Feeding habit of juvenile fishes associated with drifting seaweeds in the East China Sea with reference to oceanographic parameters

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Abstract

Many commercially important fishes associate with drifting seaweeds in their juvenile stage, however, the ecological significance of drifting seaweeds for juvenile fishes is still unclear. We postulated that the following two hypotheses may be applicable for juvenile fishes associate with drifting seaweeds, the "concentration of food supply" hypothesis: juvenile fishes are attracted by phytal animals on the drifting seaweeds and the "indicator-log" hypothesis: fish use accumulations of drifting seaweed as an indicator of productive areas (e.g. frontal areas) for food. We investigated the frontal areas, zooplankton abundance around the drifting seaweed, and the food availability of fish juveniles associated with drifting seaweed accumulations in the East China Sea in 2012 and 2013. A total of 14 drifting seaweed mass and 22 species (*n* = 408) of fish juveniles were collected. We found that 49.7 - 99.7 % of the individual fed on planktonic food and the feeding incidence on phytal animals was less than 50 %. Although drifting seaweeds were aggregated around the frontal areas of surface currents, the zooplankton abundance was not significantly different between these frontal areas and other areas. Our findings indicate that ecological significance of drifting seaweeds as feeding habit is relatively low for juvenile fishes associated with drifting seaweeds.

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Key words: Drifting seaweed; Fish juveniles; Feeding habitat; East China Sea

Drifting seaweeds are defined as floating algae or sea grasses that are detached from their base by the wind or waves (Komatsu et al. 2004). Fish juveniles (over 113 species belonging to 51 families) have been observed in conjunction with drifting seaweeds near the coastal areas of Japan, and many commercially important species associate with them, such as yellowtail *Seriola quinqueradiata*, jack mackerel *Trachurus japonicus*, greater amberjack *Seriola dumerili*, rockfish *Sebastes* spp*.,* threadsail filefish *Stephanolepis cirrhifer* and parrot bass *Oplegnathus fasciatus* (Senta 1965). Yamamoto et al. (2007) mentioned that *S. quinqueradiata* spawns around the edge of continental shelf from January to May in East China Sea (ECS) and juveniles (1.5 - 18 cm in total length) associate with drifting seaweeds (Senta 1965), which are caught by small purse seine fishery and used for aquaculture seedlings (Kubo 2004). Recently, catch of *S. quinqueradiata* juveniles has gradually decreased presumably because of dramatic changes in world climate (Nakada 2002). Komatsu et al. (2014) mentioned that the unusual distributions of drifting seaweeds observed in the ECS in 2012 may influence the marine organisms associated with drifting seaweeds; the catch of *S. quinqueradiata* juveniles around Japan in 2012 was 16 % lower compared to the prior year's catch (Minato Newspaper 2013). Although the importance of drifting seaweeds for the early life of fishes has been pointed out (e.g. Senta 1965, 1986; Hanaoka 1986; Komatsu et al. 2006), ecological significance of drifting seaweeds for juvenile fishes is still unclear. Revealing the ecological significance of drifting seaweeds for juvenile fishes will provide scientific information for stock management and sustainable utilization of *S. quinqueradiata* juveniles for the aquaculture seedlings.

It is speculated that drifting seaweeds provide a habitat, food and refuge for associated fishes (Vandendriessche et al. 2007). Of these, we postulate that the ecological importance of drifting seaweed is food habitat of juvenile fishes, since food availability is one of the most important controls in the early life stages of fishes (Sogard 1997). As for the hypotheses about food availability, the 'indicator-log' hypothesis and the 'concentration of food supply' hypothesis are proposed (reviewed by Fréon & Dagorn 2000).

The indicator-log hypothesis (Hall 1992) assumes that natural floating objects are often indicators of biologically rich water masses for tunas, because most natural floating objects originate in rich areas (i.e., river mouth, mangrove swamps) and remain within these rich water mass, or because they aggregate in rich frontal zones. This hypothesis is extended to larval and juvenile fishes, that is fish larvae and juveniles associated with drifting floating structures may benefit from drifting movements into the convergence where planktonic food is accumulated (Castro et al. 2002). Drifting seaweeds are trapped by the frontal area in the surface water's convergence area (Yoshida 1963; Komatsu et al. 2008, 2014), where it is widely recognized that oceanic frontal areas are highly productive (e.g., Lalli and Parsons 1997) because the convergence of ocean currents may aggregate organisms, which might lead to enhanced biological production (Mann and Lazier 2005). Since fish juveniles associated with drifting seaweed mostly fed on planktonic foods (Senta 1965; Ida 1967; Senta 1986), indicator-log hypothesis can be applicable for them. Although the densities of invertebrates (Kingsford and Choat 1985) and neustons (Vandendriessche et al. 2006) are higher around the drifting seaweeds than other areas, these invertebrate and neuston densities contain phytal animals associated with drifting seaweeds. It has also reported that prey densities including zooplankton around the drifting seaweeds were not high compared to open water around the San Juan Archipelago, Washington, USA (Shaffer et al. 1995). However, little is known about the zooplankton abundance in the frontal area where drifting seaweeds are accumulated and, it is still not tested if the indicator-log hypothesis is valid for juvenile fishes.

The concentration of food supply hypothesis states that certain pelagic predators aggregate around floating objects to feed upon the fauna of smaller fishes that also associate under these floating objects (Gooding and Magnuson 1967). Phytal animals (i.e., fauna on the drifting seaweeds) such as Amphipoda, Isopoda, Cirripedes and Decapod crustaceans are frequently found on drifting seaweeds forming communities (Sano et al. 2003, Aoki 2004), and we speculated that fish juveniles are also attracted to floating objects to feed on phytal animals. Splitnose rockfish *Sebastes diploproa* juveniles associated with drifting seaweeds exclusively feed on epiphytic amphipod species (Shaffer et al. 1995), and *S. cirrhifer* and hairfinned leatherjacket *Paramonacanthus japonicus* (Yamasaki et al. 2014), and *O. fasciatus* (Ida et al. 1967) fed on phytal animals as well as planktonic food.

