Continuous behavioral observation reveals the function of drifting seaweeds for *Seriola* spp. juveniles

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ABSTRACT: A large number of fish species are associated with drifting seaweeds; however, the ecological significance of such seaweeds for fishes remains unclear. Here, we developed a raft equipped with a seaweed clump, interval still/video cameras, and a GPS satellite buoy. This novel monitoring system was used to monitor the schooling and associative behavior of *Seriola* spp. juveniles with seaweed for up to 1 wk in the East China Sea. We observed diel behavioral patterns of the fish, which swam around the seaweeds during the day and remained 'attached' to the seaweed or to conspecifics at night. This nighttime behavioral pattern suggests that the fish may use drifting seaweed to maintain schools at night when vision is less effective. Solitary individuals and those in smaller schools tended to remain close to the seaweed, whereas fish in larger schools were observed swimming actively around the seaweed. Additionally, some of the solitary fish and small schools escaped into the seaweed when potential predators appeared. As the school size of the fish increased over time, solitary individuals and small schools may have used drifting seaweeds as a shelter from predators until the fish could gather to form larger schools. We suggest that drifting seaweeds have multiple ecological functions for *Seriola* spp. and other seaweed-associated fishes, and the knowledge of these functions will be useful in designing conservation and management measures for the associated fishes.

KEY WORDS: Fish-aggregating devices · Floating seaweed · *Seriola quinqueradiata* · Yellowtail · Shelter from predator hypothesis · East China Sea · Time lapse camera · GPS satellite buoy

INTRODUCTION

Seaweeds with gas-filled vesicles can float after being detached from their base by strong waves or winds (Yoshida 1963, Kingsford & Choat 1985), and these detached seaweeds are called drifting sea-weeds. Over 333 fish species (96 families) are associated with floating objects including such drifting sea-weeds, and the majority (80%) of fish are present during the juvenile stages (Castro et al. 2002). Several hypotheses have been proposed for the ecological significance of drifting seaweed for fishes, such as

the 'concentration of food supply' hypothesis, the 'indicator-log' hypothesis, the 'meeting-point' hypothesis, and the 'shelter from predator' hypothesis (reviewed by Fréon & Dagorn 2000, Castro et al. 2002). The concentration of food supply hypothesis posits that floating structures help feed small fishes, zooplankton, and sessile biota. The indicator-log hypothesis assumes that natural floating objects are often indicators of biologically rich water masses, either because most natural floating objects originate in rich areas (e.g. river mouths and mangrove swamps) and remain within these rich water masses, or because they aggregate in rich frontal zones. This hypothesis was first proposed for tunas (Hall 1992), and was extended to larval and juvenile fishes (Castro et al. 2002). The meeting-point hypothesis states that fishes make use of floating structures to increase the encounter rate between isolated individuals or small schools and other schools. The shelter from predator hypothesis posits that fishes use floating structures as a refuge from predators. Although previous studies have reported anecdotal evidence supporting each hypothesis (e.g. Druce & Kingsford 1995, Vandendriessche et al. 2007, Casazza & Ross 2008), comprehensive assessments of these different hypotheses are still limited.

Fish juveniles associated with drifting seaweed have been mostly studied by traditional methods such as net capture (e.g. Kingsford & Choat 1985, Sakakura & Tsukamoto 1997, Dempster & Kingsford 2004, Uehara et al. 2006, Vandendriessche et al. 2007) and underwater visual observation (e.g. Ikehara 1984, Hanaoka 1986, Casazza & Ross 2008). However, these methods cannot provide the continuous stream of data that is needed to monitor fish and test the hypotheses. Furthermore, the presence of an observer might affect the behavior of fishes during underwater observation (Okamoto et al. 1981, Kudo 1998, Dearden et al. 2010). Video cameras have therefore also been used for serial observation of fishes associated with drifting seaweeds; however, the possible observation time-scale (e.g. 1.3–2.0 h sequences with a total of 21.5 h [Moser et al. 1998]) is relatively short. To overcome this methodological problem, we developed a new monitoring system: a raft equipped with a clump of seaweed, interval still and video cameras, and a GPS satellite buoy, which can continuously monitor the behaviors of fishes associated with drifting seaweed for up to 1 wk.

Amberjacks (genus *Seriola*) are among the important fishery target species around the world (Sakakura & Tsukamoto 1997, Moran et al. 2007), and some species of amberjacks around Japan (mainly, yellowtail *S. quinqueradiata* and greater amberjack *S. dumerili*) are associated with drifting seaweed during their juvenile stages (Senta 1965, Ikehara 2006, Uehara et al. 2006, Yamasaki et al. 2014). *S. quinqueradiata* and *S. dumerili* sometimes form schools of dozens to hundreds of individuals around the drifting seaweed (Ikehara 2006). Several studies have examined the ecological significance of drifting seaweed for these fishes, and tested the hypotheses mentioned previously. The concentration of food supply hypothesis was rejected for *S. quinqueradiata* and *S. dumerili* juveniles, because they feed on planktonic foods such as copepods rather than on phytal animals (Anraku & Azeta 1965, Yamasaki et al. 2014, Hasegawa et al. 2016). The indicator-log hypothesis was also not supported, because food (zooplankton) abundance did not differ between areas with and without drifting seaweed (Hasegawa et al. 2016). The meeting-point and shelter from predator hypotheses remain to be tested.

Our objective was to provide novel insights into the ecological significance of drifting seaweed for *Seriola* spp. by observing a time-series of schooling and associative behavior of juveniles with seaweed clumps using the developed monitoring system. Specifically, we examined how (1) diel period, (2) time after release, (3) predator occurrence, (4) food availability, (5) sea surface temperature, and (6) drifting trajectory and speed of the system affected the schooling and associative patterns of the juveniles.

