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Spatial distribution and dietary overlap between Japanese anchovy *Engraulis japonicus* and moon jellyfish *Aurelia aurita* in the Seto Inland Sea, Japan

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SUMMARY: Biological and physical surveys were conducted in order to investigate the relationship between environmental conditions and the distribution of ichthyoplankton and jellyfish, and dietary overlap between the ichthyoplankton and jellyfish in the Seto Inland Sea (SIS), Japan. Ichthyoplankton, copepods, and jellyfish were collected during two cruises in July 2005 in the Sea of Hiuchi and in July 2006 in Hiroshima Bay within the SIS. Sea surface temperature (°C), salinity, bottom-layer dissolved oxygen (mg l^{-1}) and the abundance (no. m^{-2}) of fish eggs and larvae were significantly higher in the Sea of Hiuchi. Japanese anchovy was most dominant (69.3% in number of eggs and 52.3% in number of larvae) among the ichthyoplankton. Mean jellyfish biomass (g m^{-2}) in Hiroshima Bay was significantly higher (50-folds) than that in the Sea of Hiuchi. Moon jellyfish was the most dominant among the jellyfish collected, accounting for 85.6% in wet weight. Surface temperature had a significant effect on fish egg and larval distribution: abundance of fish eggs and larvae increased with increasing temperature. Jellyfish abundance was negatively correlated with the bottom-layer oxygen concentration. Stable isotope analysis indicated dietary overlap between the Japanese anchovy and the moon jellyfish in Hiroshima Bay.

Keywords: ichthyoplankton, stable isotope analysis, Sea of Hiuchi, Hiroshima Bay.

RESUMEN: DISTRIBUCIÓN ESPACIAL Y SOLAPAMIENTO DE DIETAS ENTRE LA ANCHOA JAPONESA *ENGRAULIS JAPONICUS* Y LA MEDUSA *AURELIA AURITA* EN EL MAR INTERIOR DE SETO, JAPÓN. – Se realizaron campañas físico-biológicas a fin de investigar la relación entre las condiciones ambientales y la distribución del ictioplancton y las medusas, y el solapamiento de sus dietas en el Mar Interior de Seto (SIS), Japón. Durante dos campañas, en julio de 2005 en el mar de Hiuchi y en julio de 2006 en la bahía de Hiroshima (SIS), se recolectaron ictioplancton, copépodos y medusas. La temperatura superficial (°C), la salinidad, el oxígeno disuelto en el fondo (mg l^{-1}) y la abundancia de los huevos y larvas de peces (no. m^{-2}) fueron significativamente mayores en el Mar de Hiuchi. La anchoa japonesa dominó el ictioplancton (69.3% en número de huevos y 52.3% de larvas). La biomasa media de medusas (g m^{-2}) en la bahía de Hiroshima fue significativamente mayor (50 veces) que en el Mar de Hiuchi. La medusa *Aurelia aurita* fue la dominante entre las medusas recogidas, lo que representó el 85.6% en peso húmedo. La temperatura superficial tuvo un efecto significativo sobre la distribución de huevos y larvas de peces: su abundancia aumentó al aumentar la temperatura. La abundancia de medusas se correlacionó negativamente con la concentración de oxígeno en la capa del fondo. Los análisis de isótopos estables indicaron una superposición en la dieta de la anchoa japonesa y la medusa *Aurelia aurita* en la bahía de Hiroshima.

Palabras clave: ictioplancton, análisis de isótopos estables, mar de Hiuchi, bahía de Hiroshima.

INTRODUCTION

An increase in the abundance and biomass of large gelatinous zooplankton such as cnidarians and ctenophores has occurred in marine ecosystems around the world (Purcell and Arai, 2001; Brodeur *et al.*, 2002), potentially causing a significant impact on smaller zooplankton and their predators in pelagic ecosystems (Uye and Ueta, 2004; Haslob *et al.*, 2007). The moon jellyfish *Aurelia aurita* is widely distributed throughout coastal waters of the world and has been considered as an important predator of zooplankton because of its high consumption rates (Möller, 1984; Nakayama *et al.*, 2003). In Japan, the biomass of moon jellyfish has increased over recent decades in coastal waters such as Tokyo Bay (Toyokawa *et al.*, 2000; Ishii, 2001) and the Seto Inland Sea (Uye and Ueta, 2004). Uye *et al.* (2003) observed moon jellyfish aggregations of up to 250 individuals m^{-2}, which were estimated to consume nearly 100% of the mesozooplankton biomass during summer months in coastal waters of the western Seto Inland Sea.

