae Huxley, 1859
Genus *Apolemia* Eschscholtz, 1829
Apolemia sp. A*
Genus *Tottonia* (Margulis, 1976)†
Tottonia contorta (Margulis, 1976)*†
Family Agalmidae Brandt, 1835
Agalmidae sp. A
Genus *Marrus* Totton, 1954
Marrus aff. *antarcticus pacifica* Stepanjants, 1967*†
Marrus sp. A*
Marrus sp. B*
Genus *Agalma* Eschscholtz, 1825
Agalma okeni Eschscholtz, 1825*
Crystallomia rigidum Haeckel, 1869*
Genus *Halistemma* Huxley, 1859
Halistemma aff. *amphytridis* Lesueur & Petit, 1807*
Genus *Nanomia* Agassiz, 1865
Nanomia bijuga (Chiaje, 1841)*
Family Pyrostephidae Moser, 1925
Genus *Bargmannia* Totton, 1954
Bargmannia elongata Totton, 1954*†
Family Forskaliidae Haeckel, 1888
Genus *Forskalia* Kölliker, 1853
Forskalia formosa*†
Forskalia aff. *asymmetrica**†
Family Rhodaliidae (Haeckel, 1888)
Genus *Sagamalia* Kawamura, 1954
Sagamalia hinomaru (Kawamura, 1954)*
Order Calycophorae Leuckart, 1854
Family Hippopodiidae Kölliker, 1853
Genus *Vogtia* Kölliker, 1853
Vogtia serrata (Moser, 1925)*
Family Diphyidae Quoy & Gaimard, 1827
Diphyidae sp. A
Family Clausophyidae Totton, 1965
Clausophyidae sp. A

Arctapodema sp. A*
Genus *Colobonema* Vanhöffen, 1902
Colobonema sericeum Vanhöffen, 1902*
Genus *Crossota* Vanhöffen, 1902
Crossota rufobrunnea (Kramp, 1913)*
Genus *Pantachogon* Maas, 1893
Pantachogon sp. A
Class Scyphozoa Goette, 1887
Order Coronatae Vanhöffen, 1892
Family Periphyllidae Haeckel, 1880
Genus *Periphylla* Haeckel, 1880
Periphylla periphylla (Péron & Lesueur, 1810)*
Genus *Periphyllopsis* Vanhöffen, 1900
Periphyllopsis sp. A
Family Atollidae Bigelow, 1913
Genus *Atolla* Haeckel, 1880
Atolla wyvillei Haeckel, 1880*
Atolla vanhoeffeni Russell, 1957*
Atolla russelli Repelin, 1962*
Order Semaeostomeae Agassiz, 1862
Family Ulmaridae (Haeckel, 1879)
Subfamily Poraliinae Larson, 1986
Genus *Poralia* Vanhöffen, 1902†
Poralia rufescens Vanhöffen, 1902*
Subfamily Tiburoniinae Matsumoto, Raskoff & Lindsay, 2003†
Genus *Tiburonia* Matsumoto, Raskoff & Lindsay, 2003†
Tiburonia granrojo Matsumoto, Raskoff & Lindsay, 2003*†
Subfamily Deepstariinae Larson, 1986
Genus *Deepstaria* Russell, 1967
Deepstaria enigmatica Russell, 1967
Phylum Ctenophora Eschscholtz, 1829
Class Nuda Chun, 1880
Order Beroida Eschscholtz, 1829
Family Beroidae Eschscholtz, 1829
Genus *Beroe* Browne, 1756
Beroe abyssicola Mortensen, 1927*
Beroe cucumis Fabricius, 1789*
Beroe forskalii Milne Edwards, 1841*
Class Tentaculata Chun, 1880
Order Lobata Agassiz, 1860

