

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

3
4 **Running page head:** Behavior of *Seriola* spp. juveniles

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

40

41 **KEY WORDS:** Fish Aggregating Devices . Floating seaweed . *Seriola quinqueradiata* . Yellowtail .
42 Shelter from predator hypothesis . East China Sea . Time lapse camera . GPS satellite buoy

43 INTRODUCTION

44 Seaweeds with gas-filled vesicles can float after being detached from their base by strong
45 waves or winds (Yoshida 1963, Kingsford & Choat 1985), and these detached seaweeds are called
46 drifting seaweeds. Over 333 fish species (96 families) are associated with floating objects including
47 drifting seaweeds, and the majority (80%) of fish are present during the juvenile stages (Castro et al.
48 2002). Several hypotheses have been proposed for the ecological significance of drifting seaweeds
49 for fishes, such as the ‘concentration of food supply’ hypothesis, the ‘indicator-log’ hypothesis, the
50 ‘meeting-point’ hypothesis, and the ‘shelter from predator’ hypothesis (reviewed by Fréon &
51 Dagorn 2000, Castro et al. 2002). The concentration of food supply hypothesis posits that floating
52 structures help feed small fishes, zooplankton, and sessile biota. The indicator-log hypothesis
53 assumes that natural floating objects are often indicators of biologically rich water masses, because
54 most natural floating objects originate in rich areas (e.g. river mouths and mangrove swamps) and
55 remain within these rich water masses, or because they aggregate in rich frontal zones. This
56 hypothesis was first proposed for tunas (Hall 1992), and was extended to larval and juvenile fishes
57 (Castro et al. 2002). The meeting-point hypothesis states that fishes make use of floating structures
58 to increase the encounter rate between isolated individuals or small schools and other schools. The
59 shelter from predator hypothesis posits that fishes use floating structures as a refuge from predators.
60 Although previous studies have reported anecdotal evidence supporting each hypothesis (e.g. Druce
61 & Kingsford 1995, Vandendriessche et al. 2007, Casazza & Ross 2008), the comprehensive
62 assessments of these different hypotheses are still limited.

63 Fish juveniles associated with drifting seaweeds have been mostly studied by traditional
64 methods such as net capture (e.g. Kingsford & Choat 1985, Sakakura & Tsukamoto 1997, Dempster
65 & Kingsford 2004, Uehara et al. 2006, Vandendriessche et al. 2007) and underwater visual
66 observation (e.g. Hanaoka 1986, Ikehara 1984, Casazza & Ross 2008). However, these methods
67 cannot provide the continuous stream of data that is needed to monitor fish and test the hypotheses.
68 Furthermore, the presence of an observer might affect the behavior of fishes during underwater

69 observation (Okamoto et al. 1981, Kudo 1998, Dearden et al. 2010). Hence, video cameras have
70 been used for serial observation of fishes associated with drifting seaweeds (Moser et al. 1998),
71 however the observation time-scale (1.3–2.0 h, a total of 21.5 h) is relatively short. To overcome
72 this methodological problem, we developed a new monitoring system: a raft equipped with a
73 seaweed clump, interval still/video cameras, and a GPS satellite buoy, which can continuously
74 monitor the behaviors of fishes associated with drifting seaweeds for up to a week.

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

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

94 MATERIALS AND METHODS

95 Study site and experimental protocol

96 This study was conducted near the Goto Islands (the Goto Sea), which is located in the
97 northeastern part of the East China Sea (Fig. 1). This location is a major fishing ground for *S.*
98 *quinqueradiata* juveniles associated with drifting seaweeds, during the months of May to June
99 (Yamashita & Iwasa 1984, Yamamoto & Tashiro 1986); the collected juveniles are used for
100 aquaculture seedlings. No artificial floating objects are deployed for the fishing of *S.*
101 *quinqueradiata* juveniles, but fish aggregating devices (FADs) for catching dolphinfish *Coryphaena*
102 *hippurus* are deployed in this region (Fujita 1986, Kuwano et al. 1982). A total of 8 cruises at the
103 shelf-break region (31°36'N–33°18'N, 129°00'E–130°06'E; Fig. 1) were conducted by the T/V
104 Kakuyo-Maru of Nagasaki University from April to June in 2013 and in 2014. In total, 14 rafts were
105 released and retrieved (See “Monitoring system” for details). The rafts were released in this area
106 because of the large number of drifting seaweeds and associated *Seriola* spp. juveniles that were
107 present (Hasegawa et al. 2016). Four rafts were released during 11–12 April and four more were
108 released on 27 May, and were retrieved during 16–18 April and 3–4 June, respectively, in 2013.
109 Three rafts were released on 12 April and three more were released on 21 May, and were retrieved
110 on 19 April and during 27–29 May, respectively, in 2014. The rafts were retrieved using near
111 real-time positional data from the attached GPS buoy and radio wave from the VHF transmitter.

