

Periodicity in the accumulation of gelatinous zooplankton during the summer season in the coastal area of Iyo-Nada, Japan

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Abstract

Gelatinous zooplankton collected and quantified daily at the sluice gate of the Ikata Nuclear Power Station along the coast of Iyo-Nada in the Seto Inland Sea were analyzed for the period 1998–2004 in an effort to correlate the number of these animals with the physical oceanographic conditions. Sudden periodic and nonperiodic increases of gelatinous zooplankton occur repeatedly from early summer to late autumn in nearshore areas. Periodic increases are synchronous with the spring tidal period. Nearshore tide-induced eddy development may play an important role for the aggregation process of gelatinous zooplankton, and the spring-neap tidal variation of the circulation induces increases of the gelatinous zooplankton population in coastal waters of the Iyo-Nada. Nonperiodic increases are attributable to typhoons and other storms. The strong shoreward currents due to the winds caused by these events transport gelatinous zooplankton to nearshore areas.

The processes of aggregation and transport of gelatinous zooplankton and their relationship with the physical environment are important scientific topics. Previous studies have shown that the magnitude of gelatinous zooplankton bloom is influenced not only by the biology and behavior of the animal, but also by the geographic setting and physical environment. Graham et al. (2001) reviewed studies on physical contexts for gelatinous zooplankton aggregations. They summarized the role of physical processes and phenomena that promote aggregation and transport of gelatinous zooplankton. These include accumulation of jellyfish along physical discontinuities. In addition, they suggested that further in situ observations are required in order to gain a better understanding of the relationship between behaviors and physical environments.

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Recently, unusually high concentrations of the scyphomedusa *Aurelia aurita* have been reported in the Seto Inland Sea (see Fig. 1). In Japanese coastal waters, the most abundant scyphozoan species is the *A. aurita* (Uye and Shimauchi 2005). The increase in *A. aurita* population is a recent phenomenon and has only become apparent in the last 10–20 yr. In a poll of fishermen, 70% of respondents answered that the *A. aurita* population had increased in the last 10 yr (i.e., 1993–2002) in Hiroshima Bay (Uye and Ueta 2004). Uye et al. (2003) reported that *A. aurita* formed dense aggregations in the coastal waters of Bungo Channel (Fig. 1) in the summer of 2000. Most of jellyfish compete with planktivorous finfish by consuming the same food resources, such as copepods, and they are also potential predators of fish eggs and larvae. Consequently, the increase in their biomass may diminish the fish standings and commercial harvest (Uye and Shimauchi 2005). Also, it has been reported that the extraordinary aggregation of gelatinous zooplankton has caused additional problems in the coastal areas, including the disturbance of fishing activities and the obstruction of seawater uptake by power plants and factories (Yasuda et al. 2003).

Gelatinous zooplankton have been collected daily at the water sluice gate of the Ikata Nuclear Power Station since the mid-1990s. The daily quantity of gelatinous zooplankton has been recorded since 1997. This is a unique record, and it indicates the temporal variation of the quantity of the gelatinous zooplankton. The purpose of the present paper is to clarify and discuss the characteristics of the variation from early summer to late autumn.

This paper is organized as follows. First, the data are explained. Next, we summarize the characteristics of the

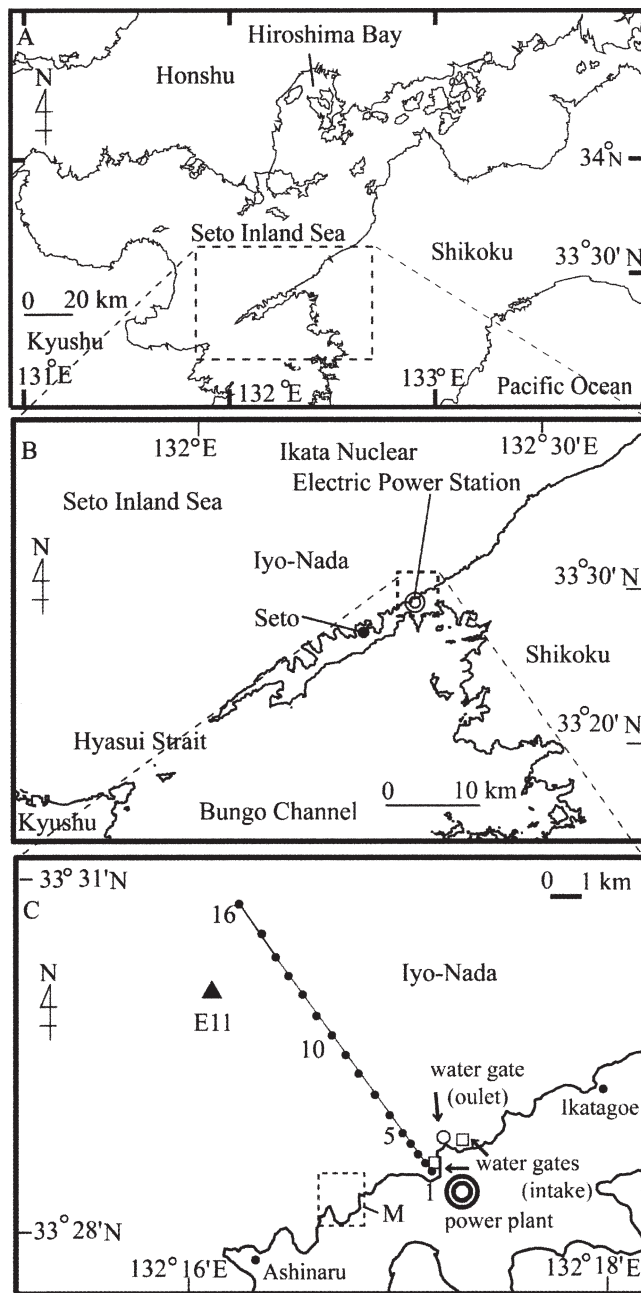


Fig. 1. Maps of the study sites. Seawater is pumped into the plant at two intake gates and discharged at a distinct gate indicated by arrows in panel C. Gelatinous zooplankton were collected at the intake gates. Water temperature and salinity from sea surface to bottom were measured at stations 1–16 from 13 to 15 September 2004. Currents were measured along the line with an ADCP. At station E11 (indicated by a triangle), the Ehime Prefecture observes water temperature and salinity once a month. A dotted square in panel C indicates the area captured by the aerial photograph in Fig. 9A.

temporal variation in the quantity of the gelatinous zooplankton, and the physical environment near the monitoring point is presented. Finally, we discuss the relationship between the temporal variability of gelatinous zooplankton in nearshore waters and the physical environment.