Lobata sp. A
Lobata sp. B ('intacta')*†
Lobata sp. C
Lobata sp. D ('Llyria')*†
Family Bathocyroidae Madin & Harbison, 1982
  Genus *Bathocyroe* Madin & Harbison, 1982
    Bathocyroe sp. A*
Family Bolinopsidae Bigelow, 1921
  Genus *Bolinopsis* Agassiz, 1860
    Bolinopsis sp. A
    Bolinopsis mikado (Moser, 1907)*
Family Leucotheidae Krumbach, 1925
  Genus *Leucothea* Mertens, 1833
    Leucothea japonica Komai, 1918*
Family Lampoctenidae Harbison, Matsumoto & Robison, 2000
  Genus *Lampocteis* Harbison, Matsumoto & Robison, 2000
    Lampocteis cruentiventer Harbison, Matsumoto & Robison, 2000*†
Family Deiopeidae Chun, 1880
  Genus *Kiyohimea* Komai & Tomioka, 1940
    Kiyohimea usagi Matsumoto & Robison, 1992*
Order Thalassocalycida Madin & Harbison, 1978
  Genus *Thalassocalyce* Madin & Harbison, 1978
    Thalassocalyce inconstans Madin & Harbison, 1978
Order Cestida Gegenbaur, 1856
  Genus *Cestum* Gegenbaur, 1856
    Cestum veneris Lesueur, 1813*
Order Cydippida Lesson, 1843
  Cydippida sp. A ('Ctenoceros')*†
  Cydippida sp. B ('Agmayeria tortugensis')*
  Cydippida sp. C†
Family Aulacoctenidae
  Aulacoctenidae sp. A*†
  Genus *Aulacoctena* Mortensen, 1932
    Aulacoctena acuminata Mortensen, 1932*
Family Bathyctenidae Mortensen, 1932
  Bathyctenidae sp. A*†
Family Pleurobrachiidae Chun, 1880
  Genus *Pleurobrachia* Fleming, 1821
    Pleurobrachia sp.

Genus *Chuniphyes*
    Chuniphyes multidentata Lens & van Riemsdijk, 1908*
Family Prayidae Kölliker, 1853
  Genus *Praya* Quoy & Gaimard, in Blainville, 1834
    Praya dubia (Quoy & Gaimard, (1833) 1834)
  Genus *Desmophyes* (Haeckel, 1888)
    Desmophyes annectens Haeckel, 1888*
Subclass Hydroidomedusae Bouillon, Boero, Cicogna, Gili & Hughes, 1992
Order Anthomedusae Haeckel, 1879
Family Pandeidae Haeckel, 1879
  Pandeidae sp. A
  Genus *Pandea* Lesson, 1843
    Pandea rubra Bigelow, 1913
Order Leptomedusae Haeckel, 1886
  Leptomedusae sp. A
Family Aequoreidae Eschscholtz, 1829
  Genus *Aequorea* Péron & Lesueur, 1810
    Aequorea sp. A
Family Tiaropsidae Boero, Bouillon & Danovaro, 1987
  Genus *Tiaropsidium* Torrey, 1909
    Tiaropsidium sp. A*
Order Narcomedusae Haeckel, 1879
  Narcomedusae sp. A†
Family Aeginidae (Gegenbaur, 1857)
  Genus *Aegina* Eschscholtz, 1829
    Aegina citrea Eschscholtz, 1829*
  Genus *Aeginura* Haeckel, 1879
    Aeginura grimaldii Maas, 1904*
  Genus *Solmundella* Haeckel, 1879
    Solmundella bitentaculata (Quoy & Gaimard, 1833)*
Family Cuninidae Bigelow, 1913
  Cuninidae sp. A
  Genus *Solmissus* Haeckel, 1879
    Solmissus incisa (Fewkes, 1886)*
    Solmissus sp. A*
Order Trachymedusae Haeckel, 1866
Family Halicreatidae Fewkes, 1886
  Genus *Halicreas* Fewkes, 1882
    Halicreas minimum Fewkes, 1882*
  Genus *Botrynema* Browne, 1908
    Botrynema brucei Browne, 1908*
Family Rhopalonematidae Russell, 1953
  Genus *Arctapodema* Dall, 1907†

DISCUSSION

Species composition differed remarkably between Toyama and Sagami Bays. As two of the most common forms that occurred below 400 m in Toyama Bay (*Beroe abyssicola* and *Bolinopsis infundibulum*) have been reported previously from the surface waters of the Sea of Okhotsk (Toyokawa et al., 2003; M. Toyokawa, personal communication) it seems to follow that, as with the hard-bodied fauna (Tyler, 2002), the deep-sea gelatinous fauna is comprised of boreal or sub-boreal species that are only now evolving into a deep-sea mode of life. This is substantiated further because diversity was found to be much lower than in Sagami Bay according to all the indices investigated (Table 2), and because an asymptote was reached in the species/form accumulation curve versus time. An asymptote was not reached, however, even after seven hours of dive time in Sagami Bay, and both new cnidarian and ctenophore forms were still being recorded (Figure 2A,B).