112 The water transparency of the Goto Sea during the study season is at least over 8.5 m
113 [2013: April, 12.1 ± 1.2 (mean \pm SD) m, $n = 7$; May, 16.6 ± 6.3 m, $n = 6$; June, 19.6 ± 10.4 m, $n = 5$,
114 2014: April, 14.6 ± 3.2 m, $n = 7$; May, 12.6 ± 3.1 m, $n = 7$] which is longer than the sum of the
115 distance between the seaweed clump and the cameras (approximately 2 m), as well as the
116 previously reported swimming range of *S. quinqueradiata* (main *Seriola* in this region) from the
117 clump (3–5 m) (Ikehara 1984). Therefore, we believe that visibility conditions had at most a trivial
118 effect in this study.

119

120 **Monitoring system**

121 Four square rafts (140 cm × 140 cm) were made with polyvinyl chloride pipes and floats
122 (Fig. 2), and repeatedly used to obtain the data in different months and years. To directly observe
123 associative behaviors of *Seriola* spp. juveniles with drifting seaweeds, each raft was equipped with
124 collected seaweeds (See next paragraph for details), a digital still camera (Optio WG-1, WG-2 or
125 W90 with a focus free wide F3.5 lens, Pentax, Japan) in a waterproof housing (WHPE-WG1, -WG2
126 or -W90, Recsea/Seatool, NTF Co., Ltd., Japan), and a video camera (Gopro Hero2 with a
127 focus-free wide F2.8 lens, Woodman Labs Inc., USA) in a custom-made waterproof housing and
128 equipped with an interval scheduling system and extra-battery (Logical Product Co., Ltd., Japan).
129 The vertical and horizontal fields of view of the still camera were 46° and 59°, respectively, and
130 those of the video camera were 62° and 100°, respectively (Fig. S1 in the Supplement). Both
131 cameras were pointed at the center of the seaweed clump (Fig. S1). To take still images at night, a
132 flash was provided for the still cameras. A water temperature logger (HOBO U22-001, Onset Corp.,
133 USA) and light logger (HOBO UA-002-64, Onset Corp., USA) were also attached to the raft to
134 monitor the sea surface temperature and to define daytime and nighttime, respectively. A drifting
135 GPS buoy (ZTB-R6-P3, Zeni Lite Buoy Co., Ltd., Tokyo Japan), which sends its position via
136 satellite, and VHF transmitter (F1860, Advanced Telemetry Systems Inc., USA) were tethered to
137 each raft to monitor location and aid in raft retrieval. A sinker (1.5 kg) was suspended below the raft
138 to lower its center of gravity and prevent it from overturning. The recording/sampling intervals for
139 the still camera and GPS buoy was once every 30 min, and it was once every 10 min for the
140 temperature and light loggers. During the daytime (06:00–19:00), the video cameras were scheduled
141 to record 2 min of video once an hour, with a few exceptions. Around the crepuscular period of May
142 2013, 2 min (05:05–05:07, 19:31–19:33) were recorded. During the crepuscular periods of April
143 2014 and May 2014, 5 min recordings were taken during 05:40–05:45 and 19:00–19:15, and 05:05–
144 05:10 and 19:25–19:30, respectively. The recordings of still and video cameras were partially
145 synchronized (every hour during the daytime).

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

151

152 **Analysis of still and video images**

153 We categorized *S. quinqueradiata* and *S. dumerili* as *Seriola* spp. and counted the number
154 of individuals in each still and video image, because *S. quinqueradiata* and *S. dumerili* (and
155 possibly yellowtail kingfish *S. aureovittata* and other *Seriola* spp.) were difficult to distinguish from
156 each other from the still or video images. We targeted juveniles of *Seriola* spp. that were associated
157 with drifting seaweeds (at most 20 cm total length, Senta 1965, Fujita & Mori 1982, Hasegawa et al.
158 2016), and thus obviously large (at least over 40 cm total length) *Seriola* spp. (identified as *S.*
159 *aureovittata*) was excluded from the analysis.

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

172 counted as one individual in both of the still and video images. To analyze the relationship between
 173 school size and the degree of association with drifting seaweeds, we categorized the degree into
 174 ‘close proximity’ in which the school or solitary fish remained inside or underneath the seaweed
 175 within the camera view (within approximately 1 m beneath the seaweed) for the whole 2-min
 176 recording period, and ‘swimming around’ in which the fish swam in and out of the camera view
 177 during the recording period. The video images during the crepuscular periods (e.g. 05:05–05:07 in
 178 April) were only used for qualitative (not quantitative) behavioral observation. The video images
 179 with potential predators were also counted, and behaviors of *Seriola* spp. juveniles in the images
 180 were noted. Nighttime was defined as a period when light intensities measured by light loggers
 181 were less than their minimum light sensitivity (1 lux): 19:30–05:30 in April and 20:00–04:30 in
 182 May–June.