Methods

Research area—The Ikata Nuclear Power Station is located on Shikoku Island, and it faces the Iyo-Nada, western part of the Seto Inland Sea (Fig. 1). The shorelines near the power plant are quite complex, including many bays of various sizes. Tides and tidal currents dominate the variability in the Iyo-Nada, and the M_2 constituent (semidiurnal tidal component) of the tide is dominant in this sea (Yanagi and Higuchi 1981; Takeoka 2002); the tidal amplitude of the M_2 tidal current in Hayasui Strait is >0.7 m (as much as 1.5 m at the center of the strait), while that in the central Iyo-Nada is ~ 0.5 m. The currents near the power plant are strongly influenced by the complex shorelines, as will be described later.

Gelatinous zooplankton data—At the power plant, to cool the turbines, seawater is continuously pumped into the plant from two gates (located 17 m below the sea surface) and subsequently discharged from a third distinct gate (Fig. 1). The western intake gate pumps in water at the rate of $76 \text{ m}^3 \text{ s}^{-1}$, while the eastern one pumps at $65 \text{ m}^3 \text{ s}^{-1}$. Since jellyfish, small fish, etc., are captured in the seawater, these are automatically removed by the screen system in the plant. The mesh size of the screen is 1.0 cm. The power plant workers record wet weights of gelatinous zooplankton and fish once a day, from Monday to Saturday, classify them manually; this record has been kept since April 1997. We analyzed data collected at the western gate from 1998 to 2004 in the present study. The quantity for Sunday and Monday was calculated as one-half the amount that was recorded on Monday.

Physical data—Our physical data include water temperature, salinity, wind, currents, and images of sea-surface temperature. The Ehime Prefectural Fisheries Experimental Station (EPFES) conducts monthly hydrographic observations at 15 locations in the Iyo-Nada. Water temperature, salinity, and transparency, etc., are measured at each location. We used data of temperature and salinity obtained at station E11 (see Fig. 1C) from 1998 to 2004. The wind data were collected at Seto (Fig. 1B) by the Japan Meteorological Agency during the same period. The images of sea-surface temperature were taken from an airplane using a multispectrum scanner (MSS) on 08 September 2000 as a part of the comprehensive survey of the marine environment in the Bungo Channel conducted by Ehime Prefecture and the Center for Marine Environmental Studies (CMES), Ehime University.

Field survey—A CMES research boat, *Tobiuo*, made observations during an expedition conducted on 13–15 September 2004. We investigated temperature, salinity, density, currents, and distributions of gelatinous zooplankton around the water gate of the plant. Observation points and a line are shown in Fig. 1. Water temperature and salinity were measured from sea surface to bottom at each point by a CTD (conductivity-temperature-depth) profiler (Alec Electric, ACL-208-PDK). Currents were measured with an ADCP (acoustic Doppler current profiler) (RD Instruments, WH-ADCP 600 kHz).

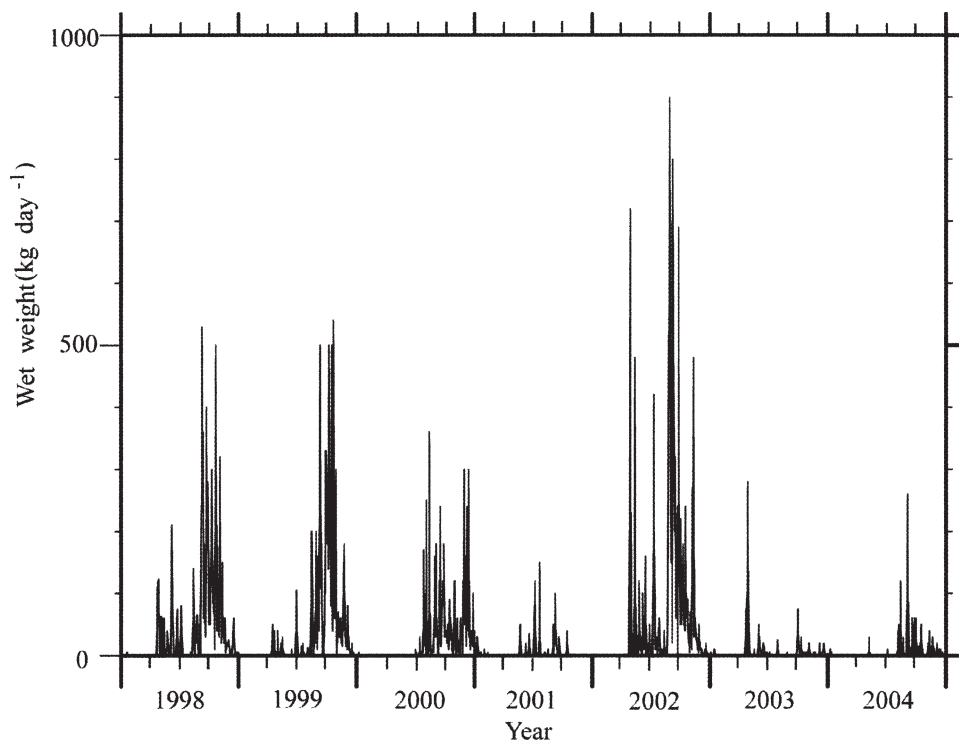


Fig. 2. Temporal variation of quantity of the gelatinous zooplankton gathered in the sluice gate of the power plant from 1998 to 2004.