In the present study we investigated the distribution of drifting seaweeds, the zooplankton abundance around the drifting seaweeds and the food availability of juvenile fishes, and we evaluated whether the indicator-log hypothesis and the concentration of food supply hypothesis are applicable for the juvenile fishes associated with drifting seaweeds. Then, we discussed ecological significance of drifting seaweeds as a food habitat for juvenile fishes.

Materials and methods

Field sampling

We chose the sea surrounding the Goto Islands in the ECS (hereinafter referred to as the Goto Islands Sea) as study field. Goto Islands Sea is located in the northeastern part of the ECS (Fig. 1) and is recognized as productive area and one of the popular fishing grounds in the ECS. A large part of the Goto Islands Sea is on the continental shelf (< 200 m depth), but the southward part exceeds 600 m in depth. The water mass distribution and ocean currents in the Goto Islands Sea are strongly affected by water masses from the Tsushima Warm Current and coastal water flowing out of estuaries in the adjacent islands in Japan, and the influence of these water masses shows large seasonal and interannual variabilities (Tsujita 1954; Inoue 1981). In the Goto Islands Sea, floating structures such as drifting seaweeds accumulate around the shelf-break region, and this area becomes a fishing ground of *S. quinqueradiata* juveniles associated with drifting seaweeds from May to June (Yamashita and Iwasa 1984). In this paper, we define “frontal area” as the area of surface water convergence.

A total of seven grid surveys at the shelf-break region (32° 06' N – 32° 30' N, 129° 18' E – 129° 36' E; Fig. 1) in the Goto Islands Sea were made by the T/V Kakuyo-Maru of Nagasaki University during 2012 (22 – 24 May and 30 July) and 2013 (11 – 12 and 17 April, 27 – 29 May, 3 – 5 June and 22 July). The observation lines were set (32° 06' N, 129° 24' E – 32° 30' N, 129° 24' E) and/or (32° 06' N, 129° 30' E – 32° 30' N, 129° 30' E) along the shelf break region (Fig. 1), except for the May 2012 survey, when observation was conducted along the lines described in Figure 1. During the daytime (06:00 – 17:30), accumulations of drifting seaweed were identified (approx. > 1 m dia.) along the observation line visually and then they were retrieved together with their associated fish juveniles, with the use of a large plankton net (2 m dia., mesh = 0.5 mm). Along one observation line, 3 to 5 sampling stations were set including the stations that covered most of the northern and southern parts of the observation line, and the shelf break region and drifting seaweeds were located. An exception was the 22 – 24 May 2012 survey, for which a total of 13 sampling stations were set (described in Fig. 3a).

At each sampling station, the vertical profiles of water temperature and salinity were measured using a conductivity-temperature-depth (CTD) profiler (SBE-911 plus, Sea-Bird Electronics, Bellevue, WA) from the sea surface to 200 m depth (mean intervals of CTD station: 9.6 km). Zooplanktons were sampled with a Norpac net (45 cm dia., mesh = 0.33 mm) towing from 20 m depth to the surface with a towing speed of 1 m s^{-1} during the hours 06:00 – 19:50. A flow meter (Rigo, Tokyo) was attached to the opening of the Norpac net to measure the volume of filtered water. Zooplankton and fish juveniles were immediately fixed in 10 % buffered formalin solution.

←Fig. 1

Sample analysis

The volume of filtered water collected during the Norpac net tow at each sampling station was calculated using a calibrated flow meter. Plankton samples of each sampling station were divided and zooplankton were strained following the method of Omori and Ikeda (1976) and dried in a desiccator over silica gel at ambient temperature for 3 days. Divided samples were also used for the measurement of the composition and density of the zooplankton. The zooplankton abundance A (mg DW m^{-3}) was calculated using the following Equation (1):

$$A = (WS^{-1})V^{-1}, \qquad (1)$$

where W is the dry weight of zooplanktons in a divided sample, S is the fraction of the sample that was divided, and V is the total volume of water sampled (m^3).

The species composition was determined by classifying the zooplankton into the lowest possible taxon, and the number of individuals for each classified group were counted according to a guideline (Chihara and Murano 1997), using a stereoscopic microscope. The density of the zooplankton Dz (number per m^{-3}) was calculated using the following Eq. (2):

$$Dz = (NS^{-1})V^{-1}, \tag{2}$$

where N is the total number of zooplankton in a divided sample.

All fish juveniles were identified at the species level (Okiyama 1988), and were grouped based on the difference in their usage of drifting seaweed as follows: (1) the fish always in the seaweed: the group of fishes that stay within the branches of the seaweed, (2) the fish that touch the seaweed: the group of fishes that touch drifting seaweed with their body, (3) the fish swimming around the seaweed: the fishes that swim around the drifting seaweeds with close association, and (4) others: undefined fish described (Senta 1965, 1986). *S. quinqueradiata* exceeding 150 mm in total length (TL) was defined as an independent group of species. Up to 30 specimens of conspecific fish juveniles were randomly sampled from each sampling station for the investigation of stomach contents.

Body size (± 0.01 mm TL) and wet weight (± 0.1 mg) of the fish juveniles were measured with calipers and an electronic balance, respectively. The intact stomachs were removed under a stereoscopic microscope, by cutting anterior to the esophagus and posterior to the large intestine. As for the agastric species, the anterior part of gut was removed. The all contents of stomach and/or anterior part of gut were removed onto a Petri dish with a few drops of 10 % formalin solution. All prey items in the stomachs were identified to the lowest possible taxon and counted. The prey items disintegrated were defined diagnostic part (e.g. head) as one item, and the prey items that could not be identified were excluded from analysis.

Chesson's selectivity index α_i (Chesson 1983) for each conspecific fish juvenile was calculated based on the following Eq. (3):

$$\alpha_i = \frac{(r_i / n_i)}{\sum_{i=1}^{m} (r_i / n_i)}, \tag{3}$$

where r_i indicates the number of items of prey type i in the consumer's diet and n_i indicates the *in situ* density of the prey items. If there were no items of prey type i *in situ* density, we defined n_i as a 1/4 density of the lowest number of the *in situ* prey items. When there were m food types, $\alpha_i = 1/m$ was defined as neutral. Positive selectivity was determined when the selectivity index significantly exceeded the neutral.