The apparently lower diversity of ctenophore forms compared to cnidarian forms evident in Figure 4A may in part, but not fully, be due to the paucity of morphological characters known to be defining for the various ctenophore taxa (Podar et al., 2001). It is noted that the number of ctenophore species currently described is much lower than the number of pelagic cnidarians, and the importance of gaining more information on taxonomically important characters in the Ctenophora cannot be overstated.

Data obtained by visual observations from submersibles will be an underestimate of the true biological diversity due to the impossibility of identifying species based on either the biological species concept (Mayr & Ashlock, 1991) or the phylogenetic species concept (DeQuerioz, 1998). As concerns the biological species concept, this is of course also the case with net-caught samples preserved in formalin, with the added disadvantage that fragile gelatinous forms are often damaged beyond recognition.

Another advantage of submersible-based studies is that information collected by submersibles allows the resolution of forms based on a combination of behaviour and morphology, and the sometimes vastly different ecology of individuals within a species and its effect on diversity can be addressed. Examples of this phenomenon include the differing ecological niches of juvenile and adult forms, such as seen in the shrimps *Funchalia* (Lindsay et al., 2001) and *Solenocera* (Youngbluth, 1982) and in chiroteuthid squid (Vecchione et al., 1992), and the differing ecological niches of dimorphic males and females such as seen in the hyperiid amphipod *Phronima* (Laval, 1968).

Submersibles also allow rigorous identification of species associations, which also have the effect of increasing diversity. Examples of such associations include the shrimp *Funchalia* and pyrosomatid tunicates (Lindsay et al., 2001), *Deepstaria enigmatica* and *Anuropus* isopods (Barham & Pickwell, 1969; Lindsay et al., 2000, and references therein), hyperiid amphipods and various medusae and ctenophores (Harbison et al., 1977), and many other examples (Lindsay et al., 2001, and references therein). Such associations were not observed during dive surveys in the species-poor Japan Sea (D.J.L. & J.C.H., personal observation).

Even a small number of submersible dives in an area can yield useful information on the biological diversity of those areas, as a comparison of Figures 2, 4 & 5 and Table 2 shows. The comparative diversity of the cnidarian and ctenophore forms in Toyama Bay is obviously much lower than that of Sagami Bay by all the indices measured. In addition, the sampling of gelatinous organisms using submersible-mounted equipment allows fragile animals to be collected in pristine condition, which in turn allows accurate morphological data to be collected for these animals. It is only with such data that cryptic species, subspecies and ontogenetic forms can be identified, and without this data we cannot have an accurate description of the biodiversity at the survey area.

Behavioural and morphological information can be gained with even a single submersible dive. This behavioural information can not only help identify cryptic species or forms but can also give valuable information on trophic ecology and consequently niche separation. For example, narcomedusae of the genus *Solmissus* were observed feeding on physonect siphonophores, cydippid ctenophores, salps and trachymedusae while the undescribed bathyctenid species had ingested an ostracod (*Conchoecia ?amblypostha*). A wide range of size-classes of cnidarians and ctenophores occurred, from the tiny 1-cm diameter cydippid ctenophore Bathyctenid sp. A to the lobate ctenophore *Kiyohimea usagi* Matsumoto & Robison, 1992 with a maximum width of 50 cm in its stomodaeal plane, and from 1-cm long diphyid calycophoran siphonophores through to the giant *Praya dubia* (Quoy & Gaimard, (1833) 1834) that can reach a total length of 40 m (Robison, 1995). Size differentiation and character displacement (Tokeshi, 1999) may therefore be important in the maintenance of diversity in this assemblage. Furthermore, usually only one species per genus was present in any given depth layer, attesting to a high degree of generic (taxonomic) spread. This also suggests a reduced potential for competition.