183

184 **Drifting trajectory**

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

$$189 \quad Dt = r \cos^{-1}(\sin y_{(t-1)} \sin y_t + \cos y_{(t-1)} \cos y_t \cos \Delta x), \quad (1)$$

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

192 To estimate the tortuosity of the raft trajectory, straightness index (Si , Benhamou 2004)
 193 during a given time period was calculated using the following Eq. (2):

$$194 \quad Si = \frac{r \cos^{-1}(\sin y_0 \sin y_n + \cos y_0 \cos y_n \cos \Delta x_{0n})}{\sum_{t=1}^n Dt}, \quad (2)$$

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

198

199 **Zooplankton abundance**

200 The main food item of *Seriola* spp. juveniles is planktonic copepoda (Anraku & Azeta
201 1965, Hasegawa et al. 2016, Senta 1965, Yamasaki et al. 2014). Therefore, to reveal the food
202 availability for *Seriola* spp. juveniles, we investigated the density of planktonic copepoda in the
203 stations where rafts were deployed and retrieved in 2014. We could not obtain zooplankton in 2013
204 due to limited ship time, and could not obtain zooplankton at the retrieved sites of the raft 2 and 3 in
205 May 2014 because these rafts were recovered after stranding on shore (Fig. 1).

206 A Norpac net (45 cm diameter, 54GG; mesh = 315 μm) was vertically towed from 20 m
207 depth during the daytime (06:00–18:00). A flow meter (Rigo, Tokyo) was attached to the opening of
208 the Norpac net to measure the volume of filtered water. Collected samples were immediately fixed
209 in 10% buffered formalin solution. The volume of filtered water collected during the Norpac net
210 tow at each sampling station was calculated using a calibrated flow meter. Because plankton
211 densities were high, plankton samples were divided more than 2, and divided samples were used for
212 the measurement of the density of the copepoda. The copepoda was identified according to a
213 guideline (Chihara & Murano 1997), using a stereoscopic microscope. The density of the copepoda
214 D (ind. per m^3) was calculated using the following Eq. (3):

$$215 \quad D = (NS^{-1})V^{-1}, \quad (3)$$

216 where N is the total number of copepod in a divided sample, S is the fraction of the sample that was
217 divided, and V is the total volume of water sampled (m^3).

218

219 **Statistical analyses**

220 We constructed a series of generalized linear models (GLMs) and generalized linear mixed
221 models (GLMMs) to evaluate the effects of different variables on the associative and schooling
222 behaviors in *Seriola* spp. juveniles; the models and variables are summarized in Table S1 in the
223 Supplement. When an objective variable was discrete, we used a Poisson or negative binomial error
224 distribution with log link function (Zuur et al. 2009); we used a negative binomial distribution
225 rather than a Poisson distribution when a fitted model was overdispersed (i.e. residual deviance/d.f.
226 was over 2). A binomial distribution with logit link function (logistic regression) was used when the
227 objective variable was categorical (Zuur et al. 2009). The diagnostics of above GLM/GLMM
228 analyses were conducted by the overdispersion parameter (residual deviance/d.f.), percentage of
229 deviance explained [R^2 for GLM, and marginal and conditional R^2 for GLMM (Nakagawa &
230 Schielzeth 2013)], quantile-quantile plots, and distribution of residuals (see Figs. S2–S10 in the
231 Supplement). All analyses were carried out using R, version 3.1.3 (R Development Core Team
232 2015) with the lme4 package (Bates et al. 2015) for the GLMM. The p-values < 0.05 were
233 considered as significant in all analyses.

234

235 Analysis of still images

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

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

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

253 To investigate the factors affecting the aggregation process of *Seriola* spp. juveniles, we
254 examined the effects of mean raft speed, tortuosity of the raft trajectory (straightness index), and
255 mean sea surface temperature (SST) on the maximum number of fish detected during the 1- to
256 6-day periods using a GLM with a negative binomial error distribution and a log link. When data
257 recorded during a 1-day period were less than 20 h due to any problems with the devices, we
258 removed them from the analysis. We conducted different analysis from the diel period and days
259 after release, because the raft speed, trajectory, and SST are likely to affect the fish colonization
260 process rather than directly affecting the fish numbers. When a significant correlation was found in
261 any pairs of the explanatory variables (i.e. raft speed, tortuosity of the raft trajectory, and SST), we
262 removed one variable from the analysis to prevent multi-collinearity (see Table 1). The
263 significances of the explanatory variables were assessed using the LR test.