Feeding incidence F (%) on planktonic food or phytal animals for each group followed by Senta

(1965, 1986) was calculated by fish species and individual based on the following Eq. (4):

$$F = F_n A_n^{-1} 100\,, \tag{4}$$

where F_n indicates the number of fish group or species that fed on prey items (planktonic food or phytal animals) and A_n indicates the total number of analyzed fish group or species.

The convergence of ocean currents is one of the most important parameters to control the aggregation of organisms, and thus the convergence was estimated in this study. The current velocity data was based on those estimated by the Japan Coastal Ocean Prediction Experiment (JCOPE2) ocean reanalysis system (Miyazawa et al. 2009). The horizontal divergence in the spherical coordinates, D, was computed using the following Eq. (5):

$$D = \frac{u_{i+1,j} - u_{i,j}}{a\cos\varphi_j \Delta\lambda} + \frac{v_{i,j+1}\cos\varphi_j - v_{i,j}\cos\varphi_j}{a\cos\varphi_i \Delta\varphi}\,, \tag{5}$$

where subscripts i and j are the grid indices in the longitudinal and meridional directions, respectively, $u_{i,j}$ and $v_{i,j}$ are the eastward and northward components of surface current velocity, φ_j is the latitude of the j-th grid in the meridional direction, $\Delta\lambda$ and $\Delta\varphi$ are the difference in longitude and latitude between two adjacent grids in the longitudinal and latitudinal directions, respectively. The convergence area was defined as the area where $D \times (-1)$ exceeds 2.0×10^{-6} (s^{-1}). The temperature data of the JCOPE2 reanalysis system were also used for illustrating the water-mass distributions. The Grid Analysis and Displaying System (version 2.0.2) and Ocean Data View (version 4.6.2) software programs were used for plotting the JCOPE2 and *in situ* CTD data, respectively.

Data analysis

The zooplankton abundance and the composition of zooplankton between the seaweed-found and other areas, and between the frontal areas and other areas were compared. In order to compare the differences in the zooplankton abundance and the composition of each zooplankton between seaweed-found and other areas and between frontal areas and other areas *t*-tests were used. Chesson's selectivity index values of fish juveniles with the neutral values were compared by *t*-test (Chesson 1983). Statistical analysis was carried out by using Stat View 5.0 (SAS Institute. Inc.), and p-values < 0.05 were considered significant in all analyses.

Results

Frontal area and distribution of drifting seaweeds

We described the frontal area by the horizontal current in 23 May and 30 July 2012, and 12 April, 17 April and 22 July 2013 (Fig. 2a–e). Areas of convergence of horizontal currents were found around the shelf break during the periods of field campaigns (Fig. 2a–e). Three latitudinally extending frontal zones were observed: between low-salinity, warm and high-salinity, cold water masses around 32° 10' N and 32° 27' N on 30 July 2012 (Fig. 3b), between warm and cold water masses around 32° 08' N on 11 – 12 April 2013 (Fig. 3c), and between low and high-salinity water masses around 32° 10' N and 32° 25' N on 22 July 2013 (Fig. 3e) based on the *in situ* CTD data.

We caught a total of 14 accumulations of drifting seaweed and two floating structures: fishing gear and bamboo, and fish juveniles associated with floating structures were excluded from the analysis. Drifting seaweeds were found around the shelf-break region between 32° 12' N and 32° 30' N, and many patches of drifting seaweed were observed at Station (Stn.) 10 on 23 – 24 May 2012 (Fig. 3a), and Stn. 2 and Stn. 5 on 17 April 2013 (Fig. 3d). Within the 14 accumulations of drifting seaweeds, seven (50.0 %) were distributed in a frontal area by the ocean current during the survey period. Drifting seaweeds were also distributed around a frontal area which was marked at the latitudinal gradient of salinity around 32° 27' N (Fig. 3b) on 30 July 2012.

←Fig. 2
Fig. 3

Zooplankton abundance and species composition

The abundance of zooplankton in the sampling stations of the frontal area with drifting seaweed was not different from those without seaweed (drifting seaweed vs. other stations, t-test, p= 0.54 – 0.92 Fig. 4a,b), (frontal area vs. other stations, t-test, p = 0.11 – 0.50 Fig. 4a,c). The compositions of zooplankton at the frontal area stations that had drifting seaweeds were basically the same as those of the without drifting seaweed stations. Thaliacea was significantly more abundant at the stations other than those with drifting seaweed in May 2012 (*t*-test, $p < 0.05$) and mysida/euphausiacea were significantly more abundant in the frontal area stations than at other stations on 11 – 12 April 2013 (*t*-test, $p < 0.01$) (Fig. 4a,c).

←Fig. 4

Fish juveniles associated with drifting seaweeds

In 2012 and 2013, we caught a total of 18 species ($n = 899$) and seven species ($n = 89$) of fishes associated with drifting seaweed, respectively. Some adult fishes, two sargassum fish *Histro histro* exceeding 7 cm TL and six dandy blenny *Petroscirtes breviceps* exceeding 5 cm TL, were excluded from the analysis. We analyzed a total of 408 fishes: 166 juveniles (fifteen species) in May and 100 juveniles (nine species) in July 2012, and 57 juveniles (seven species) in April 2013 (Table 1).

Commercially important species such as *S. quinqueradiata*, rockfish *Sebastes thompsoni*, *S. cirrhifer* and *O. fasciatus* were dominantly collected. Four species were always in the seaweeds, five species were fish that merely touched the seaweed, five species swam around the seaweed, and nine species were classified as ‘others’ (Table 1). The dominant fishes in each group were *H. histrio* and *P. breviceps* for fish always in the seaweed, *S. cirrhifer* and *P. japonicus* for fish that only touched the seaweed, and *S. quinqueradiata* and *O. fasciatus* for fish swimming around the seaweed (Table 1).