The Seto Inland Sea is a semi-enclosed basin surrounded by heavy urban, industrial and agricultural development, and receives significant freshwater from surrounding watersheds (Ochi *et al.*, 1978; Okaichi *et al.*, 1996). During summer months, excess nutrient loading from the land decreases dissolved oxygen (DO), with some areas as low as 2 mg l^{-1}. Moderate decreases in DO to near hypoxic conditions, although not lethal during short-term exposure, can reduce the ability of larval fish to escape and avoid predation and to forage for food (Breitburg *et al.*, 1994). Recent laboratory experiments reported that bell contraction rate and predation rate on fish larvae by moon jellyfish under oxygen concentrations of <2 mg l^{-1} were similar to those under higher oxygen concentrations (4–6 mg l^{-1}: Shoji *et al.*, 2005). These observations show that moon jellyfish are highly tolerant to low oxygen concentrations, as are several other jellyfish species (Breitburg *et al.*, 1994; Keister *et al.*, 2000; Thuesen *et al.*, 2005), and indicate that the relative importance of trophic flow from fish larvae to moon jellyfish may increase due to changes in predator-prey interactions during summer hypoxia in coastal waters (Shoji, 2008). Understanding the distribution of the jellyfish relative to environmental conditions is therefore important in examining the potential for compensation and predation between jellyfish and fish larvae.

In the present study, biological and physical surveys were conducted in the two innermost parts of the Seto Inland Sea (Sea of Hiuchi and Hiroshima Bay), where intermediate hypoxia prevails during summer months (Ochi *et al.*, 1978; Okaichi *et al.*, 1996). We compared the abundance, spatial distribution and effects of environmental conditions on moon jellyfish and ichthyoplankton in the two areas of the study. In addition, stable isotope analysis was applied to examine dietary overlap between the dominant fish (Japanese anchovy *Engraulis japonicus*) and jellyfish species (moon jellyfish *Aurelia aurita*) within the Hiroshima Bay, where moon jellyfish were abundant.

MATERIALS AND METHODS

Biological and physical surveys were conducted during two research cruises in July 2005 on the RV *Yakuri*, Kagawa Prefecture Fisheries Experimental Station (KPFES), in the Sea of Hiuchi, and in July 2006 on the RV *Aki*, Hiroshima Prefectural Fisheries and Ocean Technology Centre (HPFOTC), in Hiroshima Bay (Fig. 1). Ichthyoplankton and jellyfish were collected with a plankton net (0.45 m diameter, 0.33 mm mesh aperture) with a flowmeter at 17 and 13 stations in the Sea of Hiuchi and Hiroshima Bay, respectively. A vertical haul with the plankton net from 1 m above the sea bottom to the surface was made at each station. Jellyfish were sorted from the sample, identified and measured for bell diameter (mm) and wet weight (g) on the ship. Ichthyoplankton samples were preserved in 10% formalin. Vertical profiles of temperature (˚C), salinity and dissolved oxygen (DO) concentration (mg l^{-1}) were measured at each sampling event.

Ichthyoplankton were sorted in the laboratory and identified to the lowest taxa possible. Abundances of fish eggs and larvae were enumerated and expressed as the number m^{-2}, and jellyfish biomass as g m^{-2} according to the flow-meter counts. Physical (temperature, salinity and DO)