Results

Temporal variation of the gelatinous zooplankton—The time series of the quantity of the gelatinous zooplankton gathered in the sluice gate of the power plant from 1998 to 2004 (Fig. 2) exhibits the following features: (1) The quantity changed seasonally with relatively short-term fluctuations. The number of gelatinous zooplankton increased gradually from early summer and reached a maximum around late summer to autumn. After peaking, the amount collected gradually decreased until hardly any gelatinous zooplankton was found from January to March. (2) The short-term fluctuations, which were characterized as rapid increases/decreases, may indicate that the quantity of the gelatinous zooplankton existing in nearshore waters changed within several days. (3) Interannual variability was evident. For example, the quantity of the gelatinous zooplankton in 2002 was relatively large. On the other hand, it decreased in 2003.

The periodicity of the fluctuations was also examined. Figure 3 shows a result of the spectral analysis, which was calculated by using data obtained from 01 April 1998 to 09 December 2002. The peak appears at about the same point as the spring-neap tidal period (14.8 d). The fluctuation may be synchronous with the tidal period. To investigate this, we examined the increases and the timing of the spring-neap tidal period. Figure 4 shows a time series of the quantity of gelatinous zooplankton from April to November in 1998. The “S” shown in the upper horizontal axis indicates the day of the new or full moon. If the increase of gelatinous zooplankton were not synchronous with the

spring-neap modulation, the phase relation between the increase and the moon would be shifted case by case. The figure shows that the amount of the gelatinous zooplankton correlates with the spring tidal period, though the increase in gelatinous zooplankton sometimes occurs several days before or after the spring tidal period. Furthermore, Fig. 5 indicates average wet weights of gelatinous zooplankton versus each phase of the moon. We used all the data from the seven-year observation period for the calculation. In this figure, the abscissa is the time axis of 15-d length referring to the day of new or full moon. It indicates that most increases are concentrated around the day of the new or full moon, which implies that the amount of the gelatinous zooplankton in the nearshore region might be influenced by the tidal current.

On the other hand, there are some exceptional cases where rapid increases did not occur at the time of spring tidal period. The downward-pointing arrows in Fig. 4 indicate several such cases. Thus, the short-term increases are of two types: the periodic occurrence around the spring tidal period and the nonperiodic sudden increase.

Physical nearshore environment—Seasonal variation of water temperature and salinity was examined by using monthly data observed at station E11 (Fig. 1) from 1998 to 2004. Figure 6 shows that the average water temperature gradually increases from March and reaches a maximum in September. The seasonal difference in water temperature is over 10°C. Similarly, average salinity also changes seasonally. After peaking in March, it gradually decreases and reaches a minimum in August.

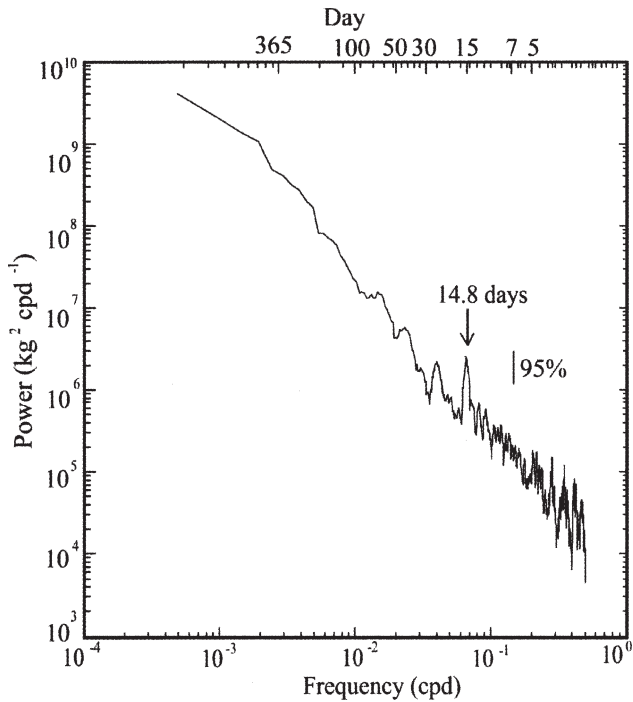


Fig. 3. Power spectra of the gelatinous zooplankton. Data collected from 01 April 1998 to 09 December 2002 were utilized ($n = 2048$, $df = 10$). The vertical line is the 95% confidence interval.

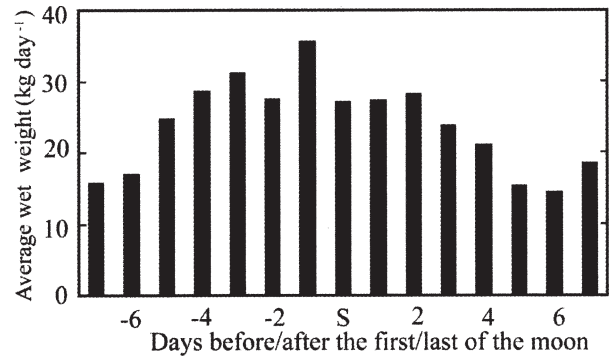


Fig. 5. Average wet weights of gelatinous zooplankton versus the phase of the moon. Data collected from 1998 to 2004 are shown.