264

265 Analysis of video images

266 To assess the change of the school size of the *Seriola* spp. juveniles over time, we
267 evaluated the effect of time after release (h) on the school size using a GLMM with a negative
268 binomial error distribution. The school size was regarded as an objective variable, while the time
269 after release was regarded as an explanatory variable. The raft was regarded as a random effect

270 because we probably repeatedly recorded the same schools or individuals. The significance of the
271 time was assessed by removing it from the model and comparing the change in deviance using the
272 LR test. To further understand the change of fish numbers over time in each raft, we examined the
273 effect of time after release on the school size in each raft using a GLM with a Poisson or negative
274 binomial error distribution and a log link. The significance of the time was similarly assessed in
275 each raft using the LR test.

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

282

283 Analysis of zooplankton

284 To examine the change of prey abundance, the copepoda density between the deployed
285 and retrieved stations were compared using a paired *t*-test.

286 **RESULTS**

287 **Drifting routes of the rafts**

288 All 14 rafts were successfully retrieved. Drifting periods ranged from 19 h to 7 d 22 h 30
289 min, with 9 rafts drifting over 5 d (Table 2). Drifting routes, and deployed and retrieved stations of
290 each raft are shown in Fig. 1. The rafts dispersed in April 2013 and in May 2014, while they moved
291 more closely to each other in May 2013 and in April 2014 (Fig. 1).

292

293 **Schooling and association patterns of *Seriola* spp. juveniles**

294 During the study periods, *Seriola* spp. juveniles occurred in 10–76 % of still images and in
295 33–95 % of video images, where on average, 1–58 individuals and 1–22 individuals were recorded
296 in still and video images, respectively (the data on other fish species are available in the
297 supplementary Tables S2 & S3). The fish were observed within 0.5–84.5 h after release in still
298 images, and 1–116 h after release in video images (Tables 2 & 3).

299 Behavior of the *Seriola* spp. juveniles differed between day and night; they often swam
300 around the seaweed clump during the day (Figs. 3a & 4; Fig. S12 & Video S1 in the Supplement),
301 and were closely attached to the seaweed clump or other individuals at night (Figs. 3b & 4; Fig. S12
302 in the Supplement). In 11 out of the 12 rafts that were successfully analyzed by GLMs, the
303 proportions of the fish that showed ‘attached’ at night were significantly larger than those during the
304 day (GLM, $\chi^2 = 1.7\text{--}1832.0$, $df = 1$, $p < 0.05$, $R^2 = 0.05\text{--}0.71$; Table 2; Fig. S12 in the Supplement).
305 The behavioral transition from the nighttime attachment pattern to the daytime swimming pattern
306 was recorded for raft 3 in 05:05–05:10 May 2014 (Video S2 in the Supplement). In the nighttime,
307 the fish number increased significantly over time in 9 out of the 13 rafts (69 %), but only in 4 out of
308 14 rafts during the day (29 %, Spearman's rank correlation test, $p < 0.05$; Table 2). In the 4 rafts in
309 which the fish number did not increase significantly at night, half of them drifted for less than 50 h,

310 indicating that the drifting periods were insufficient to provide enough information to elucidate a
311 trend with statistical significance. In 10 of the rafts (71 %), the fish numbers at night were
312 significantly larger than those during the daytime (Table 2; Fig. 5). The fish number tends to be
313 smaller in the rafts with no significant difference between day and night (maximum; 8–33, mean;
314 0.8–1.3), compared to the rafts with a significant difference between day and night (maximum; 1–
315 280, mean; 0.1–94.9).

316 The increased speed of the raft increased the maximum fish numbers detected during the
317 1-day and 2 day periods (GLM, $\chi^2 = 6.8$ – 10.0 , $df = 1$, $p < 0.01$; Table 1), while the effects during
318 the 3- to 6-day periods were not significant (GLM, $\chi^2 = 0$ – 1.7 , $df = 2$, $p = 0.19$ – 0.95 ; Table 1). Fish
319 numbers were not significantly affected by the straightness index (GLM, $\chi^2 = 0$ – 1.9 , $df = 2$, $p =$
320 0.17 – 1.00) nor SST (GLM, $\chi^2 = 0.1$ – 1.0 , $df = 2$, $p = 0.11$ – 0.76 ; Table 1) during any periods.

321 The school size increased significantly over time (GLMM, $n = 823$, $\chi^2 = 126.4$, $df = 1$, $p <$
322 0.01 , marginal $R^2 = 0.26$, conditional $R^2 = 0.81$; Fig. 6). When each raft was examined separately,
323 the school size increased significantly over time in 8 rafts (57%) (GLM, $\chi^2 = 0.2$ – 138.6 , $df = 1$, $p <$
324 0.05 , $R^2 = 0.05$ – 0.65 ; Table 3; Fig. S13 in the Supplement). The sample size of the raft (i.e. the total
325 number of schools in *Seriola* spp. juveniles recorded in each raft) without significant increase tends
326 to be low ($n = 7$ – 33), except raft 3 in April 2013 ($n = 75$) (Table 3; Fig. S13 in the Supplement). We
327 recorded one instance when two schools of *Seriola* spp. juveniles met each other to form a larger
328 school under the seaweed (Video S3 in the Supplement).