MATERIALS AND METHODS

Study site and experimental protocol

This study was conducted near the Goto Islands (in the Goto Sea), located in the northeastern part of the East China Sea (Fig. 1). This location is a major fishing ground for *Seriola quinqueradiata* juveniles associated with drifting seaweed during the months of May and June (Yamashita & Iwasa 1984, Yamamoto & Tashiro 1986); the collected juveniles are used for aquaculture seedlings. No artificial floating objects are deployed for the fishing of *S. quinqueradiata* juveniles, but fish-aggregating devices (FADs) for catching dolphinfish *Coryphaena hippurus* are deployed in this region (Kuwano et al. 1982, Fujita 1986). In total, 8 cruises were conducted in the shelf-break region (31° 36′–33° 18′ N, 129° 00′–130° 06′ E; Fig. 1) by the training vessel (T/V) 'Kakuyo-Maru' of Nagasaki University from April to June in 2013 and in 2014. In total, 14 rafts were released and retrieved
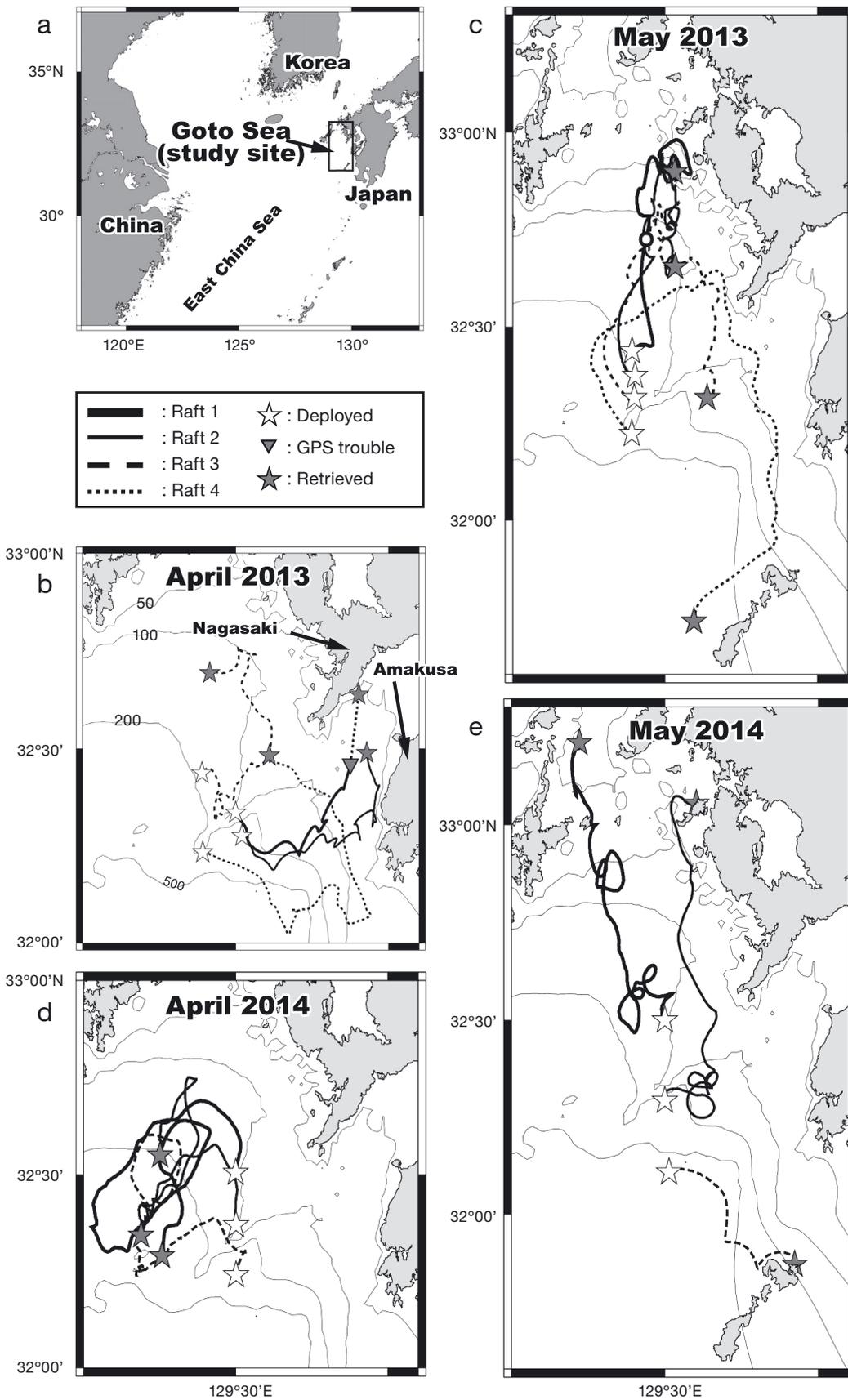
Fig. 1. (a) Study site, showing the location of the Goto Sea, and drifting routes of the rafts in (b) April 2013, (c) May 2013, (d) April 2014, and (e) May 2014. The filled inverse triangle in (b) shows the location where the GPS buoy broke. The subsequent dotted line is simply a straight line between the locations where the buoy broke and where it was retrieved. Thin solid contours with numbers (b) indicate bathymetry in meters, extracted from the Japan Oceanographic Data Center (www.jodc.go.jp)

(see 'Monitoring system' below for details). The rafts were released in this area because of the large number of drifting seaweeds and associated *Seriola* spp. juveniles that were present (Hasegawa et al. 2016). In 2013, 4 rafts were released from 11–12 April and 4 more were released on 27 May, and were retrieved from 16–18 April and 3–4 June, respectively. In 2014, 3 rafts were released on 12 April and 3 more were released on 21 May, and were retrieved on 19 April and between 27–29 May, respectively. The rafts were retrieved using near real-time positional data from the attached GPS buoy and radio waves from the VHF transmitter.

The water transparency of the Goto Sea during the study season was at least 8.5 m (2013: April, 12.1 ± 1.2 m [mean ± SD], n = 7; May, 16.6 ± 6.3 m, n = 6; June, 19.6 ± 10.4 m, n = 5, 2014: April, 14.6 ± 3.2 m, n = 7; May, 12.6 ± 3.1 m, n = 7), which is greater than the sum of the distance between the seaweed clump and the cameras (approximately 2 m) plus the previously reported swimming range of *S. quinqueradiata* (the main species of *Seriola* in this region) from the clump (3–5 m) (Ikehara 1984). Therefore, we believe that visibility conditions had at most a trivial effect in this study.

Monitoring system

Four square rafts (140 × 140 cm) were made using polyvinyl chloride pipes and floats (Fig. 2), and were repeatedly used to obtain data in different months and years. To directly observe associative behaviors of *Seriola* spp. juveniles with drifting seaweed, each raft was equipped with collected seaweed (see below for details), a digital still camera (Optio WG1, WG2, or W90 with a focus-free wide F3.5 lens, Pentax) in a waterproof housing (WHPE-WG1, -WG2, or -W90, Recsea/Seatool, NTF), and a video camera (Gopro Hero2 with a focus-free wide F2.8 lens, Woodman Labs) in a custom-made waterproof housing and equipped with an interval scheduling system and extra battery (Logical Product). The vertical and horizontal fields of view of the still camera were 46° and 59°, respectively, and those of the video camera were 62° and 100°, respectively (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m573p101_supp/). Both cameras were pointed at the center of the seaweed clump (Fig. S1). To take still images at night, a flash was provided for the still cameras. A water temperature logger (HOBO U22-001, Onset) and light logger (HOBO UA-002-64, Onset) were also attached to the raft to monitor the sea surface tem-

perature and to define daytime and nighttime, respectively. A drifting GPS buoy (ZTB-R6-P3, Zeni Lite Buoy), which sends its position via satellite, and VHF transmitter (F1860, Advanced Telemetry Systems) were tethered to each raft to monitor location and aid in raft retrieval. A sinker (1.5 kg) was suspended below the raft to lower its center of gravity and prevent it from overturning. The recording/sampling intervals for the still camera and GPS buoy were once every 30 min, and once every 10 min for the temperature and light loggers. During the daytime (06:00–19:00 h), the video cameras were scheduled to record 2 min of video once an hour, with several exceptions. Around the crepuscular period in May 2013, 2 min (05:05–05:07 h, 19:31–19:33 h) were recorded. During the crepuscular periods in April 2014 and May 2014, 5 min recordings were taken from 05:40–05:45 h and 19:00–19:15 h, and 05:05–05:10 h and 19:25–19:30 h, respectively. The recordings of still and video cameras were partially synchronized (every hour during the daytime).