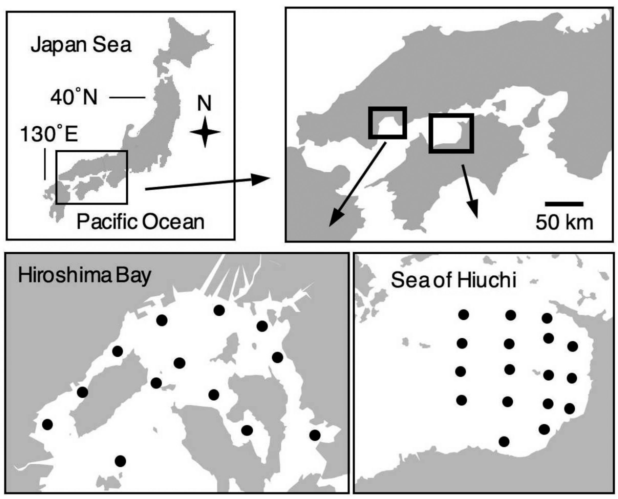

FIG. 1. – Map showing sampling stations in the Sea of Hiuchi and Hiroshima Bay, Seto Inland Sea, southwestern Japan.

and biological data (abundance of fish eggs and larvae and jellyfish) were compared between the surveyed areas (Sea of Hiuchi and Hiroshima Bay). Possible effects of the environmental factors (temperature, salinity and DO) on variability in ichthyoplankton and jellyfish abundance were examined by regression analysis. Temperature, salinity, and DO in surface, middle and bottom layers were used as explanatory variables and abundance of fish eggs (number m^{-2}), larvae (number m^{-2}) and jellyfish (g m^{-2}) as dependent variables. Data from the two sampling areas (Sea of Hiuchi and Hiroshima Bay) was combined for the regression analysis due to the small sample size (n=30).

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were analysed from a limited number of taxa collected from the 2006 survey in coastal areas of Hiroshima Bay. Collections included moon jellyfish (75-259 mm bell diameter, n=12), sub-samples of Japanese anchovy larvae (22.1-54.8 mm body length, n=10), copepods (n=6), particulate organic matter (POM: n=6), benthic fish (gobiids: 31.4-52.8 mm body length, n=6), crustacean zooplankton (decapods: 18.1-34.2 mm carapace length, n=6) and benthic microalgae (n=6). Copepods were collected using a plankton net (250 μm mesh) at 6 separate stations (randomly selected from the 13 stations). The POM samples were collected from six stations at just below the sea surface, pre-filtered with a 200 μm mesh to remove macrozooplankton, then filtered onto Whatman GF/C glass-fibre filters. All samples were preserved frozen at -30°C until further processing for stable isotope analysis; final processing of drying and preparation followed the methods of Nagata and Miyajima (2008). Stable isotope ratios of carbon and nitrogen were measured with a mass spectrometer fitted with an elemental analyser (ANCA-SL, PDZ Europa Inc). Isotope ratios are expressed as:

$$\delta X = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000$$

where δX is the stable isotope ($\delta^{13}C$ or $\delta^{15}N$) in units of ‰, and $R = {}^{13}C/{}^{12}C$ (${}^{15}N/{}^{14}N$). Atmospheric nitrogen (N_2) and PeeDee belemnite were used as the standards for nitrogen and carbon stable isotopes, respectively. To verify the accuracy of the analysis, DL-alanine was used as a secondary standard for carbon. Precision for isotopic analysis was within ±0.28‰ for both $\delta^{13}C$ and $\delta^{15}N$.

RESULTS

Environmental conditions

Sea surface (0.5 m in depth) temperatures ranged between 25.7 and 30.9°C (mean±SD = 28.2±1.6) in the Sea of Hiuchi and was higher in the southeastern part and lower in the northwest (Figs. 2a and 3a). In Hiroshima Bay, sea surface temperatures ranged between 22.5 and 25.3°C (24.0±0.8), with higher temperatures in the southern region and lower ones in the upper part of the bay. The area surveyed had a significant effect on the surface temperature (Wilcoxon test, d.f.=1, $p<0.0001$, Fig. 2a).

Surface salinity also differed between the survey areas (Fig. 2b, $p<0.0001$). Mean (SD) and range of surface salinity was 31.9±0.4 and 30.8-32.3 in the Sea of Hiuchi, and 25.3±1.9 and 19.8-27.5 in Hiroshima Bay. Surface salinities were lower in the upper part of Hiroshima Bay.