329 The degree of association with drifting seaweeds changed in response to the school size.
330 The proportion of the fish that exhibited ‘close proximity’, in which the school or solitary fish
331 remained close proximity to the seaweed, decreased in response to the increase in school size;
332 whereas the proportion of the fish that exhibited ‘swimming around’, in which the school or solitary
333 fish swam around the seaweed, increased in response to the increase in school size (GLMM, $\chi^2 =$
334 82.8 , $df = 1$, $p < 0.01$; Fig. 7). This result indicates that the solitary individual and smaller schools
335 tended to remain close to the seaweeds, whereas the larger schools tended to actively swim around

336 the seaweeds.

337 Among 945 video images, potential predators (i.e. *Coryphaena hippurus*, *S. aureovittata*
338 and Belonidae spp.) occurred in 172 (16%), 19 (2%) and 4 (0.4%) images, respectively. Of these
339 images, *Seriola* spp. juveniles were recorded together with *C. hippurus* in 153 images (89%), with *S.*
340 *aureovittata* in 7 images (37%) and with Belonidae spp. in no images (0%). Although in many cases
341 *Seriola* spp. juveniles remained schooling around the seaweeds or did not show observable
342 responses, they escaped into the seaweeds in 5 cases (4 cases with *C. hippurus*, and 1 case with *S.*
343 *aureovittata*). See Video S4 in the Supplement for the example of the escaping behavior. Solitary
344 fish escaped into the seaweed in 4 cases (3 cases with *C. hippurus*, and 1 case with *S. aureovittata*),
345 whereas a school of 4 individuals escaped into the seaweed in 1 case with *C. hippurus*.

346

347 **Zooplankton abundance**

348 Although the sample size was quite small ($n = 4$) and thus the statistical test should be
349 considered with care, the density of copepoda (a main food item of *Seriola* spp. juveniles) at the
350 release sites was not significantly different from that at the retrieved sites (paired *t*-test, $df = 3$, $t =$
351 -0.61 , $p = 0.59$; Fig. 8). We did not find a positive relationship between the copepoda density and
352 the maximum fish numbers detected by still cameras (Fig. 8).

353

354 **DISCUSSION**

355 In the still image analysis, the numbers of fish at night were higher than those during the
356 day in 71% of the rafts (Table 2). The fish numbers at night tended to increase over time (increase:
357 69%, decrease: 8%, no significant trend: 23%) but the trend was less obvious during the day
358 (increase: 29%, decrease: 14%, no significant trend: 57%). These diel differences are likely to be
359 attributed to the difference in the diel behavioral pattern, since the still and video images showed
360 that the fish attached closely to the seaweed or other individuals at night and that many fish swam in

361 and out of the camera view during the daytime (Figs. 3 & 4; Videos S1 & S2 in the Supplement).
362 Furthermore, *S. quinqu radiata* juveniles actively swim around the seaweeds (ranging 3–5 m) in the
363 daytime (05:00–19:00), and cease swimming and stay inside and/or around the seaweeds in the
364 nighttime (21:00–03:00) (Ikehara 1984). Thus, it is highly likely that the fish numbers around the
365 raft increased over time, and the diel behavior is the cause of the observed difference in fish
366 numbers between day and night.

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

378 Our results provide circumstantial evidence supporting the shelter from predator
379 hypothesis in *Seriola* spp. juveniles, since we observed that solitary individuals and a small school
380 escaped into the seaweed clump when potential predators appeared (Video S4 in the Supplement).
381 Fréon & Dagorn (2000) disagreed with the shelter from predator hypothesis for fishes swimming
382 around the floating structures, because sometimes they are too numerous to take shelter under small
383 objects and/or they are too far from the objects to be in the “blind zone” of predators. However, it is
384 important to note that the color (yellow-brown) of the *Seriola* spp. juveniles matches with the color
385 of the seaweeds (Uchida 1963, Senta 1965), and the background-matching coloration is an
386 anti-predator adaptation in general (e.g. Stuart-Fox et al. 2008, Wang & Schaefer 2012, Morgans &

387 Ord 2013). Furthermore, *S. quinqueradiata* juveniles escape into the drifting seaweeds when threats
388 such as boats approach them (Hanaoka 1986). Drifting seaweeds have highly complex thallus
389 morphology that can be used for sheltering, like driftwoods and manmade FADs with complex
390 structures (Hunter & Mitchell 1966, Gooding & Magnuson 1967). Therefore, the juveniles that hide
391 into the drifting seaweeds may have better survival rates when predators are nearby. Considering
392 these facts, drifting seaweeds likely function as shelters from predators for *Seriola* spp. juveniles,
393 especially for the isolated individuals or small schools.