A clump of *Sargassum horneri* was used as the drifting seaweed because this species is the dominant species of drifting seaweed in the East China Sea (e.g. Komatsu et al. 2008). *S. horneri* was collected from the coastal areas of Amakusa Island, Kumamoto Prefecture, and Nagasaki Prefecture, Japan (Fig. 1). A clump of *S. horneri* was standardized by weight (7.2–8.3 kg) and attached to each raft.
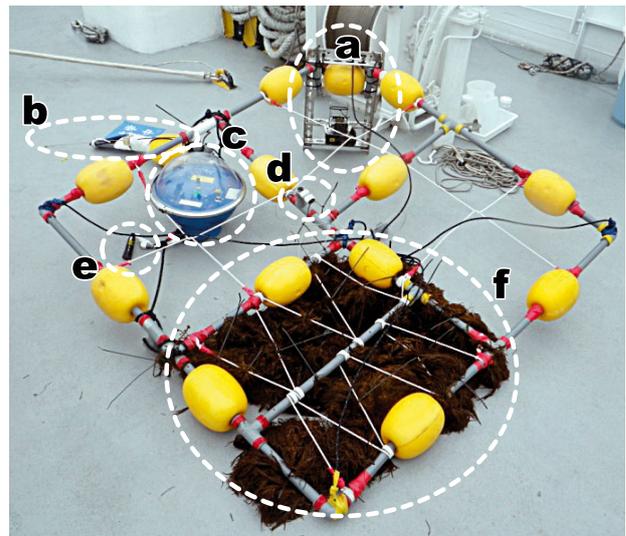

Fig. 2. Monitoring system used in our study. A raft was equipped with still and video cameras (a), a VHF transmitter with float (b), a drifting GPS buoy (c), a light logger (d), a water temperature logger (e), and a clump of *Sargassum horneri* (f)

Analysis of still and video images

We categorized *S. quinqueradiata* and *S. dumerili* as *Seriola* spp. and counted the number of individuals in each still and video image, because these 2 species (and possibly yellowtail kingfish *S. aureovittata* and other *Seriola* spp.) were difficult to distinguish from each other in the images. We targeted juveniles of *Seriola* spp. that are associated with drifting seaweeds (≤20 cm total length; Senta 1965, Fujita & Mori 1982, Hasegawa et al. 2016), whereas large (at least >40 cm total length) *Seriola* spp. (identified as *S. aureovittata*) were excluded from the analysis.

From all still images (recorded both during the day and at night), we counted the total number of *Seriola* spp. juveniles in each image. To analyze the diel difference in the degree of association with drifting seaweed from the still images, we also categorized fish position as being 'attached,' in which the fish was attached to the seaweed or conspecifics, and 'around,' in which the fish was not attached to the seaweed or conspecifics but was in the water column. From the video images, we detected all schools and solitary individuals, and counted the numbers of fish in each school. A school was defined as a group of fish (nearest neighbor distance is within approximately 2 body lengths) that swam synchronously (Pitcher 1983). Because the fish often swam in and out of the camera view, the maximum number during a 2 min video image was defined as the school size during that period. The school size of a solitary individual was regarded as 1. Since the images during the crepuscular periods were too dark to correctly measure the school size, we only used the video images recorded during the daytime (06:00–19:00 h in April and 05:00–19:30 h in May–June). A portion of a fish (e.g. if only the head or only the tail was visible) was counted as 1 individual in both the still and video images.

To analyze the relationship between school size and the degree of association with drifting seaweed from the video images, we used the categories (1) 'close proximity', in which the school or solitary fish remained inside or underneath the seaweed within the camera view (within approximately 1 m beneath the seaweed) for the whole 2 min recording period, and (2) 'swimming around', in which the fish swam in and out of the camera view during the recording period. The video images during the crepuscular periods (e.g. 05:05–05:07 h in April) were only used for qualitative (not quantitative) behavioral observation. The video images with potential predators were also counted, and behaviors of *Seriola* spp. juveniles in these images were noted. Nighttime was defined as a period when light intensities measured by light loggers were less than their minimum light sensitivity (1 lux): 19:30–05:30 h in April and 20:00–04:30 h in May–June.

Drifting trajectory

To reveal the drifting trajectory of the rafts, the positions of each raft were plotted every half hour using GMT ver. 4.5.9 (www.soest.hawaii.edu/gmt; Wessel & Smith 1998). We applied the cosine formula of spherical trigonometry. A distance between the position at time $t - 1$, and that at time t of a raft (D_t) can be calculated as:

$$D_t = r \cos^{-1}(\sin y_{(t-1)} \sin y_t + \cos y_{(t-1)} \cos y_t \cos \Delta x) \quad (1)$$

where r is the equatorial radius (6378.137 km), and $y_{(t-1)}$ and y_t are latitudes of the positions at $t - 1$ and at t. Δx is the difference in longitudes of those 2 sites.

To estimate the tortuosity of the raft trajectory, a straightness index (Si, Benhamou 2004) during a given time period was calculated as:

$$Si = \frac{r \cos^{-1}(\sin y_0 \sin y_n + \cos y_0 \cos y \cos \Delta x_{0n})}{\sum_{t=1}^{n} D_t} \quad (2)$$

where y_0 is the latitude of the initial position of the raft, and y_n is the latitude of the last position recorded during the given time period. Δx_{0n} is the difference in longitudes of those 2 sites, and n is the number of records during the given time period.

Zooplankton abundance

The main food of *Seriola* spp. juveniles is planktonic copepods (Anraku & Azeta 1965, Senta 1965, Yamasaki et al. 2014, Hasegawa et al. 2016). Therefore, to reveal the food availability for *Seriola* spp. juveniles, we investigated the density of planktonic copepods at the stations where rafts were deployed and retrieved in 2014. We could not obtain zooplankton in 2013 due to limited ship time, and we were unable to obtain zooplankton at the retrieval sites of rafts 2 and 3 in May 2014 because these rafts were recovered after stranding on shore (Fig. 1).