Dissolved oxygen concentration (DO) in the bottom layer ranged between 3.9 and 7.1 mg l^{-1} (5.5±0.9) in the Sea of Hiuchi and 2.8 and 6.1 mg l^{-1} (4.5±1.0) in the Hiroshima Bay (Fig. 2c). The effect of area surveyed on bottom DO was significant ($p=0.008$). Bottom DO was <4.0 mg l^{-1} in one area in the eastern part of the Sea of Hiuchi and <3.0 mg l^{-1} in the eastern part of Hiroshima Bay (Fig. 3a).

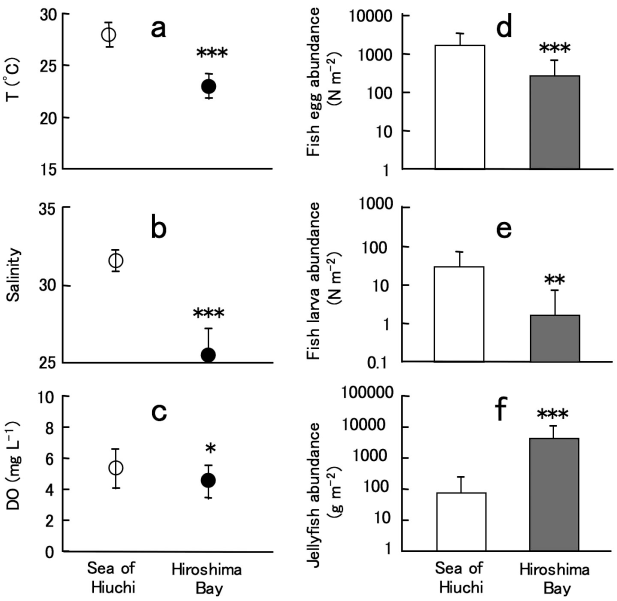

FIG. 2. – Comparison of physical and biological conditions between the Sea of Hiuchi and Hiroshima Bay. (a) Mean sea-surface temperature (T), (b) salinity, (c) bottom dissolved oxygen concentration (DO), (d) abundance of fish eggs, (e) larvae and (f) jellyfish; vertical bars denote standard deviation. Asterisks indicate significant difference between areas (*: $p<0.01$; **: $p<0.001$; ***: $p<0.0001$).

Distribution of ichthyoplankton and jellyfish

A total of 612 fish eggs were collected during the two cruises in the Sea of Hiuchi and Hiroshima Bay. Japanese anchovy eggs were the most dominant, accounting for 69.3% of the total number. The mean (range) of fish egg abundance was 1592.8±1812.9 m^{-2} (0-5875.7) in the Sea of Hiuchi and 36.6±74.5 m^{-2} (0-265.5) in Hiroshima Bay (Fig. 2d); abundance was significantly higher in the Sea of Hiuchi (p<0.0001). Fish eggs were almost exclusively found in the central Hiroshima