Almost all of the fish species fed on planktonic food. The feeding incidence on planktonic food by individuals was 49.7 % in the group of always in the seaweeds, 64.2 % in the group touching the seaweeds, 99.7 % in the group swimming around the seaweed, and 68.8 % in the ‘others’ group (Table 2). Among the fish juveniles that fed on planktonic food, 50 % (10 species) of the fish juveniles fed on copepoda, appendicularia and bivalve larvae selectively ($\alpha = 0.13 – 0.87$) (Fig. 5 a–c). The following percentages of the fish juvenile species fed on phytal animals on drifting seaweeds were 100 % for always in the seaweeds, 75.0 % for touching the seaweed, 40.0 % for swimming around the seaweeds and 14.3 % for others (Table 3). These fish fed mostly on gammarids, isopods, caprellids and fish eggs on the drifting seaweeds. Aside from the fish that were always in the seaweed, the feeding incidence of the fish juveniles on phytal animals by individual fish were low: 41.0 % for the fish always in the seaweed, 13.4 % for the fish touching the seaweed, 5.3 % for the fish swimming around the seaweeds, and 11.1 % for the others (Table 3).

←Fig. 5
Table 1
Table 2
Table 3

Discussion

Frontal areas and the distribution of drifting seaweeds

Relatively high-velocity ocean currents from west to east were observed around the continental shelf (Fig. 2a–e), which were considered as Tsushima Warm Current Branch. We assumed that a frontal area was possibly formed by Tsushima Warm Current Branch and continental water that has a different current velocity and direction in the Goto Islands Sea, as confirmed by our convergence model (Fig. 2a–e). During 11 – 17 April 2013, a warm water mass was observed in the southern part of the study area, and the average sea surface temperature increased by 2.5 °C within 6 days, indicating that a branch of the Tsushima Warm Current intruded into the study area leading the high-velocity current around the shelf-break region from west to east (Fig. 2a–e). The Tsushima Warm Current intrudes into the Goto Islands Sea from the west (Kondo 1985) and is affected by the continental water and land water from the Ariake Sea (Inoue 1981). Nakata et al. (1989) observed a frontal area with a marked current shear between the offshore water flowing into Sagami Bay, Japan and the comparatively sluggish coastal water in Sagami Bay.

In our study, a frontal area which marked the gradient of temperature and/or salinity could not explain the distributions of drifting seaweed, and 50 % of the collection sites of drifting seaweeds corresponded with the frontal area. Thus, drifting seaweeds may be accumulated in frontal areas created by surface currents on large scale in the Goto Islands Sea. Yoshida (1963) mentioned that most drifting seaweeds around Japan were found in coastal waters in the vicinity of the frontal zone off the west or north of Kyushu Island in the ECS. Recently, it has been reported that large amount of drifting seaweeds from China were distributed in the area located between the continental shelf waters and the oceanic front of the Kuroshio Current in the ECS (Konishi 2000; Komatsu et al. 2008). On the other hand, Michida et al. (2006, 2009) found that the area where drifting seaweeds were accumulated coincided with strong convergence by surface currents in Suruga Bay, Japan.

One to three drifting seaweeds were found along the one observation line (aprrox. 45 km distance), suggesting that the scale of our study (the horizontal resolution of the JCOPE2 ocean reanalysis system is 1/12°, or approx. 9.3 km (Miyazawa et al. 2009), and the average interval between the CTD stations was

9.6 km) could explain the distributions of drifting seaweeds. Although the resolution could be too large to explain the frontal structure, we assumed that drifting seaweeds were accumulated in frontal areas created by ocean currents around the shelf-break region in the Goto Islands Sea. A massive bloom of drifting macro algae was observed to accumulate in a pattern dominated by linear bands and the distance between neighboring bands ranged from hundreds of meters to 6 km in the western Yellow Sea (Qiao et al. 2009). Uehara et al. (2006) reported that a frontal structure indexed using a station-to-station ⊿SST analysis did not explain the spatial variation in the drifting seaweeds' distribution at the southeast coast of Japan, near the Kuroshio current, and they speculated that the frontal structure was too small to detect by their station intervals (up to 15 km). On the other hands, Komatsu et al. (2008) revealed that over 1,800 drifting seaweeds were distributed in the area located between the continental shelf waters and the oceanic front of the Kuroshio Current (along over 180 km transect) in the ECS in March 2004, indicating that drifting seaweeds were accumulated in large scale of frontal area. Thus, the scale of frontal area that accumulates drifting seaweeds can show a wide range. It may be possible to predict the distribution of drifting seaweeds by analyzing the frontal areas created by surface currents.

There were two cases (in July 2012 and on 17 April 2013) in which the frontal area created by ocean currents could not explain the distribution of drifting seaweeds. In July 2012, the drifting seaweeds corresponded with a frontal area that was marked by a latitudinal gradient of salinity and temperature, which may be attributed to a strong intrusion of land water due to a northern Kyushu district heavy rainstorm. The case of many patches of drifting seaweeds on 17 April 2013 was thought that the drifting seaweeds had not yet been trapped by a frontal area.

Abundance and species composition of zooplankton

Our present findings demonstrated that drifting seaweeds that were accumulated in the frontal areas did not have a high abundance of zooplankton. A frontal area, formed between fast-flowing and stagnant water when a current strikes a peninsula or an island, is highly abundant in plankton, and the convergence may act as a nursery ground for juvenile fishes (Uda 1983). Nakata et al. (1989) revealed that Japanese sardine *Sardinops melanosticta* larvae were most abundant in the frontal areas created by ocean currents in

Sagami Bay, Japan. In light of previous study, planktons can be accumulated in frontal zones by ocean currents. On the other hand, prey densities including zooplankton around the drifting seaweeds were not high compared to open water around the San Juan Archipelago, Washington, USA (Shaffer et al. 1995). Senta (2001) found that fish eggs, fish larvae and juveniles were not highly abundant in the frontal area compared to surrounding areas except for the fish juveniles associated with drifting seaweeds in Goto Islands Sea. Although it has been reported that the densities of invertebrates (Kingsford and Choat 1985) and neustons (Vandendriessche et al. 2007) are higher around drifting seaweed compared to other areas, frontal areas where drifting seaweeds are accumulated cannot ensure the high abundance of planktons.