A Norpac net (45 cm diameter, 54GG; mesh = 315 μm) was vertically towed from 20 m depth during the daytime (06:00–18:00 h). A flow meter (Rigo) was attached to the opening of the net to measure the volume of filtered water. Collected samples were immediately fixed in 10% buffered formalin

solution. The volume of filtered water collected during the net tow at each sampling station was calculated using a calibrated flow meter. Because plankton densities were high, plankton samples were divided into between 4 and 64 samples, and these divided samples were used for the measurement of copepod density. Copepods were identified according to Chihara & Murano (1997), using a stereoscopic microscope. The density of copepods C (ind. m^{-3}) was calculated as:

$$C = (NS^{-1})V^{-1} \qquad (3)$$

where N is the total number of copepods in a divided sample, S is the number by which they were divided (i.e. between 4 and 64), and V is the total volume of water sampled (m^3).

Statistical analyses

We constructed a series of generalized linear models (GLMs) and generalized linear mixed models (GLMMs) to evaluate the effects of different variables on the associative and schooling behaviors of *Seriola* spp. juveniles; the models and variables are summarized in Table S1 in the Supplement. When an objective variable was discrete, we used a Poisson or negative binomial error distribution with a log link function (Zuur et al. 2009); we used a negative binomial distribution rather than a Poisson distribution when a fitted model was overdispersed (i.e. when residual deviance/df was >2). A binomial distribution with a logit link function (logistic regression) was used when the objective variable was categorical (Zuur et al. 2009). The diagnostics of the above GLM/ GLMM analyses were conducted by the overdispersion parameter (residual deviance/df), percentage of deviance explained (R^2 for GLM, and marginal and conditional R^2 for GLMM; Nakagawa & Schielzeth 2013), quantile–quantile plots, and distribution of residuals (see Figs. S2–S10 in the Supplement). All analyses were carried out using R version 3.1.3 (R Development Core Team 2015) with the lme4 package (Bates et al. 2015) for the GLMM, and p values <0.05 were considered significant in all analyses.

Analysis of still images

To reveal patterns in diel association of *Seriola* spp. juveniles, the effect of day or night on the number of individuals in the still images was assessed for each raft using a GLM with a Poisson or negative binomial error distribution and a log link. The number of individuals was regarded as the objective variable, while the diel period and 'days after release' were regarded as categorical explanatory variables. Days after release was included as a categorical variable because the fish numbers substantially fluctuated depending on the days (see Fig. S11 in the Supplement). The significance of the diel period was assessed by removing it from the model and comparing the change in deviance using the likelihood-ratio (LR) test.

To further assess the behavioral difference between day and night, we evaluated the effect of diel period on the degree of association ('attached' or 'around') using a GLM with a binomial error distribution and a logit link. The degree of association was regarded as an objective variable, while the diel period was regarded as an explanatory variable. The significance of the diel period was assessed using the LR test.

To assess the general trend of the change in fish number over time, we examined the relationship between the days after release and fish numbers for each raft using a Spearman rank correlation test. Because there were significant effects of diel period on fish numbers in many rafts (see 'Results'), daytime and nighttime were examined separately.

To investigate the factors affecting the aggregation process of *Seriola* spp. juveniles, we examined the effects of mean raft speed, tortuosity of the raft trajectory (straightness index), and mean sea surface temperature (SST) on the maximum number of fish detected during 1 to 6 d periods using a GLM with a negative binomial error distribution and a log link. When data recorded during a 1 d period were less than 20 h due to any problems with the devices, we removed them from the analysis. We conducted a different analysis than was used for the diel period and days after release, because the raft speed, trajectory, and SST are likely to affect the fish colonization process rather than directly affecting the fish numbers. When a significant correlation was found in any pairs of the explanatory variables (i.e. raft speed, tortuosity of the raft trajectory, and SST), we removed 1 variable from the analysis to prevent multi-collinearity (see Table 3). The significances of the explanatory variables were assessed using the LR test.

Analysis of video images

To assess the change in school size of *Seriola* spp. juveniles over time, we evaluated the effect of

time after release (h) on school size using a GLMM with a negative binomial error distribution. School size was regarded as an objective variable, while time after release was regarded as an explanatory variable. The raft was regarded as a random effect because we probably repeatedly recorded the same schools or individuals. The significance of time was assessed by removing it from the model and comparing the change in deviance using the LR test. To further understand the change in fish numbers over time for each raft, we examined the effect of time after release on school size at each raft using a GLM with a Poisson or negative binomial error distribution and a log link. The significance of time was similarly assessed for each raft using the LR test.

To understand the relationship between school size and the degree of association with drifting seaweeds, we evaluated the effect of school size on the degree of association ('close proximity' or 'swimming around') using a GLMM with a binomial error distribution and a logit link. The degree of association was regarded as an objective variable, while school size was regarded as an explanatory variable. The raft was regarded as a random effect. The significance of school size was assessed using the LR test.

Analysis of zooplankton

To examine changes in prey abundance, copepod densities were compared between the raft deployment and retrieval stations using a paired *t*-test.

RESULTS

Drifting routes of the rafts

All 14 rafts were successfully retrieved. Drifting periods ranged from 19 h to 7 d 22 h 30 min, with 9 rafts drifting for >5 d (Table 1). Drifting routes and deployment and retrieval stations of each raft are shown in Fig. 1. The rafts dispersed in April 2013 and in May 2014, while they moved closer to each other in May 2013 and in April 2014 (Fig. 1).

Schooling and association patterns of *Seriola* spp. juveniles

During the study periods, *Seriola* spp. juveniles were observed in 10–76% of still images and in 33–95% of video images, with, on average, 1–58 and 1–22 individuals recorded in still and video images, respectively (data on other fish species are available in Tables S2 & S3 in the Supplement). The fish were observed within 0.5–84.5 h after release in still images, and within 1–116 h after release in video images (Table 1, and see Table 4).

Behavior of the *Seriola* spp. juveniles differed between day and night; they often swam around the seaweed clump during the day (Figs. 3a & 4; Fig. S12 in the Supplement & Video S1 in the Supplementary videos at www.int-res.com/articles/suppl/m573p101_supp/), and were closely attached to the seaweed clump or to other individuals at night (Figs. 3b & 4; Fig. S12). In 11 out of the 12 rafts that were success-