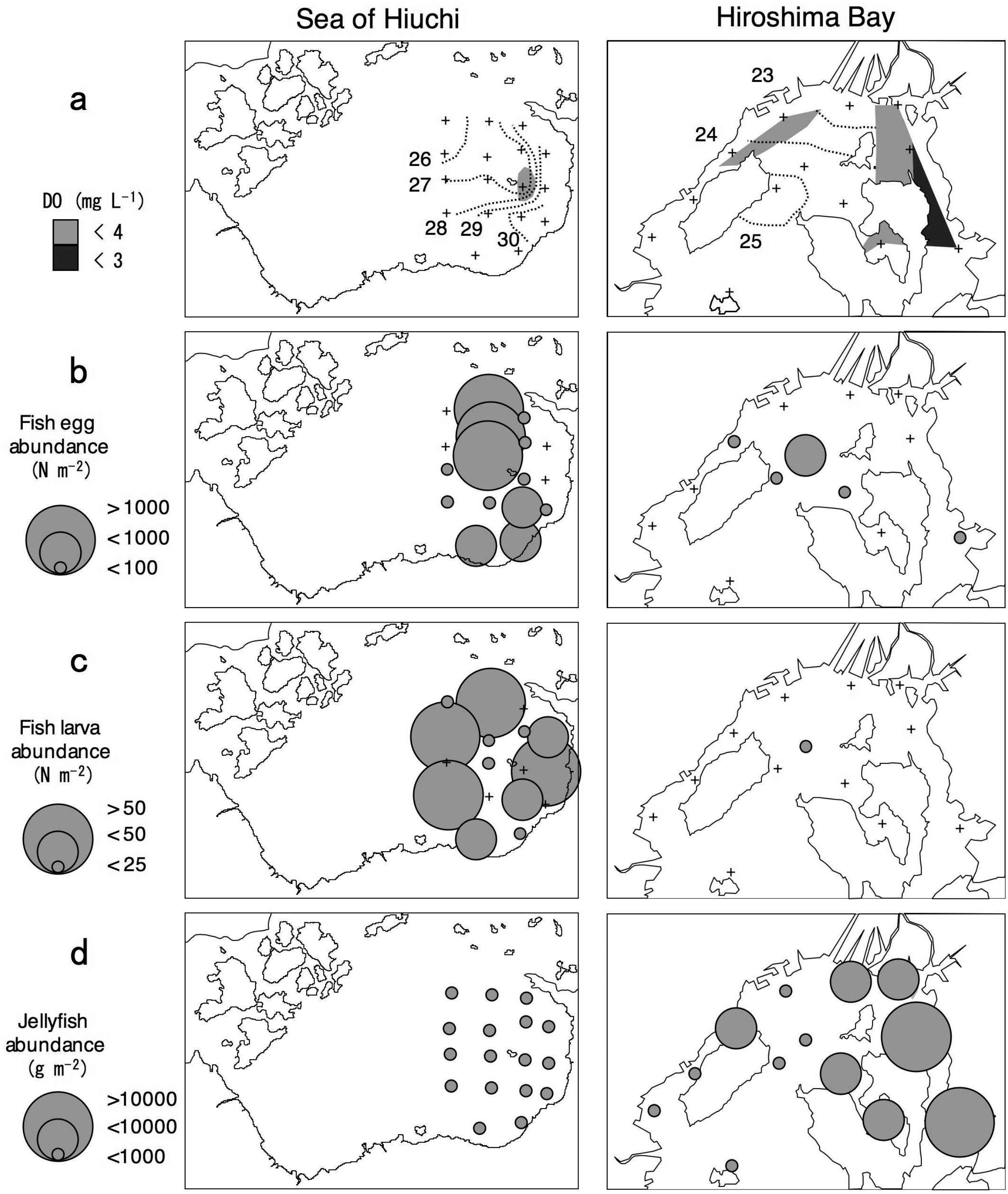

FIG. 3. – Horizontal distribution of sea-surface temperature (°C, contours) and (a) bottom oxygen concentration (DO), (b) fish egg, (c) fish larvae and (d) jellyfish abundance in the Sea of Hiuchi and Hiroshima Bay. Crosses indicate sampled stations.

Bay, while they were more evenly distributed over the whole Sea of Hiuchi. (Fig. 3b).

Of 258 fish larvae collected, Japanese anchovy (52.3% in number) were the most dominant during the two cruises. The mean±SD (range) of fish larvae abundance was 29.6±32.5 m^{-2} (0-97.8) in the Sea of Hiuchi and 1.1±3.9 m^{-2} (0-14.0) in Hiroshima Bay (Fig. 2e); abundance was significantly higher in the Sea of Hiuchi (p=0.0005). Fish larvae were only collected in the middle of Hiroshima Bay, whereas they were widely distributed in the Sea of Hiuchi (Fig. 3c).

Jellyfish were more abundant in Hiroshima Bay (Fig. 2f: p<0.0001). The mean (range) of jellyfish abundance was 82.9±150.4 g m^{-2} (1.0-419.3) in the Sea of Hiuchi and 4681.7±5477.8 g m^{-2} (637.5-16975.0) in Hiroshima Bay. Of the total jellyfish catch for the two cruises, the moon jellyfish *Aurelia aurita* was the most dominant, accounting for 85.6% of the total wet weight. Jellyfish were sparsely distributed throughout the Sea of Hiuchi, whereas they were more abundant in the northwestern and eastern parts of Hiroshima Bay (Fig. 3d).