Feeding incidence of juvenile fishes

Castro et al. (2002) pointed out that fish associated with drifting objects may benefit from drifting movements into the frontal convergence areas where planktonic food is accumulated (the indicator-log hypothesis). However, our results show that the indicator log hypothesis is not applicable for the juvenile fishes associated with drifting seaweed as examined in the present study. In our study, almost all of the fish species fed on planktonic food, notably, 99.7 % of the individual fish juveniles in the swimming-around-the-seaweeds group (including *S. quinqueradiata*) fed on planktonic food (Table 2). Of the fish juveniles always in the seaweeds, approx. 50 % fed on planktonic food. These fish juveniles selectively feed on copepoda, appendicularia and bivalve larvae (Fig. 5 a–c). However, mysida/euphausiacea that was significantly more abundant in the frontal area stations than at other stations were not selectively fed in April 2013. Commercially important specie such as *S. quinqueradiata*, *S. thompsoni*, *S. cirrhifer* and *O. fasciatus* fed on copepod in common, and our results confirmed that planktonic foods such as copepod, appendicularia and bivalve larvae are one of the most important prey for fish juveniles associated with drifting seaweeds. Ida (1967) and Senta (1965, 1986) revealed that a number of fish juveniles associated with drifting seaweed fed mostly on planktonic food. Notwithstanding the importance of planktonic food for juvenile fishes, the areas around drifting seaweeds are not highly abundant in zooplankton compared to other areas.

We also concluded that the concentration of food supply hypothesis is not applicable for fish juveniles associated with drifting seaweeds in the study area. Although, the feeding incidence of phytal animals by individual fish (41.0 %) for the fish juveniles always in the seaweeds was higher than the incidences in the other three groups of juvenile fishes, concentration of food supply hypothesis cannot be applied for the fish juveniles always in the seaweeds. Because fish juveniles always in the seaweeds are considered as a group that utilize drifting seaweeds for their habitat, and they are not attracted drifting seaweeds by phytal animals. Feeding incidence of phytal animals for other three groups (including *S. quinqueradiata*, *S. thompsoni*, *S. cirrhifer* and *O. fasciatus*) were low (5.3 - 13.4 %). Vandendriessche et al. (2007) mentioned that macrofauna associated with drifting seaweeds can serve as a food source for *Cyclopterus lumpus*, while seaweed-associated food items appear to represent opportunistic prey items for some fish species, such as Atlantic horse-mackerel *Trachurus trachurus*, lesser pipefish *Syngnathus rostellatus* and thicklip grey mullet *Chelon labrosus* in the North Sea. Senta (1986) reported that fish juveniles that touch seaweeds and swim around seaweed fed mainly on copepoda, ostracoda, appendicularia and cladocera, and that notably smaller juveniles fed on planktonic food, whereas fish juveniles that were always in the seaweeds (tidepool gunnel *Pholis nebulosa*, *H. histrio* and spottybelly greenlings *Hexagrammos agrammus*) fed on isopoda and amphipoda. The feeding habitat of fish juveniles associated with drifting seaweeds shifts depending on the species, growth stage and swimming activity (Ida et al. 1967, Ida 1986; Senta 1965, 1986), planktonic food abundance of the ambient surroundings (Senta 1986) and season (Shaffer et al. 1995). For instance, concentration of food supply hypothesis can be applicable in the season and area that is low in the abundance of zooplankton.

In conclusion, during our field survey, fish juveniles fed on planktonic food although the zooplankton abundance around the drifting seaweeds was not high, and they did not feed on phytal animals. These results are inconsistent with both the concentration of food supply hypothesis and the indicator-log hypothesis. Thus, it is revealed that food habitat is not a major ecological role of drifting seaweeds for fish juveniles associating with them. Further investigations using high resolution are necessary to determine the relationships among frontal areas, the distribution of drifting seaweeds, and zooplankton abundance in order to retest the indicator log hypothesis. Based on the results from laboratory observations, Sakakura and Tsukamoto (1997) suggested that *S. quinqueradiata* juveniles associate with drifting seaweed to maintain their schools during the night-time. Hanaoka (1986) observed that *S. quinqueradiata* juveniles recognized a boat as a predator and escaped into the drifting seaweeds. Therefore, other hypotheses such as the 'meeting point' hypothesis: fish can make use of floating objects to increase the encounter rate between isolated individuals or small schools and other schools, and/or the 'shelter from predator' hypothesis: the floating object can be used as a refuge or blind zone from predator (Fréon and Dagorn 2000) for fish juveniles associated with drifting seaweeds, should also be evaluated.

Acknowledgements

We thank the crews of the T/V Kakuyo-Maru of Nagasaki University for their help during the research cruises, and Drs. Y. Miyazawa and R. Zhang of JAMSTEC for providing the JCOPE2 data and for their assistance. This study was financially supported by Sustainable Aquatic Food and Environment Project in the East China Sea by MEXT Japan (to YK, RK, YS), Research Initiative for Adaptation to Future Ocean Change by Nagasaki University Major Research Project (to YS), and Grants-in-Aid for Scientific Research, JSPS, Japan (16H05794 to YS, 16H05795 to RK, 23880023 to YK).

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要約

流れ藻には多くの水産上重要種の稚魚が付随するが，流れ藻の稚魚にとっての生態学的意義は明らかにされていない。筆者らは次の2仮説のいずれかが流れ藻付随稚魚に当てはまると考え，“concentration of food supply hypothesis”（流れ藻葉上生物を摂餌するため）と“indicator log hypothesis”（流れ藻をフロント域のような餌豊度の高い海域の目印とするため）を検証するため，2012年と2013年に東シナ海の流れ藻周辺の海洋環境，フロント域，動物プランクトン豊度，流れ藻付随稚魚の摂餌個体率を調べた。流れ藻は表層流の収束帯に集積されていたが，収束帯のプランクトン豊度は高くなかった。合計14個の流れ藻を採集し，合計22種（408尾）の稚魚の胃内容物を調査した結果，稚魚の49.7 - 99.7 %の個体はプランクトンを選択的に摂餌していたが，葉上生物の摂餌個体率は高くなかった（50 %未満）。以上の結果から流れ藻の稚魚にとっての生態学的意義は摂餌場でないことが示唆された。

Fig. 1. Map of the study area. Frame: the sampling area. Dashed thick line: the observation line crossing the shelf-break region in July 2012 and April, May, July 2013. Dashed thin line: the observation line on 23 – 24 May 2012. Solid contours indicate the bathymetry in meters, provided by the Japan Oceanographic Data Center (http://www.jodc.go.jp).