A survey of the physical environment near the power plant was conducted on 13–15 September 2004 using the research boat *Tobiuo* of Ehime University. The observation points are shown in Fig. 1. Additionally, an annual set of oceanic observations (Ehime Prefecture 2003) that summarizes the data of comprehensive observations around the power plant was examined. The survey data were from three vertical transects of water temperature, salinity, and density, and six transects of currents along the line (Fig. 1). The current data showed that currents near the power plant

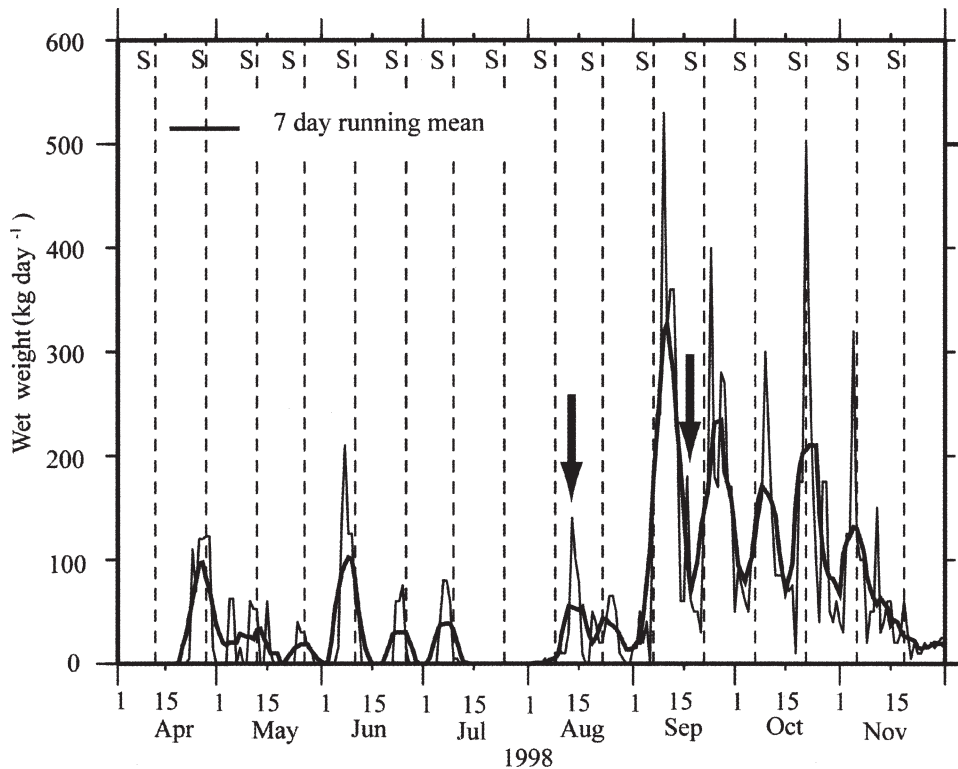


Fig. 4. Time series of the quantity of gelatinous zooplankton from July to November 1998. The raw data (thin line) and averaged data (a 7-d running mean, thick line) are shown. The “S” shown in the upper horizontal axis indicates the day of the spring tide. The increase in gelatinous zooplankton correlates with the spring tidal period, except in several cases indicated by the arrows.

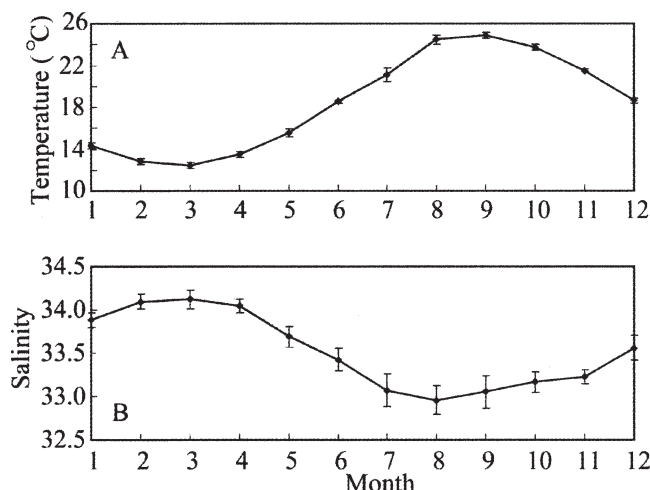


Fig. 6. Seasonal variation in (A) average water temperature and (B) salinity (\pm SE) at station E11. Monthly data collected from 1998 to 2004 were used.

were strongly influenced by the complex shoreline and the strong tidal currents offshore. Clockwise and counterclockwise topographic eddies caused by the tidal currents offshore formed in the bay where the sluice gate of power plant is. The vertical distributions in water temperature, salinity, and density were also influenced by the complex coastal geometries.

Figure 7 shows an example of currents observed with an ADCP. Panel A shows current vectors at 5 m below the sea surface during the ebb tidal period (southwestward currents developed offshore during this period.) on September 14 2004. We found that a counterclockwise eddy had formed in the bay. A clockwise eddy developed in the bay during the flood tidal period (see panel C). Other observations confirm this finding. An annual set of oceanic observations reported by Ehime Prefecture (2003) shows horizontal distributions of currents in the nearshore waters from Ashinaru to Ikatagoe (Fig. 1C), which indicate eddies like the one we observed (not shown). Next, we show the vertical distributions of water temperature, salinity and density observed on 14 September 2004 (Fig. 8). The offshore-stratified water was separated from the mixed water in the bay by a transition zone near station 10, where the temperature, salinity, and density of the surface water changed abruptly. Takeoka et al. (1997) studied the physical environment in the bay of the Bungo Channel (Fig. 1) and showed that the mixed region was formed by an integrated effect of vertical mixing due to the complicated geometries presented by groups of islands or a series of bays, because the mixing energy was supplied from the tidal kinetic energy. On the basis of the previous study, we concluded that the turbulence induced by the horizontal current shear would effectively mix the water column near the coast. The data of currents showed that the tide-induced eddy caused by the strong tidal currents offshore and the complicated geometry is predominant in the bay.

Finally, we examined the characteristics of wind variation measured in the Seto Inland Sea (see Fig. 1).