Effects of environmental factors on the distribution

Of the environmental conditions tested, only sea surface temperature had an effect on fish egg (p=0.006: Fig. 4a) and larval abundance (p=0.006: Fig. 4b), and bottom DO on jellyfish abundance (p=0.0002: Fig. 4c). Fish eggs and larvae were more abundant in waters of higher sea surface temperature and jellyfish at lower levels of bottom water DO.

Analysis of stable isotope ratios of moon jellyfish and Japanese anchovy

Mean carbon and nitrogen isotope values of Japanese anchovy ($\delta^{13}C$=-18.2±1.5, $\delta^{15}N$=13.2±0.6) and moon jellyfish ($\delta^{13}C$=-18.2±1.3, $\delta^{15}N$=13.7±4.5) were similar, with higher variation expressed in nitrogen isotope values of moon jellyfish (Fig. 5). Mean nitrogen isotope values of benthic fish (gobiids: $\delta^{15}N$=13.0±0.4) were also similar to those of Japanese anchovy and moon jellyfish, but their mean carbon isotope value ($\delta^{13}C$=-13.8±0.7) was higher than both Japanese anchovy and moon jellyfish. All mean nitrogen isotope values of the two fish groups and moon jellyfish were higher than those of POM ($\delta^{15}N$=7.8±1.8), copepods ($\delta^{15}N$=9.2±1.1) and pelagic decapod larvae ($\delta^{15}N$=10.4±2.0).

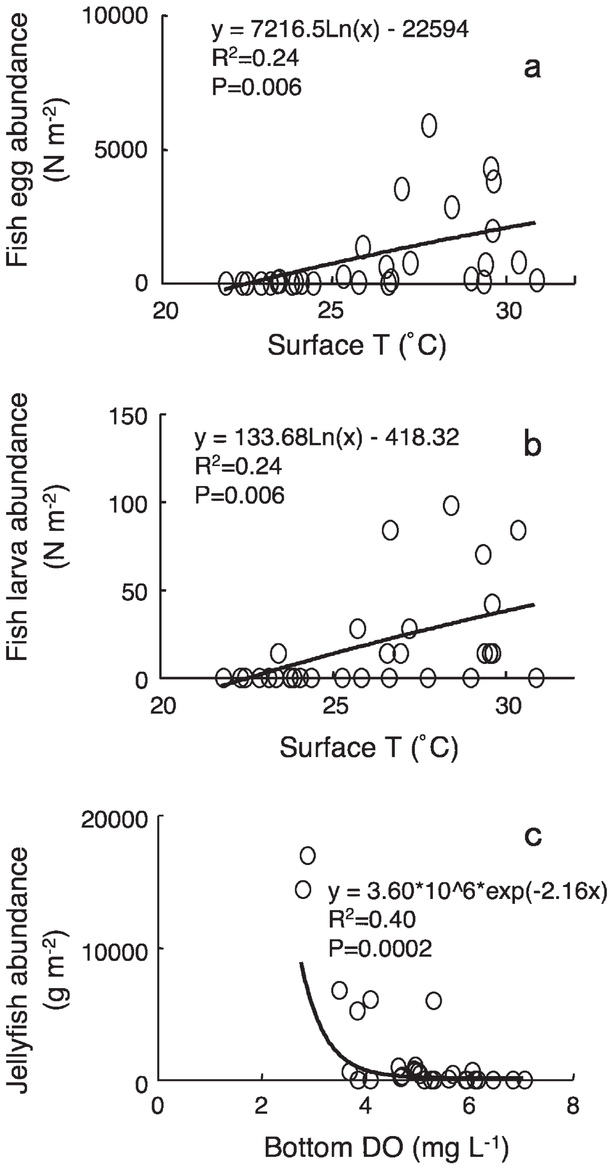

FIG. 4. – Plots of (a) fish egg and (b) fish larval abundance to sea surface temperature (T, °C), and (c) jellyfish abundance to bottom oxygen concentration (DO). Data from the Sea of Hiuchi and Hiroshima Bay are combined.