Fig. 2. Horizontal current velocities (vector), convergence area (colored contour) and water temperature (°C, thin black line) at a depth of 10 m in (a) 23 May and (b) on 30 July 2012, and on (c) 12 April, (d) 17 April and (e) 22 July 2013, estimated using the JCOPE2 reanalysis data (24h average, Miyazawa et al. 2009). The red frame shows areas that are also shown in Fig. 3.

Fig. 3. The distributions of drifting seaweed around the shelf-break region in the Goto Islands Sea. The dashed thick contour shows the convergence of the horizontal current velocities overlaid with those shown in Fig. 2 (the outer counter line is 2.0×10^{-6} s^{-1}), and the water temperature and salinity at a depth of 10 m (thin black lines) on (a) 23–24 May and (b) 30 July 2012 and on (c) 11–12 April, (d) 17 April and (e) 22 July 2013, except for Stn. 6 in May 2012 and Stn. 5, where the temperature data at a depth of 11 m and 13 m, respectively, were used. Filled triangles: the stations where drifting seaweeds were found. Open triangles: the stations where floating structures were found. Filled circles: the stations of conductivity-temperature-depth (CTD) casting and zooplankton sampling. At Stn. 1 and Stn. 5 in May 2012, we could not scoop drifting seaweed or cast the CTD profiler and tow the Norpac net, respectively. The locations of each station are not consistent with those of the other survey periods.

Fig. 4. Zooplankton abundance (upper) and composition (lower) of the study area in (a) 22 – 24 May and (b) 30 July 2012, and in (c) 11 – 12 April, (d) 17 April and (e) 22 July 2013. Filled and open inverted triangles indicate stations where drifting seaweeds and floating structures were found, respectively. Station name enclosed by dashed circles in abscissa in each panel indicates the station where the convergence of horizontal velocity was observed. The locations of each station are different among survey periods. ND means no data.

Fig. 5. Chesson's selectivity index of fish juveniles associated with drifting seaweeds in (a) May and (b) July 2012, and in (c) April 2013. The colors of column show zooplankton classifications same as Fig. 4. +; *t*-test, $p < 0.05$, ++; *t*-test, $p < 0.01$, neutral = 0.063 (2012), 0.059 (2013). *Fed phytal animals aggregated to drifting seaweeds. Figures upper the columns represent the number of fish juveniles that fed on zooplanktons. ND means no data.

Table 1. Number of total catch and analysis, and total length range of analyzed fish juveniles associated with drifting seaweeds

Species	Group	Number of total catch	Number of analysis	Total length range of analyzed fish [average] (mm)
Hexagrammos agrammus	A	2	2	90.98 – 97.27 [94.13]
Histrio histrio	A	35	33	11.42 – 77.71 [24.27]
Petroscirtes breviceps	A	138	36	16.80 – 48.16 [31.96]
Pholis nebulosa	A	4	4	76.98 – 110.04 [90.68]
Paramonacanthus japonicus	T	65	58	13.00 – 44.14 [24.22]
Rudarius ercodes	T	9	9	11.45 – 17.12 [14.44]
Sebastes thompsoni	T	133	67	37.49 – 51.68 [43.06]
Stephanolepis cirrhifer	T	316	38	21.15 – 67.59 [32.40]
Abudefduf vaigiensis	S	7	7	15.47 – 42.60 [30.99]
Kyphosus vaigiensis	S	15	15	75.40 – 104.00 [89.19]
Oplegnathus fasciatus	S	32	32	13.86 – 38.25 [20.58]
Seriola quinqueradiata	S	203	78	9.74 – 122.89 [45.57]
S. quinqueradiata (> 150 mm TL)	S	1	1	195.33
Engraulis japonicas	O	1	1	17.50
Girella punctata	O	3	3	14.43 – 30.57 [20.70]
Hyperoglyphe japonica	O	3	3	59.39 – 91.29 [75.17]
Leptoscarus vaigiensis	O	1	1	35.21
Macroramphosus scolopax	O	6	6	9.33 – 17.65 [13.08]
Oplegnathus punctatus	O	7	7	22.17 – 91.39 [49.16]
Psenes cyanophrys	O	3	3	24.71 – 63.86 [39.13]
Seriola dumerili	O	3	3	42.38 – 74.52 [63.01]
Trachurus japonicas	O	1	1	60.01

The groups follow the description by Senta (1965, 1986), as follows. A: always in the seaweed, T: touches the seaweed, S: swims around the seaweed, O: others. Values in square brackets are the average total length.

Table 2. Feeding incidence of fish juveniles on planktonic food

Group*	Species	Individual	Feeding incidence by species (%)	Feeding incidence by individual (%)
A	4	75	100	49.7
T	4	172	100	64.2
S	5	133	100	99.7
O	9	28	77.8	68.8

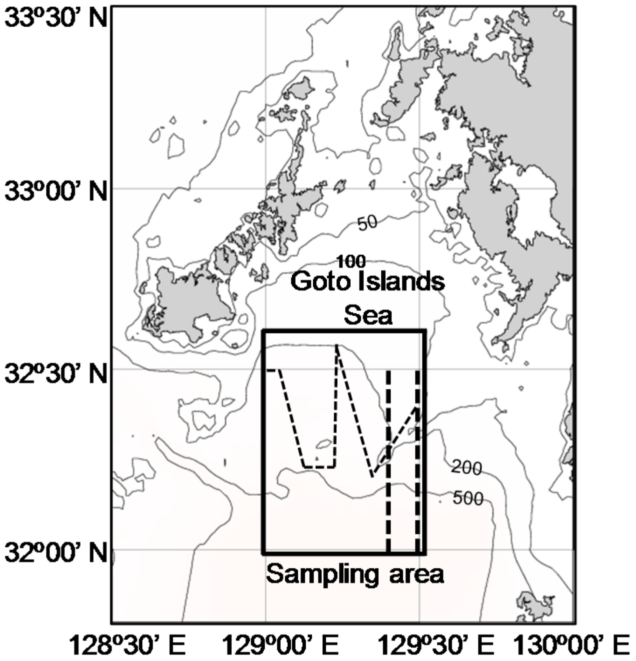
* The groups are explained in the Table 1 footnote.