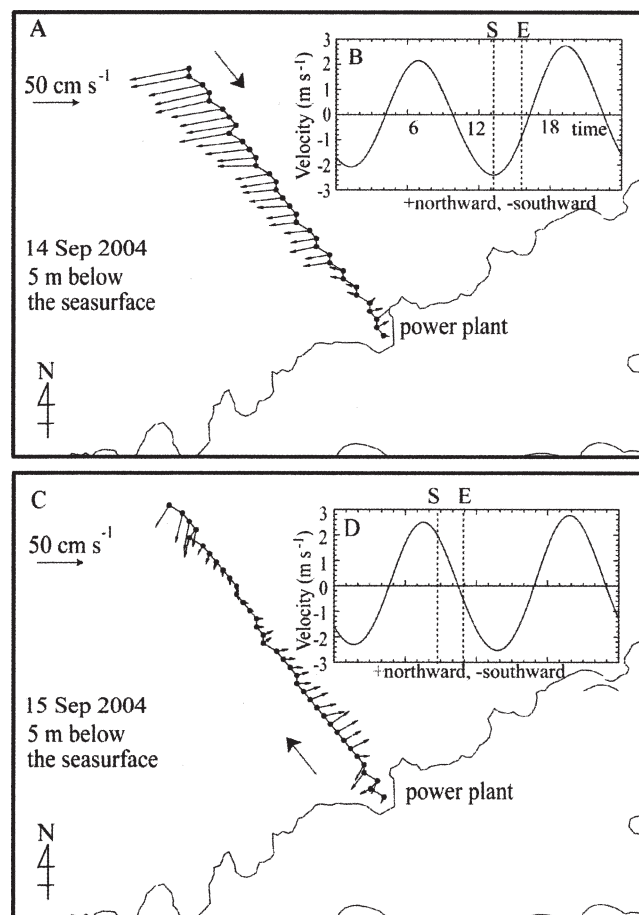


Fig. 7. (A) Currents measured at 5 m below the sea surface on 14 September 2004. Southwestward currents developed offshore. A counterclockwise eddy formed near the shore. (B) A time series of predicted tidal current at the Hayasui Strait. “S” and “E” indicate the start and end of the observation period, showing that the period was during the ebb tidal period. (C) Currents measured at 5 m below the sea surface on 15 September 2004. (D) A time series of predicted tidal current at the Hayasui Strait. “S” and “E” indicate the start and end of the observation period as in panel B. A clockwise eddy developed in the bay.

Clear seasonal variation and occurrences of sudden strong wind are evident (the figure is not shown). From autumn (around September) to early spring (around March), there was a northwestern wind. However, from spring (around April), a southerly wind increased gradually. After that, until the end of summer, the southerly wind was most frequent, although occasional strong northerly winds occurred due to the passage of a typhoon or a cold front.

Discussion

The daily accumulation of gelatinous zooplankton has two components: a periodic component related to the spring tidal period and a nonperiodic one. In this section, we discuss the process of these temporal variations of amounts of gelatinous zooplankton.

Kohama (pers. comm.) has frequently classified the gelatinous zooplankton sample gathered at the gates and

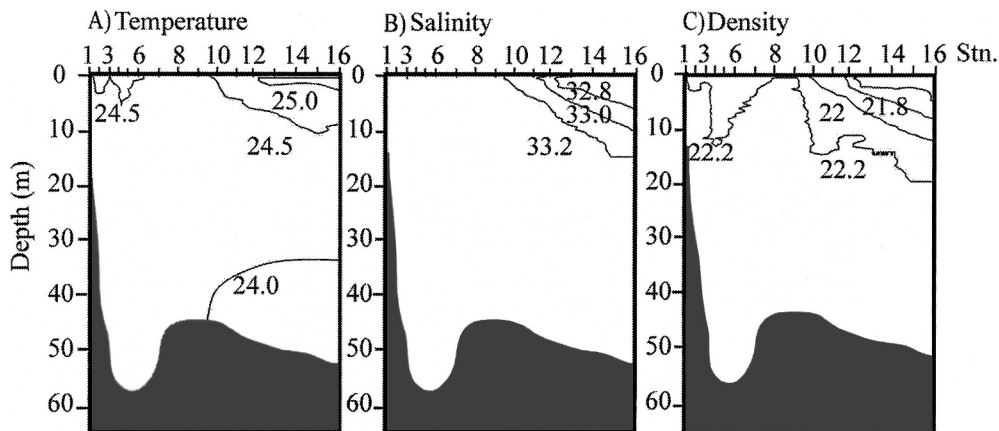


Fig. 8. Vertical distributions of (A) water temperature, (B) salinity, and (C) σ_t observed on 14 September 2004. Station locations are shown in Fig. 1C.

has shown that *Aurelia aurita* is the predominant species. *A. aurita* can swim, albeit slowly. It is well known that the gelatinous zooplankton are attracted to a certain bands of temperature or salinity (Arai 1997; Graham et al. 2001). Recently, Rakow and Graham (2006) showed that jellyfish swimming is associated with current shear. Consequently, jellyfish swimming does play a role in the accumulation of gelatinous zooplankton. On the other hand, it is known that the physical environment also plays a role. The convergence areas in the upper layer of fronts and the outer edges of eddies serve as aggregation points for gelatinous zooplankton, phytoplankton, and nongelatinous zooplankton (e.g., Farrell et al. 1991; Shanks et al. 2000; Helfrich and Pineda 2003). Thus, both biological behavior and physical environment probably play a role in the distribution of the gelatinous zooplankton in the Seto Inland Sea, but we consider the most important factor in this study to be the physical environment, taking into consideration this study's scale (1–2 km). Biological and physical effects operate at different scales (Genin et al. 2005; Rakow and Graham 2006). At large spatial scales (10–100 km), the horizontal distribution is dictated by physical features, while active swimming behavior by plankton is dominant at small scales (0.001–100 m) (Genin et al. 2005).

The data presented here show both periodic and nonperiodic increases in gelatinous zooplankton. Both tide-induced eddy and wind effects may be critical factors associated with the aggregation and transportation of gelatinous zooplankton in the coastal waters of Iyo-Nada. The periodic increase may possibly be due to the transport by tide-induced eddies. As described here, a tide-induced eddy develops in the bay where the sluice gate of the plant is located, and the convergence flow forms along the outer edge of the tide-induced eddy (e.g., Wolanski and Hamner 1988). It is considered that this convergence flow may assist the accumulation and transport of the gelatinous zooplankton, and therefore, the tidal eddy plays an important role for the transport and aggregation of the gelatinous zooplankton in this area. On the other hand, the nonperiodic increase is more likely caused by wind effect. The strong wind directed onshore may change the quantity

of the gelatinous zooplankton in the coastal sea. Recently, S. Magome (pers. comm.) observed movement of patches of *A. aurita* with aerial photography and drift experiments in the bay of the Bungo Channel (see Fig. 1). These gelatinous zooplankton did not move over large distances autonomously but were moved passively by currents induced by wind. On the basis of these studies, we consider that wind effects may induce nonperiodic increases in gelatinous zooplankton.