Table 1. Summary of the analysis of still images of *Seriola* spp. at each raft

| Year	Month	Raft no.	Drifting period (h)	Max. no. of fish at raft (mean ± SD) Day	Night	First *Seriola* spp. occurrence after release (h)
2013	April	1	121.5	8 (0.8 ± 1.8)	9 (0.9 ± 1.7)	11.5
		2	118.5	51 (0.7 ± 4.6)	33 (3.9 ± 7.3)	11.0
		3	145.5	7 (0.8 ± 1.4)	6 (0.2 ± 0.8)	5.0
		4	142.0	18 (1.4 ± 3.5)	131 (35.3 ± 36.2)	3.5
	May	1	19.0	8 (0.9 ± 2.0)	6 (2.9 ± 1.9)	5.0
		2	190.5	47 (0.5 ± 3.2)	31 (2.9 ± 4.3)	5.5
		3	186.0	48 (1.5 ± 4.8)	25 (6.3 ± 5.9)	2.0
		4	166.5	11 (1.3 ± 2.0)	7 (1.2 ± 1.3)	1.5
2014	April	1	150.0	2 (0.1 ± 0.3)	1 (0.1 ± 0.3)	84.5
		2	51.5	12 (4.7 ± 3.9)	13 (4.6 ± 4.7)	1.5
		3	169.5	20 (3.3 ± 5.1)	21 (4.8 ± 5.8)	12.0
	May	1	161.5	69 (5.1 ± 11.5)	52 (14.0 ± 13.6)	0.5
		2	43.5	33 (0.8 ± 4.6)	6 (1.1 ± 1.5)	7.5
		3	45.0	165 (10.5 ± 27.0)	280 (94.9 ± 74.0)	3.0
Summary			19.0–190.5	2–165 (0.1–10.5)	1–280 (0.1–94.9)	0.5–84.5
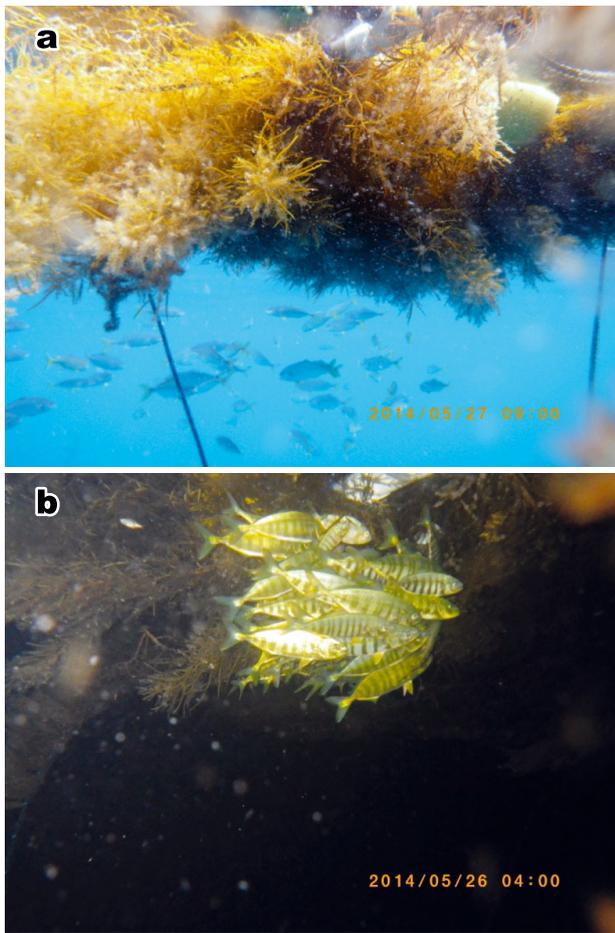
Fig. 3. Typical still pictures of *Seriola* spp. during (a) daytime (09:00 h on 27 May 2014, raft 1) and (b) nighttime (04:00 h on 26 May 2014, raft 1)
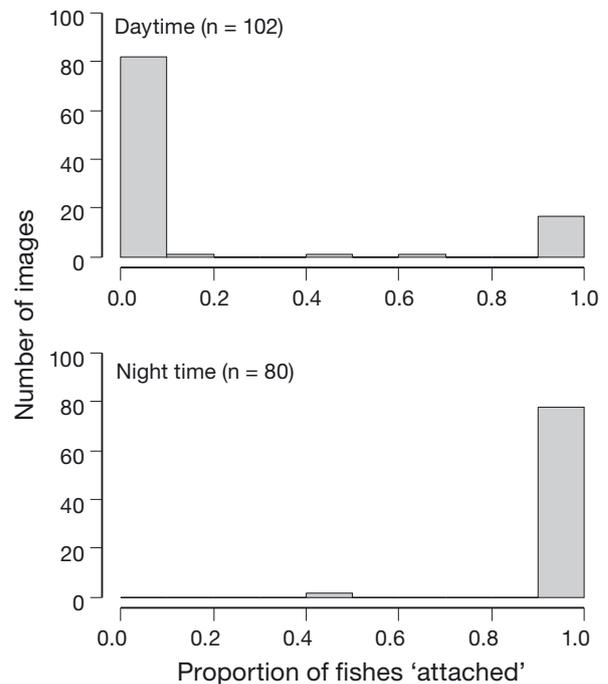

Fig. 4. Typical diel differences in the degree of association of *Seriola* spp. with drifting seaweeds (raft 4 in May 2013, categorized either as 'attached' or 'around;' see 'Materials and methods' for details). See Fig. S12 in the Supplement for data from the other rafts

fully analyzed by GLMs, the proportions of fish that were 'attached' at night were significantly larger than those during the day (GLM, χ^2 = 1.7–1832.0, df = 1, p < 0.05, R^2 = 0.05–0.71; Table 2; Fig. S12). The behavioral transition from the nighttime attachment pattern to the daytime swimming pattern was recorded for raft 3 from 05:05–05:10 h in May 2014 (Video S2). The number of fish increased significantly over time in 9 out of the 13 rafts (69%) at night, but only in 4 out of 14 rafts during the day (29%, Spearman's rank correlation test, p < 0.05; Table 2). Of the 4 rafts in which the fish number did not increase significantly at night, half drifted for <50 h, indicating that the drifting periods were insufficient to provide enough information to elucidate a trend with statistical significance. For 10 of the rafts (71%), fish numbers were significantly larger at night than during the daytime (Table 2; Fig. 5). The number of fish tended to be smaller at rafts that showed no significant difference between day and night (maxi-

mum: 8–33; mean: 0.8–1.3), compared to rafts with a significant difference between day and night (maximum: 1–280; mean: 0.1–94.9).

With increasing speed of the raft, the maximum fish numbers detected during 1 and 2 d periods also increased (GLM, χ^2 = 6.8–10.0, df = 1, p < 0.01; Table 3), while the effects during 3 to 6 d periods were not significant (GLM, χ^2 = 0–1.7, df = 2, p = 0.19–0.95; Table 3). Fish numbers were not significantly affected by the straightness index (GLM, χ^2 = 0–1.9, df = 2, p = 0.17–1.00) or by SST (GLM, χ^2 = 0.1–1.0, df = 2, p = 0.11–0.76; Table 3) during any period.

School size increased significantly over time (GLMM, n = 823, χ^2 = 126.4, df = 1, p < 0.01, marginal R^2 = 0.26, conditional R^2 = 0.81; Fig. 6). When each raft was examined separately, school size increased significantly over time in 8 rafts (57%) (GLM, χ^2 = 0.2–138.6, df = 1, p < 0.05, R^2 = 0.05–0.65; Table 4; Fig. S13 in the Supplement). There were no significant increases in some rafts, but the sample size (i.e. the total number of schools of *Seriola* spp. juveniles recorded at each of these rafts) tended to be low (n = 7–33), except raft 3 in April 2013 (n = 75) (Table 4; Fig. S13 in the Supplement). We recorded 1 instance when 2 schools of *Seriola* spp. juveniles met each other to form a larger school under the seaweed (Video S3).