394 We observed that solitary individuals and small schools tended to remain close to the
395 drifting seaweeds, whereas the large schools tended to actively swim around the seaweeds (Fig. 7).
396 This may reflect the adaptive significance of association with drifting seaweeds and schooling in
397 *Seriola* spp. juveniles. Juvenile fishes generally must balance the demands of feeding and safety
398 from predators. For example, fish normally prefer to utilize high density areas of prey, but when
399 predation risk becomes higher, they prefer to utilize safer but lower density areas of prey (Milinski
400 & Heller 1978, Werner et al. 1983). Schooling decreases per capita predation risk of animals
401 through several mechanisms such as dilution, predator confusion, and improved vigilance for
402 predators (Pitcher & Parish 1993). Thus, *Seriola* spp. juveniles may stay close to the seaweed
403 shelter when the school size is small and per capita predation risk is high. Then, when the school
404 size becomes larger and the per capita predation risk becomes lower, they may explore wider areas
405 around the seaweeds in search for high density areas of zooplankton prey. This hypothesis is also
406 supported by the fact that solitary individuals and a small school hid in drifting seaweeds but the
407 large schools kept schooling around the seaweeds regardless of the appearance of potential
408 predators. Further experiments are required to verify the adaptive significance of schooling in
409 *Seriola* spp. juveniles observed in this study.

410 Our results show that the school size of *Seriola* spp. juveniles associated with drifting
411 seaweeds increased over time (Fig. 6; Tables 2 & 3). One possible explanation for this pattern is that
412 the fish in solitude or in smaller schools might have utilized drifting objects as a meeting-point to

413 form larger schools. Our observation of an instance when two schools met each other to form a
414 larger school (Video S3 in the Supplement) is consistent with this explanation. However, we should
415 also note that this study lacks the record of the instance of dissociation from the seaweeds,
416 information of which is also essential for testing the meeting-point hypothesis (Fréon & Dagorn
417 2000, Soria et al. 2009). Another possibility is that the increase of the school size is a by-product of
418 the fish gathering at drifting seaweeds for alternative purposes, such as nighttime school
419 maintenance and shelter from predators as mentioned previously, and thus the increase simply
420 reflected the colonization process of the fish because no fish were associated with the rafts at the
421 time of release. This explanation also includes the possibility that larger schools already formed
422 around the natural drifting seaweeds, FADs, and/or food-rich areas have recruited to our rafts for
423 some purposes. There were natural drifting seaweeds and manmade FADs (for *C. hippurus* fishing)
424 around the study area (Fujita 1986, Kuwano et al. 1982). In addition, although we did not find any
425 relationship between the fish numbers and zooplankton abundance (Fig. 8), the possibility that there
426 were zooplankton hotspots between the release and retrieval sites cannot be excluded. Nonetheless,
427 schooling should provide some benefit as well, because the fish exhibited more than just
428 aggregation at seaweeds; they showed clear schooling behavior in which the fish swam
429 synchronously (See Videos S1, S2 & S3 in the Supplement). Further research measuring
430 dissociation process of the fish from the seaweeds, fish behaviors after the colonization period, and
431 distributions of other floating objects and zooplankton abundance is needed to clarify the reason for
432 the increase of school size over time.

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

439 process of *Seriola* spp. juveniles.

440 Although our monitoring system was useful for continuously monitoring the schooling and
441 associative behaviors of fishes with the same drifting seaweeds, there are some limitations. First, as
442 described above, the camera view is limited and thus the fish numbers (specifically, in still images)
443 can be variable when the fish swim around the system. Second, the fish numbers (specifically, in
444 still images) can be underestimated when the fish completely hide into the seaweeds such as those
445 at night. In contrast, we observed an opposing phenomenon: the fish numbers at night were larger
446 than those during the day, and thus the effect of this bias was relatively small compared to that of
447 the diel behavioral difference. Third, due to the darkness, video images can only be obtained in the
448 daytime. However, these three limitations can be overcome by modifying our system with
449 omni-directional, infrared video cameras. Fourth, since tracking the same individual or school over
450 time is not possible, we cannot detect all instances when the fish actually meet with other
451 conspecifics at the drifting objects (but see Video S3 for the instance of meeting), and the instances
452 when the individuals or schools leave the drifting objects. This limitation cannot be overcome by
453 modifying our system itself, and thus incorporation of other methods are required. Specifically,
454 combining our system with acoustic telemetry can provide stronger evidence of the meeting-point
455 function because our system can record the increase or decrease of the school size but cannot record
456 the timing of the meeting among individuals or schools and the timing of dissociation from the
457 drifting objects, and acoustic telemetry can do vice versa (Soria et al. 2009). Combining our system
458 with an echo-sounder buoy can also be useful because the echo-sounder buoy provides rough
459 estimates of aggregated biomass over larger scales (Lopez et al. 2014, Moreno et al. 2016) and our
460 system can allow species identification and behavioral categorization.