DISCUSSION

Distribution of ichthyoplankton and jellyfish in Hiroshima Bay

The highest abundances of fish eggs and larvae were observed in the central part of Hiroshima Bay. Nutritional input through the Ohta River—the northernmost part of Hiroshima Bay—and estuarine circulation enhance both primary and secondary production within the greater Hiroshima Bay (Hashimoto *et al.*, 2006). Chlorophyll-*a*

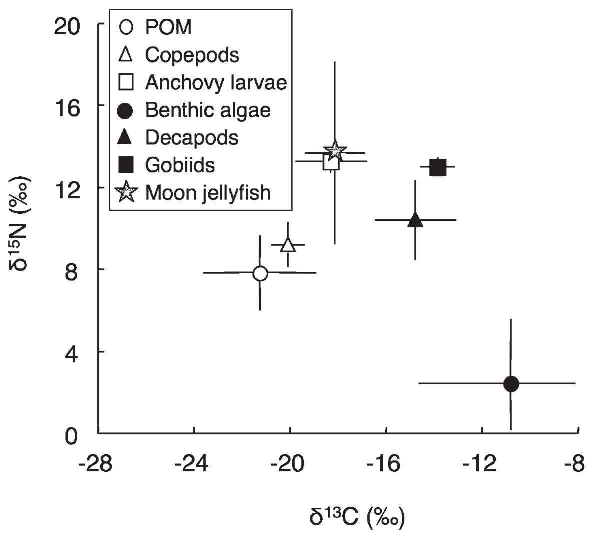

FIG. 5. – Plots of $\delta^{13}C$ versus $\delta^{15}N$ for samples collected in Hiroshima Bay in summer 2006. Points are mean values and bars represent standard deviation.

levels and therefore primary production of Hiroshima Bay is among the highest of the nine bays (from east to west: Kii Channel, Osaka Bay, Sea of Harima, Bisan Archipelago, Sea of Hiuchi, Sea of Aki, Hiroshima bay, Sea of Iyo, Sea of Suo) of the Seto Inland Sea (Okaichi *et al.*, 1996).

On the other hand, bottom-layer hypoxia (<3 mg l^{-1}) prevails in the coastal area of the northern Hiroshima Bay (Oceanographic Society of Japan, 1992; present study), and this was similarly observed by the present study with jellyfish abundance being higher in the northern coastal areas of the bay. In a laboratory study Shoji *et al.* (2005) observed moon jellyfish to have a high tolerance to low DO conditions (<2.0 mg l^{-1}); bell contract rate (an indices of feeding activity) of the moon jellyfish was constant through the DO levels tested (1.0-5.8 mg l^{-1}). High densities of the ctenophore *Mnemiopsis leidyi* in low DO concentrations have also been reported in Chesapeake Bay (Keister *et al.*, 2000) and are considered to have a substantial negative impact on ichthyoplankton through predation.

Fish larvae probably have a greater chance to survive due to higher prey concentrations in the central part of Hiroshima Bay in July, whereas fish eggs and larvae may be more vulnerable to starvation and predation in the northern coastal areas of the bay where biological production and water quality is low and jellyfish abundance is high. The spatial difference in the abundance of fish eggs and larvae between the central and coastal parts of the bay indicates that: 1) fish spawning was more concentrated in and around the central part of Hiroshima Bay, and/or 2) egg and larval mortality was higher in the coastal part of northern Hiroshima Bay.