Table 2. Summary of the statistical analyses on the still images of *Seriola* spp. at each raft. Correlations between fish numbers and days after release were analyzed by Spearman's rank correlation test (+: $p < 0.05$; ++ and −: $p < 0.01$, where + and − represent positive and negative correlations, respectively), while diel differences in fish numbers and proportions were analyzed by a generalized linear model (GLM; *$p < 0.05$, **$p < 0.01$); in the correlation and diel difference columns, the numbers shown are p-values. NA: not analyzed. See 'Materials and methods' for a definition of 'attached' fish. Images with *Seriola*: no. of images that captured *Seriola* spp.

Month	Raft no.	No. of images Day	No. of images Night	Correlation between fish nos. and days after release Day	Correlation between fish nos. and days after release Night	Diel difference in fish nos.	R^2	Images with *Seriola* Day	Images with *Seriola* Night	Diel difference in proportion of fish 'attached'	R^2
2013											
April	1	139	105	0.36	0.05	0.22[c]	0.29	30	39	Night > day**	0.15
	2	133	105	0.88	++	Night > day**[d]	0.34	17	53	NA[f]	
	3	158	122	0.47	++	Day > night**[d]	0.22	54	13	0.19	0.05
	4	159	126	−	++	Night > day**[d]	0.54	43	120	Night > day**	0.71
May	1	21	18	0.86	NA[a]	Night > day*[d]	0.17	5	15	Night > day**	0.44
	2	238	144	+	++	Night > day**[d]	0.50	28	116	Night > day**	0.21
	3	203	126	0.91	++	Night > day**[d]	0.21	41	120	Night > day**	0.43
	4	208	126	−	0.99	0.30[c]	0.22	102	80	Night > day**	0.62
2014											
April	1	175	126	++	++	Night > day*[c]	0.27	8	6	NA[f]	
	2	62	42	++	++	Night > day**[d]	0.62	45	26	Night > day**	0.56
	3	193	147	++	++	Night > day**[d]	0.67	112	119	Night > day**	0.46
May	1	198	126	0.06	++	Night > day**[d]	0.35	75	106	Night > day**	0.65
	2	52	36	0.25	0.08	0.48[d]	NA[e]	4	21	Night > day**	0.62
	3	55	36	0.42	−	Night > day**[d]	0.29	34	35	Night > day**	0.18
Summary		21–238	18–147	28.6%[b]	69.2%[b]	71.4%[b]	0.17–0.67	4–112	6–120	91.7%[b]	0.05–0.71

[a]Not analyzed due to small sample size; [b]Percentage of rafts that had increasing trends or increasing trends at night; [c]With a Poisson distribution; [d]With a negative binomial distribution; [e]Not calculated because no significant effects were found in any variable; [f]Not analyzed because the algorithm did not converge
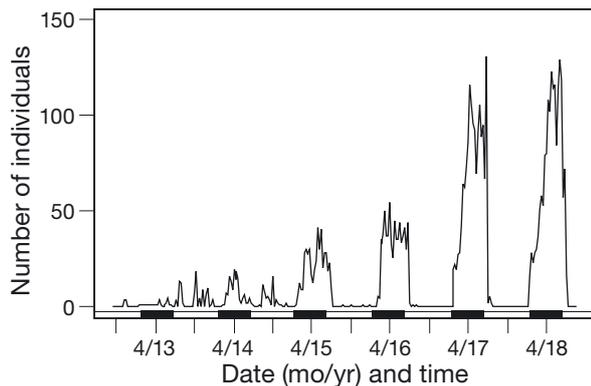

Fig. 5. Typical change in the numbers of *Seriola* spp. in the still images over time (raft 4 in April 2013). Black horizontal bars indicate nighttime (19:30–05:30 h). See Fig. S11 in the Supplement for data from the other rafts

Table 3. Summary of the effect of different factors on the maximum number of *Seriola* spp. Day: time since deployment of rafts. Factors were analyzed by a generalized linear model. +: significant positive interaction ($p < 0.01$). Numbers in the columns are p-values; NA: not analyzed

Day	No. of rafts	Factors Speed	Factors Straightness index	Factors Sea surface temperature	R^2
1	13	+	0.85	NA[a]	0.39
2	13	+	NA[a]	0.32	0.56
3	10	0.30	1.00	0.55	NA[b]
4	9	0.25	0.24	0.42	NA[b]
5	9	0.19	0.28	0.76	NA[b]
6	7	0.95	0.17	0.11	NA[b]

[a]Factor removed from analysis because there was a correlation with speed; [b]Could not be calculated because no significant effects were found in any variable

The degree of association with drifting seaweeds changed in response to school size. The proportion of the fish that exhibited 'close proximity,' in which the school or solitary fish remained in close proximity to the seaweed, decreased in response to the increase in school size, whereas the proportion of

the fish that were 'swimming around,' whereby the school or solitary fish swam around the seaweed, increased in response to an increase in school size (GLMM, $\chi^2 = 82.8$, df = 1, $p < 0.01$; Fig. 7). This result indicates that solitary individuals and smaller schools tended to remain close to the seaweeds,
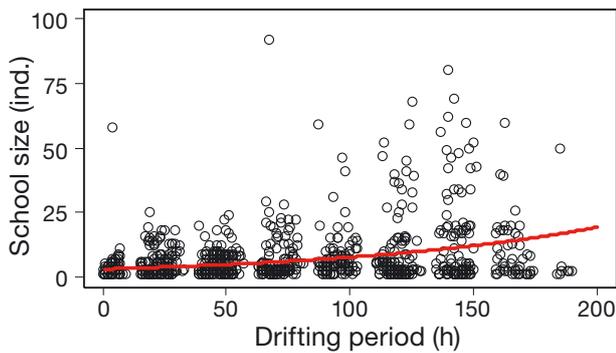
Fig. 6. Effect of the drifting period (h) on the school size of *Seriola* spp. around the rafts, measured from the video images. The red solid line indicates the estimate from the generalized linear mixed model. See Fig. S13 for data from the other rafts
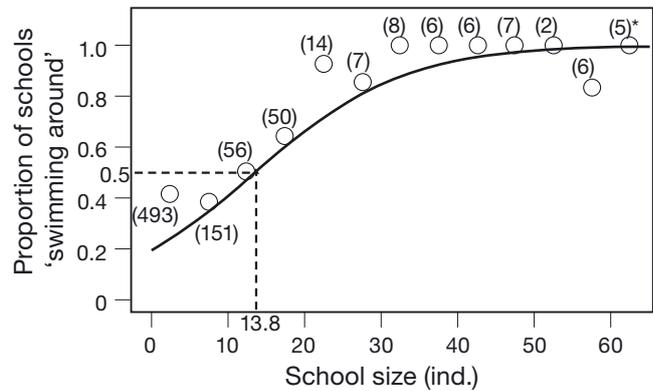

Fig. 7. Effect of *Seriola* spp. school size on the degree of association with drifting seaweeds (categorized either as being in 'close proximity' or 'swimming around;' see 'Materials and methods' for details). Circles represent the proportion of fish schools that were 'swimming around' in every school size class (binned by 5 individuals). The solid line indicates the estimate from the generalized linear mixed model (GLMM). Numbers in parentheses indicate numbers of schools examined. Dashed lines represent the school size (13.8 ind.) in which 50% of schools showed 'swimming around' behavior, estimated from the GLMM. The asterisk (*) indicates that this number includes all fish schools exceeding 60 individuals

whereas larger schools tended to actively swim around the seaweeds.