461

462 **CONCLUSION**

463 The ecological significance of drifting seaweeds for fish juveniles has been reported as a
464 hiding place and feeding habitat in many waters (e.g. Ida et al. 1967, Kingsford 1992, Shaffer et al.

465 1995, Vandendriessche et al. 2007). Our results, together with a previous study (Hasegawa et al.
466 2016), indicate that the ecological significance of the seaweeds for *Seriola* spp. juveniles would
467 include the habitat for school maintenance at night, hiding place for predator avoidance, and
468 possibly the meeting-point for school formation, but not the habitat for feeding. The abundance,
469 distribution, and species composition of seaweed forests and drifting seaweeds have been
470 dramatically changing due to global warming (Komatsu et al. 2014, Yamasaki et al. 2014, Wernberg
471 et al. 2011), which may in turn affect the populations of *Seriola* and other fishes associated with
472 drifting seaweeds. In these cases, knowledge on the significance of drifting seaweeds for fishes as
473 obtained in this study, will be useful in designing conservation and management measures of fishes
474 associated with drifting seaweeds. For example, the installation of artificial drifting objects with
475 complex structures could provide suitable habitats that facilitate the school maintenance and
476 predator avoidance of *Seriola* spp. juveniles, as shown in this study for the drifting seaweeds.
477 However, we also should be cautious about the implementation because fish associated with the
478 artificial drifting objects may obtain less food items, as shown in other fishes associated with
479 manmade FADs (Marsac et al. 2000, Hallier & Gaertner 2008).