First, we discuss the detailed accumulation process of gelatinous zooplankton associated with the tide-induced eddy and the spring-neap tidal period. Aerial photographs taken on 07 July 1990 were examined in order to understand the role of physical features in the aggregation of gelatinous zooplankton. An example taken at ebb tide is shown in Fig. 9. The dotted square shown in Fig. 1C indicates the location of this area. The horizontal scale of the bay is almost the same as the bay where the sluice gate of the power plant is located. This picture was taken after heavy rain and floods caused lumber and other debris to be washed out into the Iyo-Nada of the Seto Inland Sea. Obviously, the flotsam had accumulated at the edge of a tide-induced eddy. Since the picture was taken at the ebb tidal period, a tide-induced eddy would form in the west-side sea area of the tip of the headland. In a previous study on the tide-induced eddy, the formation process leading to the eddy and its expansion were examined by Takeoka and Higuchi (1982). They demonstrated experimentally that an eddy can be induced by the ideal topology of the shoreline. Their findings are summarized schematically in Fig. 10. At slack tide (Fig. 10A), a counterclockwise eddy, which may have developed during flood tide, remains inside the bay. As the speed of the tidal current increases (Fig. 10B,C), the current around the mouth of the bay gradually turns until it is recognizable as a clockwise eddy. The diameter of the eddy increases until the end of ebb tidal period, and it reaches a maximum at the next slack tidal period (Fig. 10F). The eddies observed in coastal waters of the Iyo-Nada have a quite similar features. On the basis of the study, we considered that a portion of the flotsam reached the shore as a result of eddy expansion. Considering the

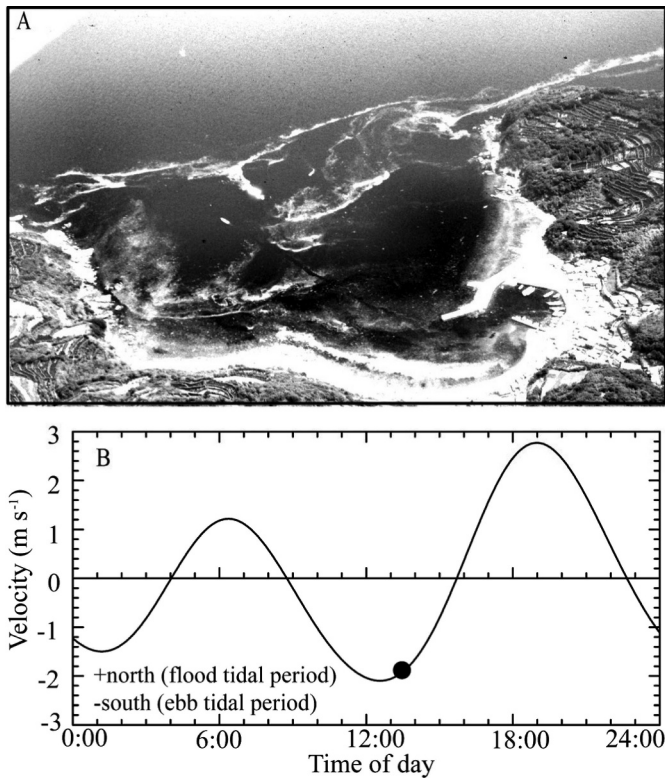


Fig. 9. (A) Aerial photograph taken on 07 July 1990. Many lumber, wood, and chips are aggregated along the edge of the tide-induced eddy, and a portion of the flotsam has reached the shore. (B) A time series of the predicted tidal current in the Hayasui Strait. The photograph in panel A was taken during the ebb tidal period, as shown by the time indicated by the dot.

results presented here and those previous studies mentioned earlier, this distribution may reflect what happens with the gelatinous zooplankton. Figure 9 shows that the convergence area reaches a very nearshore region due to the expansion of the tide-induced eddy, and it implies that the gelatinous zooplankton may also approach the nearshore region in the same way. Indeed, during our survey of 13–15 September 2004, we observed that the number of gelatinous zooplankton was relatively high around the edge of the eddy, though there were unfortunately no dense patches of gelatinous zooplankton during the observation period. This implies that the convergence flow caused by the tide-induced eddy serves to accumulate gelatinous zooplankton in this area.

The spring-neap tidal change of the eddy may be a critical factor in inducing the periodic increase of the gelatinous zooplankton at the sluice gate. The size and strength of the eddy change according to the speed of the current in the mainstream region (Wolanski et al. 1984; Wolanski et al. 1989). The diameter of the induced tidal eddy becomes larger during the spring tidal period. The observation data during 13–15 September 2004 and the photograph shown in Fig. 9 indicate the scale of the eddy. The diameter of the tide-induced eddy during spring tidal period observed on 13–15 September 2004 was almost 2 km, which is larger than the horizontal scale of the bay. On the other hand, the