The fine scale distribution data able to be gained by submersibles to a resolution of metres if not centimetres is valuable in determining mechanisms by which biodi-

versity is maintained and in estimating resource partitioning. For example, Leptomedusa sp. A was observed within the layer of maximum krill (*Euphausia similis* Sars, 1883 + *E. nana* Brinton, 1962) abundance and was also observed to capture these krill. Likewise, *Praya dubia* was observed immediately above this krill layer, suggesting a lie-in-wait strategy for feeding on krill or their predators during their diel migration. Submersible surveys during and after sundown should further elucidate the form of such resource partitioning. In addition to this data, biogeographical information pertaining to the presence of a species or form at the survey site can be obtained. It would seem that confirming the absence of a species or form at that site is considerably more difficult as we have observed some forms only once over the course of more than 150 hours of observations in Sagami Bay.

Due to the patchiness of distributions and the consequent between-dive variability in observed abundances (Figure 6), it is probably difficult to accurately estimate evenness/equitability. Even with nets, the between-tow variance in zooplankton species abundances has been reported to be in the order of 20–500% (Wiebe & Holland, 1968). Such patchiness, however, was determined not to contribute to diversity maintenance mechanisms during a study on the copepod assemblage of the North Pacific gyre over a range of temporal and spatial scales with ranked abundance curves being highly stable (McGowan & Walker, 1985). An accurate ranked abundance curve of the cnidarian forms at the survey site is probably difficult to obtain with only one or two dive surveys due to this patchiness, although it would be useful for investigating the degree of dominance of the community by common species and for approximation of the stability of the system. The use of far-ranging survey systems such as autonomous underwater vehicles (AUVs) for such studies should be investigated.

The depth layer with highest diversity of cnidarian and ctenophore forms (400–600 m; Figures 4A & 5A, Table 2) overlaps the depths at which diel vertical migrant populations and non-migrating populations of fish and shrimps co-occur during the day (500–700 m, Murano et al., 1976; D.J.L., unpublished data). The calanoid copepod community, as sampled by MTD nets (Motoda, 1971) of 80 cm mouth diameter and 0.5 mm mesh aperture, also exhibited a species richness maximum of 53 species at 500 m depth on 23 July 2000, although species richness remained high in deeper layers (D.J.L., unpublished data). The high richness of gelatinous forms in the 400–600 m depth layer during the day may be due to niche separation linked to predator and prey abundances and diversity, or alternatively to the overlapping daytime distributional

ranges of vertically migrating gelatinous plankton. The major micronektonic shrimp species in Sagami Bay include *Sergestes similis* Hansen, 1903, *Sergia prehensilis* Hanamura, 1979, *Bentheogennema borealis* (Rathbun, 1902) and *Hymenodora frontalis* Rathbun, 1902, all of which feed on cnidarians as part of their diet (Roe, 1984; Nishida et al., 1988; D.J.L., unpublished data). Preliminary night-time surveys of Sagami Bay on 5 May 2002 using the ROV 'HyperDolphin' identified several gelatinous diel vertical migrants (*Nanomia bijuga*, *Bargmannia elongata* Totton, 1954, *Solmissus* sp., *Atolla* sp., *Bathocyroe* sp.; D.J.L., unpublished data,) lending support to the hypothesis that the daytime peak in richness at 400–600 m depth was due to the effect of diel migrations. The lack of a clear richness peak for ctenophore forms in the 400–600 m depth layer may signify that a lower proportion of ctenophore forms undergo diel vertical migration compared with cnidarians. A combination of day and night surveys by submersibles and surveys using layered nets on the midwater community in Sagami Bay is necessary to conclusively determine the factors leading to the observed patterns in diversity.

In conclusion, submersibles can yield valuable information on many aspects of the biodiversity present at a given survey site provided that a sufficient number of dives by a suitably trained observer are conducted. Although valuable information on biogeography, taxonomy, trophic ecology and resource partitioning can be gained even with a single dive, it is only with multiple dives that accurate estimates of species/form diversity, richness and evenness, can be obtained. Inter-dive variability in abundances suggests that a bare minimum of three dives per hydrographic season is necessary to gain basic information on the biodiversity at any survey site. The present survey did, however, with only a limited number of dives, determine that the biodiversity of cnidarian and ctenophore forms in Toyama Bay is lower than that in Sagami Bay. It also identified a number of undescribed species and determined that a peak in the richness of cnidarian forms occurs in Sagami Bay at 400–600 m depth during the day.

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