Difference between the Sea of Hiuchi and Hiroshima Bay

Fish eggs, larvae and jellyfish abundance were significantly different between the two surveyed areas. Abundance of moon jellyfish, the dominant jellyfish species, was higher and temperature and salinity were lower in Hiroshima Bay than in the Sea of Hiuchi. Since higher abundance of moon jellyfish has been reported to be associated with higher temperatures in coastal waters of Japan (Uye and Ueta, 2004), other factors may be considered to have contributed to the higher jellyfish abundance in Hiroshima Bay. Uye and Ueta (2004) suggested that eutrophication and increases in reclamation and exploitation of shallow waters have been more favourable for moon jellyfish blooms in coastal waters of Japan. Moon jellyfish polyps readily use artificial substrate such as concrete blocks and plastic floats, which may have contributed to the increase in jellyfish abundance. In Hiroshima Bay, the natural shoreline has decreased to less than 40% of its original existence (Okaichi *et al.*, 1996), with much of it replaced by concrete seawalls which are favourable for jellyfish polyps. In addition, eutrophication coupled with summer hypoxia of coastal waters has been common in innermost parts of the Seto Inland Sea, such as Osaka Bay and Hiroshima Bay (Okaichi *et al.*, 1996, present study). We conclude that a combination of environmental factors such as increases in artificial shoreline eutrophication and summer hypoxia have a favourable influence, directly or indirectly, on moon jellyfish abundance in Hiroshima Bay.

In the present study, however, data obtained from two different areas in different years were analysed. The contrastive distribution and abundance of ichthyoplankton and jellyfish between Hiroshima Bay and the Sea of Hiuch (Figs. 2 and 3) might have reflected year-to-year variability physical and biological conditions in each area. For example, the total precipitation in Hiroshima City (899 mm) during the three months (from April to June in 2006) prior to the sampling in Hiroshima Bay was triple the values in the same period in 2005 (242 mm: Japan Meteorological Agency: http://www.jma.go.jp/jma/). Higher freshwater flow through the Ohta River—the northernmost part of Hiroshima Bay—increases primary and secondary production within the bay by enhancing the nutritional input and estuarine circulation (Hashimoto *et al*., 2006). Previous stomach contents analysis (Uye *et al*., 2003) and recent stable isotope analysis (present study) have shown copepods to be the main prey source of moon jellyfish in the Seto Inland Sea. An increase in freshwater flow through the Ohta River should enhance growth and survival of moon jellyfish in Hiroshima Bay by increasing production of their prey organisms, although the underlying mechanism would be complicated. Further investigation on the influence of variability in the physical and biological conditions on primary and secondary production of the coastal areas of the Seto Inland Sea in relation to growth and survival of moon jellyfish and ichthyoplankton would help to clarify the mechanism of moon jellyfish bloom, distribution and spatio-temporal fluctuation

Dietary overlap between moon jellyfish and Japanese anchovy

The application of stable isotopes (carbon and nitrogen) is an effective means of analysis for determining past feeding of moon jellyfish because: 1) direct observation of stomach contents of jellyfish cannot identify prey ingested by jellyfish collected from sampling gear, 2) information on night-time feeding of jellyfish cannot be obtained by usual day-time sampling, 3) inequalities in digestion rates of different prey contribute to underestimation or over-estimation of certain prey, and 4) diet analysis by visual inspection of stomach contents only provides a very short-term observation of diet. Brodeur *et al*. (2002) applied the stable isotopes to examine the Bering Sea pelagic food web and observed competition for food resources among the jellyfish community and age-0 walleye pollock *Theragra chalcogramma*. In the present study, strong overlaps in the feeding habits between moon jellyfish and Japanese anchovy were shown by stable isotope analysis. The feeding of moon jellyfish on zooplankton is size-selective, being performed by making a current through contraction by the bell (Costello and Colin, 1994; Uye *et al*., 2003). The Japanese anchovy, a dominant small pelagic fish in the Seto Inland Sea, feeds on zooplankton such as copepods from larvae and adults. The spatial distribution of the moon jellyfish and Japanese anchovy did not overlap in summer 2006 in Hiroshima Bay, but the result from stable isotopes suggests strong trophic overlap, which may result in significant competition for prey when their biomass becomes high. In the Seto Inland Sea, the annual catch of Japanese anchovy decreased from 100000 t in the mid-1980s to 16000 t in the late 1990s (Nagai, 2005). Expansion of summer hypoxia due to eutrophication, global warming and an increase in moon jellyfish biomass within the Seto Inland Sea may have led to significant pressure on larval Japanese anchovy, which has been expressed in the form of fisheries recruitment.

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