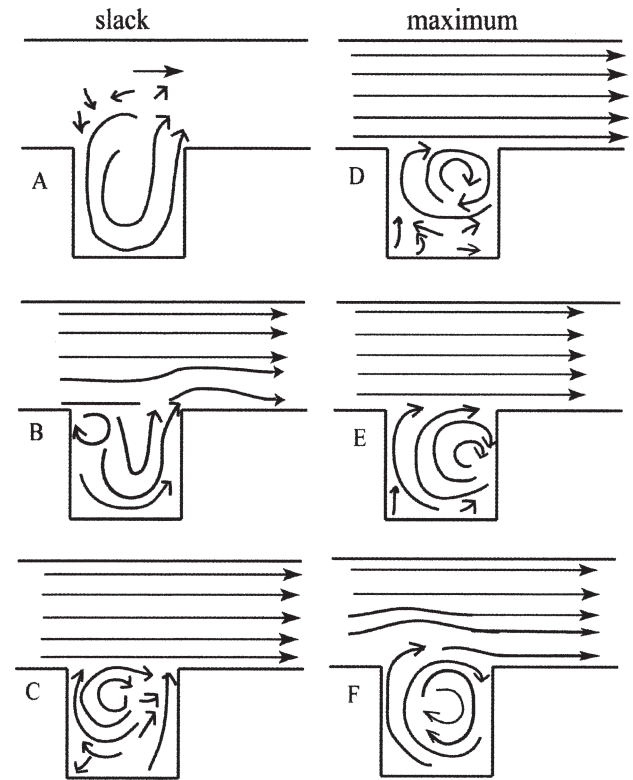


Fig. 10. Schematic of the process by which the tide-induced eddy forms in the idealized bay (after Takeoka and Higuchi 1982).

photograph (Fig. 9) was taken during the neap tidal period. The size of the eddy developing during the neap tidal period was nearly the same size of the bay (diameter ~ 1 km), since the drifting flotsam reached the shore. Biomass difference between the spring and neap tidal periods may be induced by this difference of the scale and angular velocity of the eddy. During the spring tidal period, the eddy can entrain the gelatinous zooplankton existing in a larger area, and entrained gelatinous zooplankton are transported to the inner area of the bay by faster flows. Therefore the quantity collected at the water gate periodically increases during the spring tidal period (Figs. 4, 5). Wind effects may cause the nonperiodic increases in gelatinous zooplankton. The large-scale increases that are not related to the spring tidal period may be related to strong shoreward winds due to typhoons and storms. As described before, a southerly shoreward wind predominates during the summer, and occasional bursts of strong northerly seaward winds occur during this time due to the typhoons and storms. The nonperiodic increases in gelatinous zooplankton correlate with these bursts of strong onshore winds. As an example, Fig. 11 shows the temporal variations of the quantity of gathered gelatinous zooplankton and wind in August 2000. The data indicate that the increase of gelatinous zooplankton occurred around the spring tidal period, but a spiky peak appeared on 14 August, a time outside this period. During mid-August in 2000, a shoreward temporal strong wind occurred, though southwesterly winds were dominant during this period. Therefore, we conclude that the wind

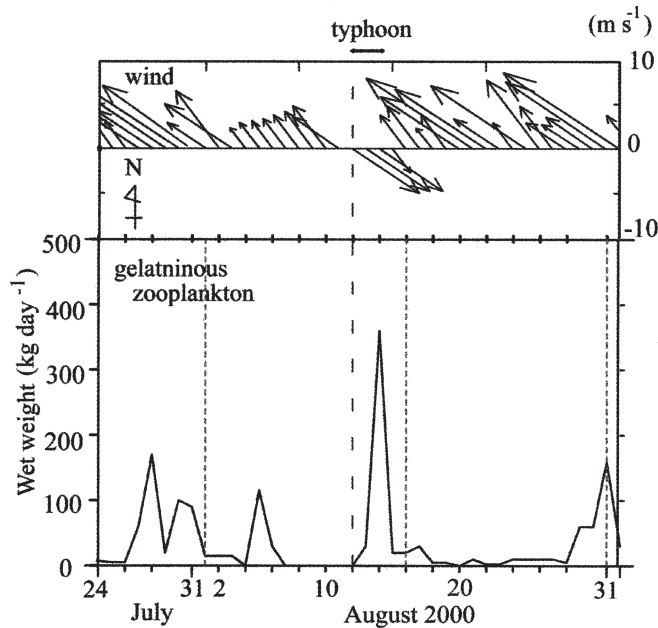


Fig. 11. Temporal variations of the quantity of gathered gelatinous zooplankton and wind from 24 July to 31 August 2000. The number of captured gelatinous zooplankton increased when wind direction was shoreward. The dotted lines indicate the spring tide.

effect due to the typhoon likely induced this aggregation event. Furthermore, besides the time of passage of a typhoon or a front, the wind affects transportation of gelatinous zooplankton. In Fig. 4, the biomass peak sometimes appears at times just before and after the spring tidal period. We consider that the wind effects may cause these shifting patterns. Wind speed and direction changes day by day. Hence, the wind effects for the transport of the gelatinous zooplankton also change. Since the wind effects overlap with the tidal effect, the biomass peaks are not completely coincident with the spring tidal period.

Next, we examined sea-surface temperature observed with a multispectral scanner (MSS) for evidence of an eddy in other bays of the Iyo-Nada. Curving flows such as the tide-induced eddy generate vertical secondary circulation that is characterized by upwelling near the center of the eddy and downwelling near the outer edge (e.g., Wolanski et al. 1984; Geyer and Signell 1990; Geyer 1993). The secondary circulation caused by the eddy generates locally vertical mixing and induces the horizontal difference in sea-surface temperature. Wolanski et al. (1984) showed that eddies developing around islands can be mapped from horizontal distributions of sea-surface temperature and satellite images of turbidity patterns. Prompted by this, we analyzed data of sea-surface water temperature in the coastal area of the Iyo-Nada from an image taken on 08 September 2000 (Fig. 12). From the figure, it is evident that cold-water patches appeared at the tip of headlands, implying that the flow separation downstream of the headlands generated the eddy. (Unfortunately, we cannot recognize the eddy developing in the bay where the sluice gate is located, because the resolution of the image is not