Table 3. Feeding incidence of fish juveniles on phytal animals

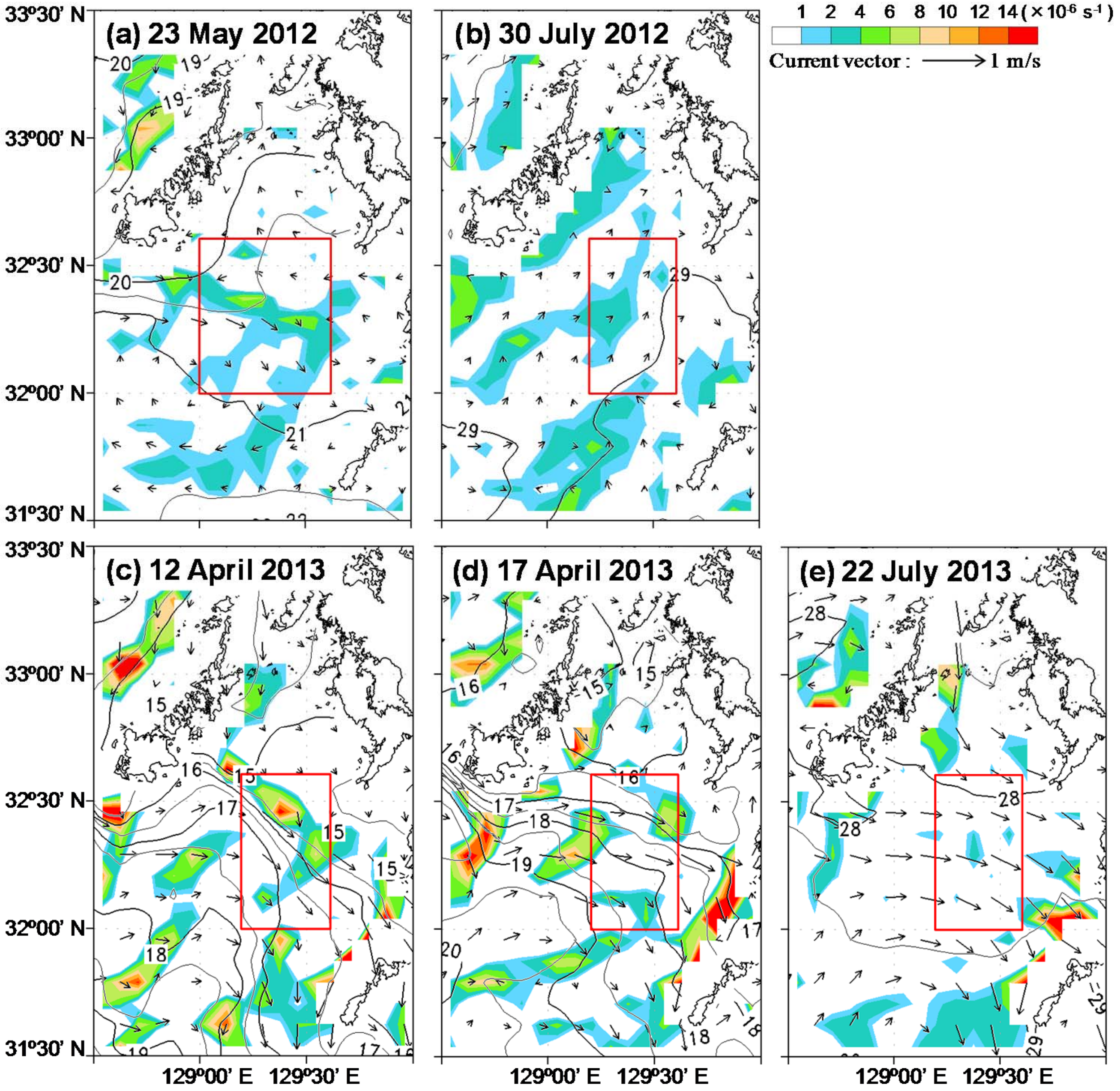
Group*	Species	Individual	Feeding incidence by species (%)	Feeding incidence by individual (%)
A	4	75	100	41.0
T	4	172	75.0	13.4
S	5	133	40.0	5.3
O	9	28	14.3	11.1

* The groups are explained in the Table 1 footnote.