Among 945 video images, potential predators (i.e. *Coryphaena hippurus*, *S. aureovittata*, and Belonidae spp.) occurred in 172 (16%), 19 (2%), and 4 (0.4%) images, respectively. Of these images, *Seriola*

spp. juveniles were recorded together with *C. hippurus* in 153 images (89%), with *S. aureovittata* in 7 images (37%), and with Belonidae spp. in no images (0%). Although in many cases *Seriola* spp. juveniles remained schooling around the seaweeds or did not show observable responses, they escaped into the seaweeds in 5 cases (4 cases with *C. hippurus*, and 1 case with *S. aureovittata*). (See Video S4 for an example of this escaping behavior.) Solitary fish escaped into the seaweed in 4 cases (3 cases with *C. hippurus*, and 1 case with *S. aureovittata*), whereas a school of 4 individuals escaped into the seaweed in 1 case with *C. hippurus*.

Zooplankton abundance

Although the sample size was quite small (n = 4) and thus the statistical test should be interpreted with caution, the density of cope-

Table 4. Summary of the statistical analyses of the video images of *Seriola* spp. at each raft. The effect of time after release on school size was analyzed by a generalized linear model (+ indicates a significant [p < 0.01] increase); numbers in the column represent p-values. NA: could not be calculated because no significant effects were found in any variable

Month	Raft no.	Drifting period (h)	First *Seriola* spp. occurrence after release (h)	No. of fish schools	Effect of time (h) after release on school size	R^2
2013						
April	1	121.5	41	33	0.17[a]	NA
	2	118.5	16	33	+[a]	0.35
	3	145.5	2	75	0.29[a]	NA
	4	142.0	3	93	+[a]	0.20
May	1	19.0	2	7	0.06[b]	NA
	2	190.5	6	106	+[a]	0.06
	3	186.0	1	72	+[a]	0.05
	4	166.5	1	116	+[a]	0.05
2014						
April	1	150.0	116	21	0.31[b]	NA
	2	51.5	2	28	+[b]	0.51
	3	169.5	16	84	+[a]	0.65
May	1	161.5	1	119	+[a]	0.43
	2	43.5	2	8	0.70[a]	NA
	3	45.0	1	33	0.11[a]	NA
Summary		19.0–190.5	1–116	7–119	57.1%[c]	0.05–0.65

[a]With a negative binomial distribution; [b]With a Poisson distribution; [c]Percentage of rafts that had increasing trends
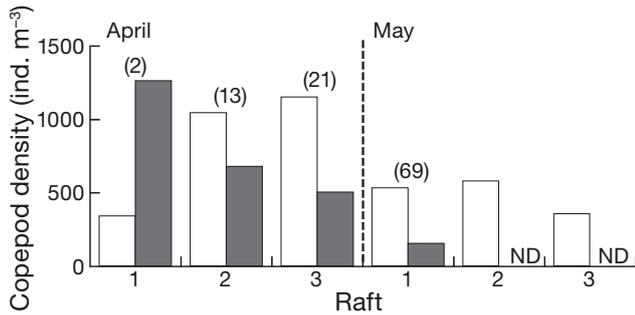
Fig. 8. Copepod density at the sites of raft deployment (white bars) and retrieval (black bars), obtained in 2014. ND: no data (due to stranding of the rafts). Numbers in parentheses are maximum fish numbers in the still images during the drifting periods (shown in Table 1)

pods (a main food item of *Seriola* spp. juveniles) at the release sites was not significantly different from that at the retrieval sites (paired *t*-test, df = 3, *t* = −0.61, p = 0.59; Fig. 8). We did not find a positive relationship between copepod density and the maximum number of fish detected by still cameras (Fig. 8).

DISCUSSION

In the still image analysis, the numbers of fish were higher at night than during the day at 71% of the rafts (Table 2). Fish numbers at night tended to increase over time (increase: 69%, decrease: 8%, no significant trend: 23%), but the trend was less obvious during the day (increase: 29%, decrease: 14%, no significant trend: 57%). These diel differences are likely due to the difference in the diel behavioral patterns, since the still and video images showed that the fish attached closely to the seaweed or other individuals at night and that many fish swam in and out of the camera view during the daytime (Figs. 3 & 4; Videos S1 & S2 in the Supplement). Furthermore, *Seriola quinqueradiata* juveniles actively swam around the seaweed (ranging 3–5 m) in the daytime (05:00−19:00 h), and ceased swimming and stayed inside and/or around the seaweed at night (21:00−03:00 h) (Ikehara 1984). Thus, it is highly likely that the fish numbers around the raft increased (both during the day and at night) over time, and the diel behavioral pattern is the cause of the observed difference in fish numbers between day and night.

The nighttime behavioral pattern (i.e. close attachment to the seaweed or to conspecifics) of *Seriola* spp. juveniles can be related to the maintenance of schools. Sakakura & Tsukamoto (1997) speculated that *S. quinqueradiata* juveniles are associated with drifting seaweeds to maintain their schools at night when their visual acuity is limited. In addition, another carangid, *Pseudocaranx dentex*, maintains an association with floating objects by mechanosensory cues at night, although it uses vision during the day (Masuda & Tsukamoto 2000). Although chemical and auditory cues have also been suggested as potential cues to locate floating objects (Dempster & Kingsford 2003, 2004), the sensing ranges for these cues are generally larger than visual and mechanosensory cues during both day and night. Therefore, the nighttime dense aggregation of *Seriola* spp. juveniles near seaweed may be due to the use of mechanosensory signals by the fish when vision is less effective.