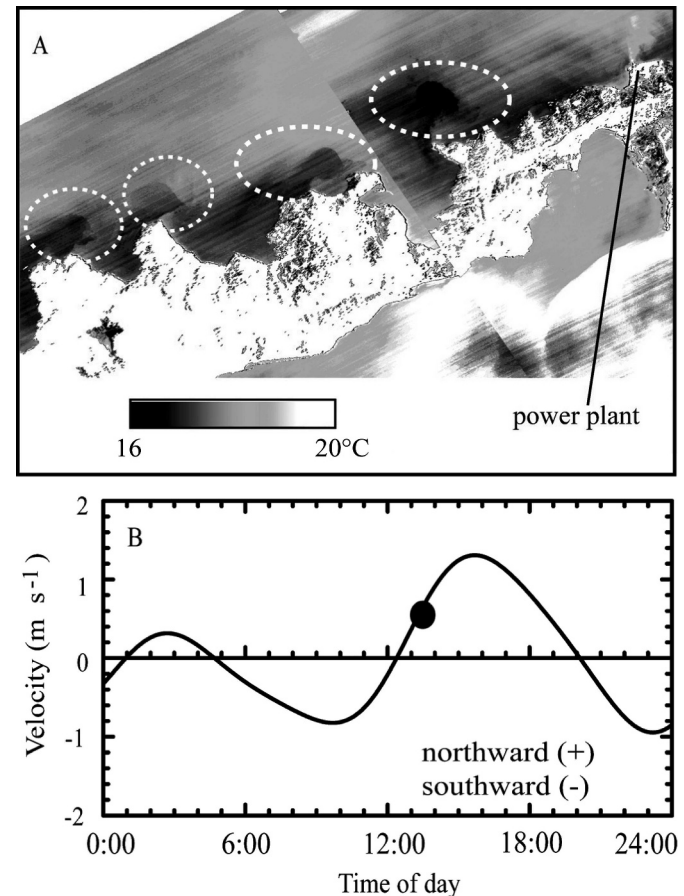


Fig. 12. (A) Sea-surface temperature observed on 08 September 2000. Dotted lines show the relatively cold areas near the tip of the headlands. (B) A time series of predicted tidal current in the Hayasui Strait. The dot indicates the time that the picture was taken, which was during the flood tidal period.

enough.) We speculate that the physical characteristics due to the complicated geometry may play an important role for the accumulation and transport of *A. aurita* in the coastal waters of the Iyo-Nada.

To predict the quantity of the gelatinous zooplankton is an urgent and important issue for fishermen, power plants, and factories. The data show that the temporal variation of gelatinous zooplankton collected at the sluice gate of the plant is not random, but exhibits a strong regularity. In this area, the spring-neap tidal period and the tangent of wind speed and direction will be good indexes. As described already, the data indicate a year-to-year variation of the abundance of gelatinous zooplankton. This is another important scientific problem and should be analyzed, since investigation into the cause of the year-to-year variation may provide some indications of the cause of the recent abundance of gelatinous zooplankton.

References

- ARAI, M. N. 1997. A functional biology of Scyphozoa. Chapman & Hall.
- EHIME PREFECTURE. 2003. Observation report on the Ikata nuclear power plant [in Japanese].

- FARRELL, T. M., D. BRACHER, AND J. ROUGHGARDEN. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr.* **36**: 279–288.
- GENIN, A., J. S. JAFFE, R. REEF, C. RICHTER, AND P. J. S. FRANKS. 2005. Swimming against the flow: A mechanism of zooplankton aggregation. *Science* **308**: 860–862.
- GEYER, W. R. 1993. Three-dimensional tidal flow around headlands. *J. Geophys. Res.* **98**: 955–966.
- , AND R. P. SIGNELL. 1990. Measurements of tidal flow around a headland with shipboard acoustic Doppler current profiler. *J. Geophys. Res.* **95**: 3189–3197.
- GRAHAM, W. G., F. PAGES, AND W. M. HAMNER. 2001. A physical context for gelatinous zooplankton aggregations: A review. *Hydrobiologia* **451**: 199–212.
- HELFRICH, K. R., AND J. PINEDA. 2003. Accumulation of particles in propagating fronts. *Limnol. Oceanogr.* **48**: 1509–1520.
- RAKOW, K. C., AND W. M. GRAHAM. 2006. Orientation and swimming mechanics by the scyphomedusa *Aurelia* sp. in shear flow. *Limnol. Oceanogr.* **51**: 1097–1106.
- SHANKS, A. L., J. LARGIER, L. BRINK, J. BRUBACKER, AND R. HOOFF. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol. Oceanogr.* **45**: 230–236.
- TAKEOKA, H. 2002. Progress in Seto Inland Sea Research. *J. Oceanogr.* **58**: 93–108.
- , AND H. HIGUCHI. 1982. Water exchange due to local eddies in harbors and embayments. *Bull. Coast. Oceanogr.* **19**: 175–182.
- , A. KANEDA, AND H. ANAMI. 1997. Tidal fronts induced by horizontal contrast of vertical mixing efficiency. *J. Oceanogr.* **53**: 563–570.
- UYE, S., N. FUJII, AND H. TAKEOKA. 2003. Unusual aggregations of the scyphomedusa *Aurelia aurita* in coastal waters along western Shikoku, Japan. *Plankton Biol. Ecol.* **50**: 17–21.
- , AND H. SHIMAUCHI. 2005. Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the inland sea of Japan. *J. Plankton Res.* **27**: 237–248.
- , AND Y. UETA. 2004. Recent increase of jellyfish populations and their nuisance to fisheries in the inland sea of Japan. *Bull. Jpn. Soc. Fish. Oceanogr.*, **68**: 9–19 [in Japanese with English abstract].
- WOLANSKI, E., D. BURRAGE, AND K. BRAIAN. 1989. Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. *Cont. Shelf Res.* **9**: 479–496.
- , AND W. M. HAMNER. 1988. Topographically controlled fronts in the ocean and their biological influence. *Science* **241**: 177–181.
- , J. IMBERGER, AND M. L. HERON. 1984. Island wakes in shallow coastal waters. *J. Geophys. Res.* **89**: 10553–10569.
- YANAGI, T., AND H. HIGUCHI. 1981. Tide and tidal current in the Seto Inland Sea, p. 555–558. *In* Proceedings of the 28th Conference of Coastal Engineering. JSCE.
- YASUDA, T., S. UENO, AND A. ADACHI. 2003. Umi no UFO kurage. Kouseisyakouseikaku [in Japanese].

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