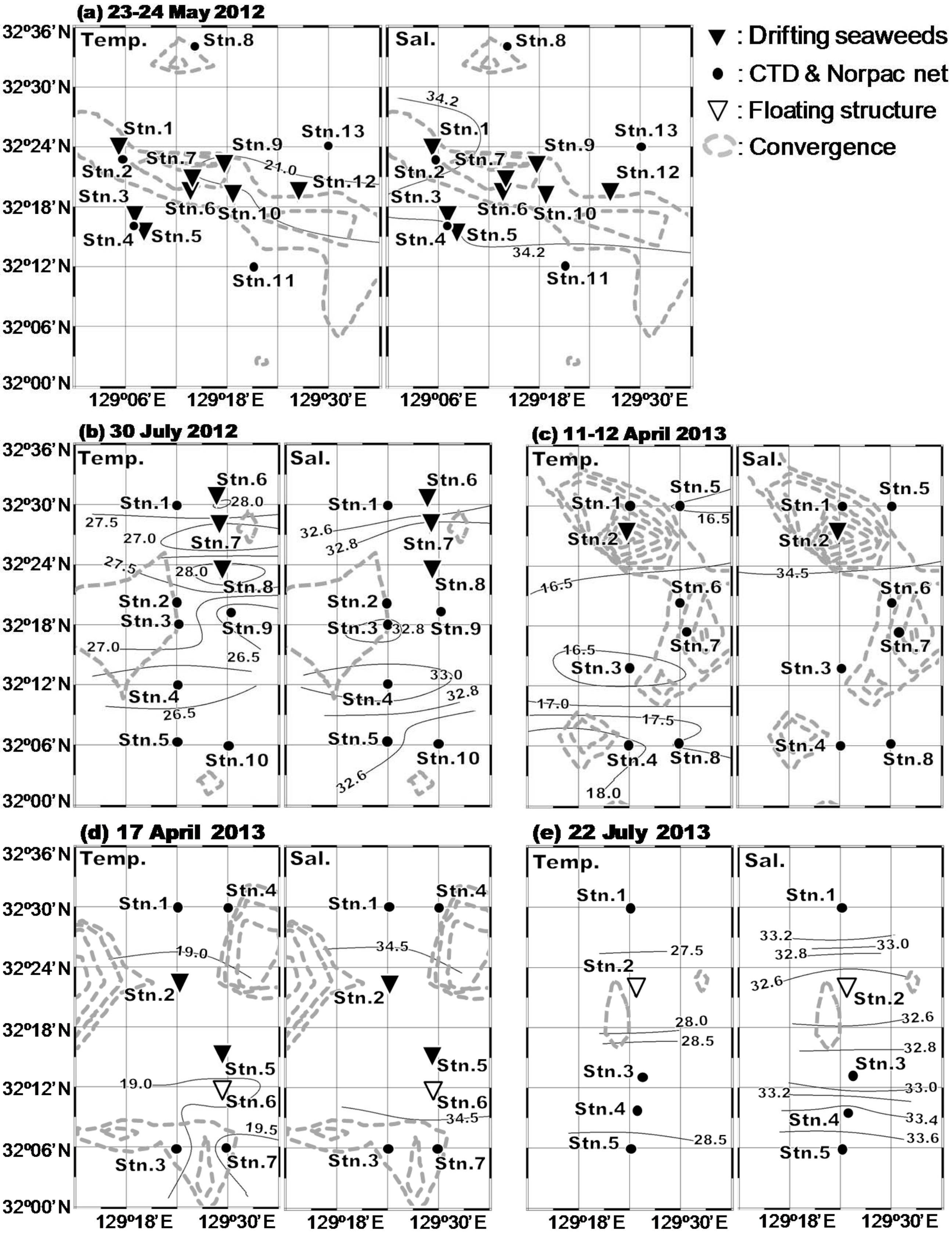
Hasegawa et al. Figure 1 希望縮尺率 100 %



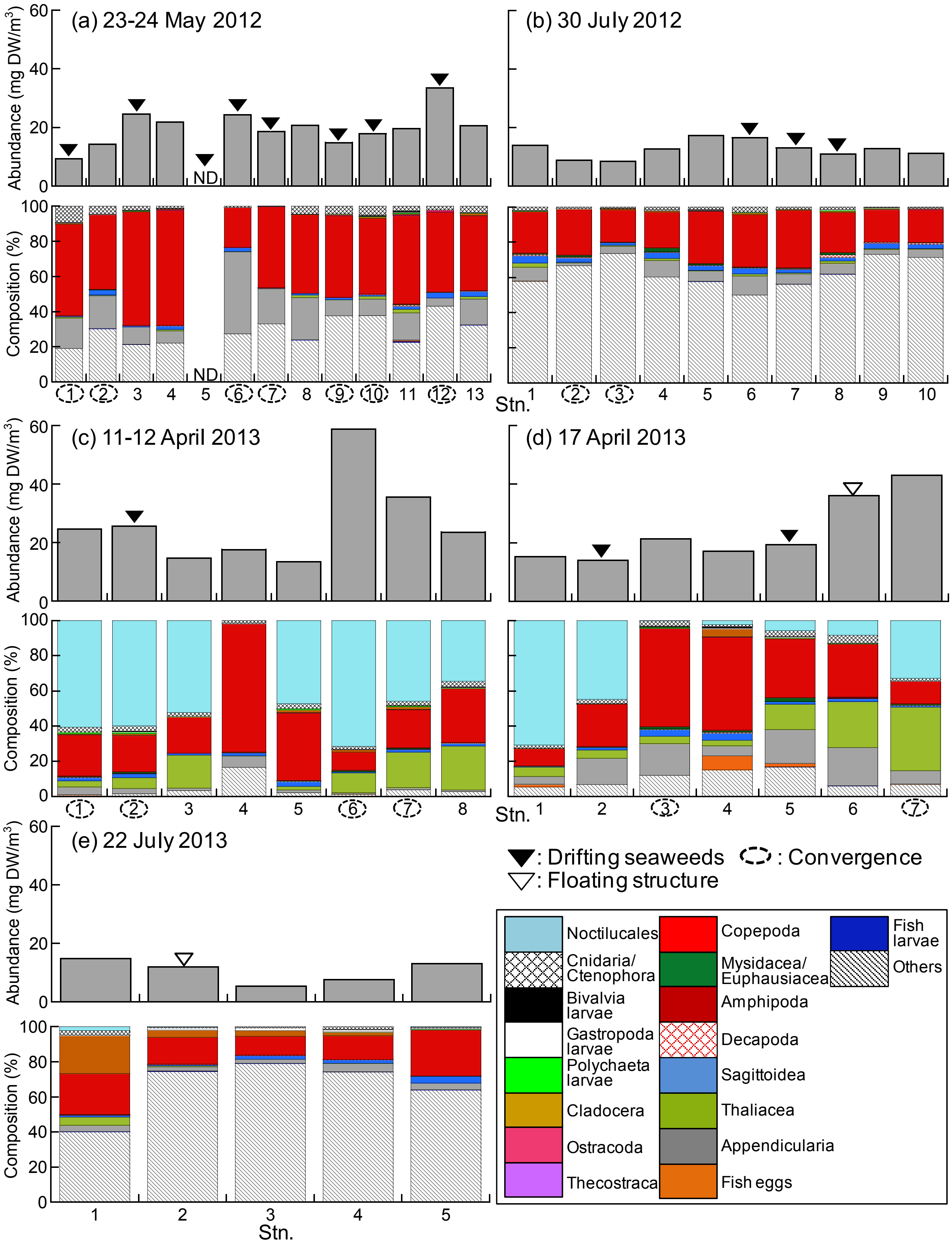
Hasegawa et al. Figure 2 希望縮尺率 100 % カラー希望



Hasegawa et al. Figure 3 希望縮尺率 100 %



Hasegawa et al. Figure 4 希望縮尺率 100 % カラー希望



Hasegawa et al. Figure 5 希望縮尺率 100 % カラー希望