Our results provide circumstantial evidence supporting the shelter from predator hypothesis in *Seriola* spp. juveniles, since we observed that solitary individuals and a small school escaped into the seaweed clump when potential predators appeared (Video S4). Fréon & Dagorn (2000) disagreed with the shelter from predator hypothesis for fishes swimming around floating structures, because sometimes they are too numerous to take shelter under small objects and/or they are too far from the objects to be in the 'blind zone' of predators. However, it is important to note that the color (yellow-brown) of *Seriola* spp. juveniles matches the color of the seaweed (Uchida 1963, Senta 1965), and background-matching coloration is a general anti-predator adaptation (e.g. Stuart-Fox et al. 2008, Wang & Schaefer 2012, Morgans & Ord 2013). Furthermore, *S. quinqueradiata* juveniles escape into drifting seaweed when threats such as boats approach them (Hanaoka 1986). Drifting seaweeds have highly complex thallus morphology that can be used for sheltering, similar to driftwood and manmade FADs with complex structures (Hunter & Mitchell 1966, Gooding & Magnuson 1967). Therefore, juveniles that hide in drifting seaweed may have better survival rates when predators are nearby. Considering these facts, drifting seaweeds likely function as shelters from predators for *Seriola* spp. juveniles, especially for isolated individuals or small schools.

We observed that solitary individuals and small schools tended to remain close to the drifting seaweed, whereas large schools tended to actively swim around the rafts (Fig. 7). This may reflect the adaptive significance of association with drifting seaweed and schooling in *Seriola* spp. juveniles. Juvenile fishes generally have to balance the demands of feeding and safety from predators. For example, fish normally prefer areas of high-density prey, but when predation risk increases, they prefer to use areas that

are safer, but have a lower prey density (Milinski & Heller 1978, Werner et al. 1983). Schooling decreases per capita predation risk of animals through several mechanisms such as dilution, predator confusion, and improved vigilance for predators (Pitcher & Parrish 1993). Thus, *Seriola* spp. juveniles may stay close to the seaweed shelter when the school size is small and the per capita predation risk is high. Then, when the school size becomes larger and the per capita predation risk becomes lower, they may explore wider areas around the seaweed in search of high-density areas of zooplankton prey. This hypothesis is also supported by the fact that solitary individuals and a small school hid in drifting seaweed but the large schools continued schooling around the seaweed regardless of the appearance of potential predators. Further experiments are required to verify the adaptive significance of schooling in *Seriola* spp. juveniles observed in this study.

Our results show that the school size of *Seriola* spp. juveniles associated with drifting seaweeds increased over time (Fig. 6; Table 4). One possible explanation for this pattern is that solitary fish or those in smaller schools might have used drifting objects as a meeting-point to form larger schools. Our observation of an instance when 2 schools joined each other to form a larger school (Video S3) is consistent with this explanation. However, we should also note that this study lacks records of the instances of dissociation of the fish from the seaweed, information that is also essential for testing the meeting-point hypothesis (Fréon & Dagorn 2000, Soria et al. 2009). Another possibility is that the increase in school size is a by-product of fish gathering at drifting seaweed for alternative purposes, such as nighttime school maintenance and shelter from predators as mentioned previously, and thus the increase simply reflects the colonization process of the fish because no fish were associated with the rafts at the time of release. This explanation also includes the possibility that larger schools which had previously formed around natural drifting seaweeds, FADs, and/or food-rich areas recruited to our rafts for some other purpose(s). There were natural drifting seaweeds and manmade FADs (for *C. hippurus* fishing) around the study area (Kuwano et al. 1982, Fujita 1986). In addition, although we did not find any relationship between fish numbers and zooplankton abundance (Fig. 8), the possibility that there were zooplankton hotspots between the release and retrieval sites cannot be excluded. Nonetheless, schooling should provide some benefit as well, because the fish exhibited more than just aggregation at seaweeds; they

showed clear schooling behavior in which they swam synchronously (See Videos S1, S2 & S3 in the Supplement). Further research documenting the dissociation process of the fish from the seaweeds, fish behaviors after the colonization period, and the distribution of other floating objects and zooplankton abundance is needed to clarify the reason(s) for the increase in school size over time.

Our study also provides insight into a factor affecting the colonization process of *Seriola* spp. juveniles; increased raft speed enhanced the colonization of *Seriola* spp. juveniles during the 1 and 2 d periods (but not during the 3 to 6 d periods; Table 3). The increased raft speed might have increased the encounter rate between the raft and *Seriola* spp. juveniles, and consequently the juveniles could rapidly colonize the rafts. Because our monitoring periods were up to 1 wk, further long-term study is needed to clarify other factors affecting the colonization process of *Seriola* spp. juveniles.

Although our monitoring system was useful for continuously monitoring the schooling and associative behaviors of fishes with the same drifting seaweeds, there are some limitations. First, as described above, the camera view is limited and thus fish numbers (especially in still images) can be variable when the fish swim around the system. Second, fish numbers (specifically in still images) can be underestimated when the fish are completely hidden in the seaweeds, e.g. at night. However, we observed the opposite phenomenon: fish numbers at night were larger than during the day, and thus the effect of this bias was relatively small compared to that of diel behavioral differences. Third, due to the darkness, video images can only be obtained in the daytime. However, these 3 limitations can be overcome by modifying our system with omni-directional, infrared video cameras. Fourth, since tracking the same individual or school over time is not possible, we cannot detect all instances when the fish actually meet with other conspecifics at the drifting objects (but see Video S3 for such a case), and the instances when the individuals or schools leave the drifting objects. This limitation cannot be overcome by modifying our system alone, and thus other methods need to be incorporated. Specifically, combining our system with acoustic telemetry can provide stronger evidence of the meeting-point function because our system can record increases or decreases in the school size but cannot record the timing of the meeting among individuals or schools and the timing of dissociation from the drifting objects, whereas acoustic telemetry can (Soria et al. 2009). Combining our system with echo-

sounder buoys can also be useful, because echo-sounder buoys provide rough estimates of aggregated biomass over larger scales (Lopez et al. 2014, Moreno et al. 2016), and our system enables species identification and behavioral categorization.

CONCLUSION

The ecologically significant functions of drifting seaweeds for juvenile fish include providing hiding places and feeding habitats (e.g. Ida et al. 1967, Kingsford 1992, Shaffer et al. 1995, Vandendriessche et al. 2007). Our results, together with a previous study (Hasegawa et al. 2016), indicate that the ecological significance of the seaweeds for *Seriola* spp. juveniles include providing habitat for school maintenance at night, a hiding place for predator avoidance, and possibly a meeting-point for school formation, but not a habitat for feeding. The abundance, distribution, and species composition of seaweed forests and drifting seaweeds have been dramatically changing due to global warming (Wernberg et al. 2011, Komatsu et al. 2014, Yamasaki et al. 2014), which may in turn affect populations of *Seriola* and other fishes associated with drifting seaweeds. Knowledge of the significance of drifting seaweeds for fishes as obtained in this study will be useful in designing conservation and management measures for fishes associated with drifting seaweeds. For example, the installation of artificial drifting objects with complex structures could provide suitable habitats that facilitate school maintenance and predator avoidance of *Seriola* spp. juveniles, as shown in this study for the drifting seaweeds. However, we must be cautious about the implementation of such measures because fish associated with artificial drifting objects may obtain less food, as shown in other fishes associated with manmade FADs (Marsac et al. 2000, Hallier & Gaertner 2008).

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