480

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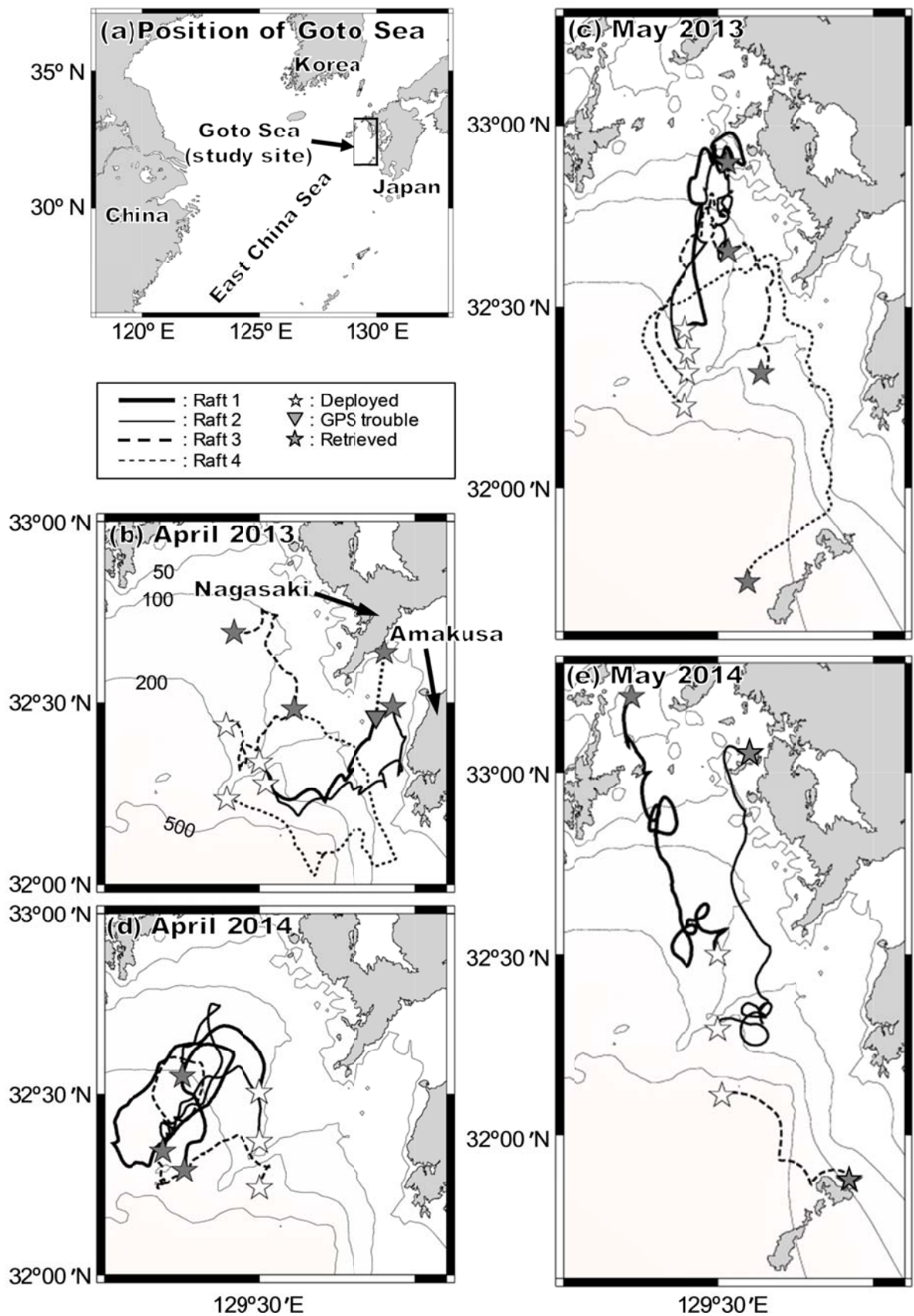
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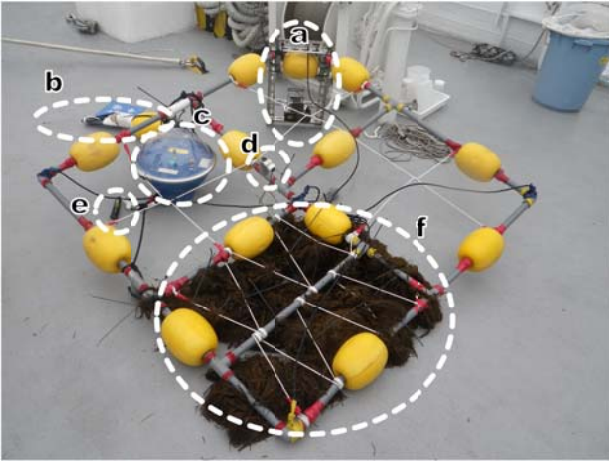
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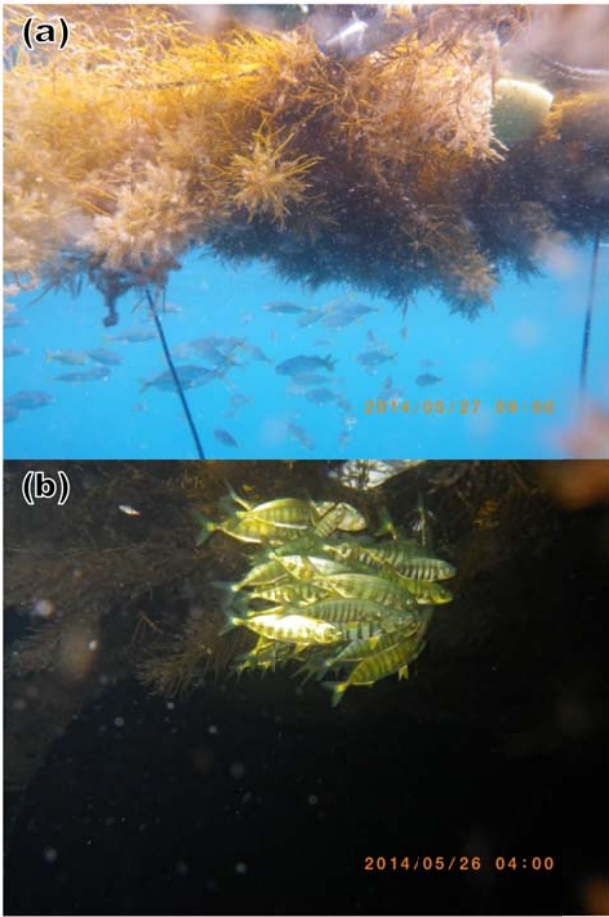
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629 Fig. 1. (a) Map of the study site showing the position of the Goto Sea, and drifting routes of the
 630 rafts in (b) April 2013, (c) May 2013, (d) April 2014 and (e) May 2014. Open and filled stars

631 indicate deployed and retrieved locations of monitoring systems, respectively. Bold solid line, thin
632 solid line, bold break line and thin break line represent the drifting routes of the raft 1, raft 2, raft 3
633 and raft 4, respectively. The filled inverse triangle in (a) April 2013 shows the location where the
634 GPS buoy was broken. The subsequent thin break line is a straight line between the locations where
635 the GPS buoy was broken and where the system was retrieved. Thin solid contours with numbers
636 indicate the bathymetry in meters, extracted from the Japan Oceanographic Data Center
637 (<http://www.jodc.go.jp>)

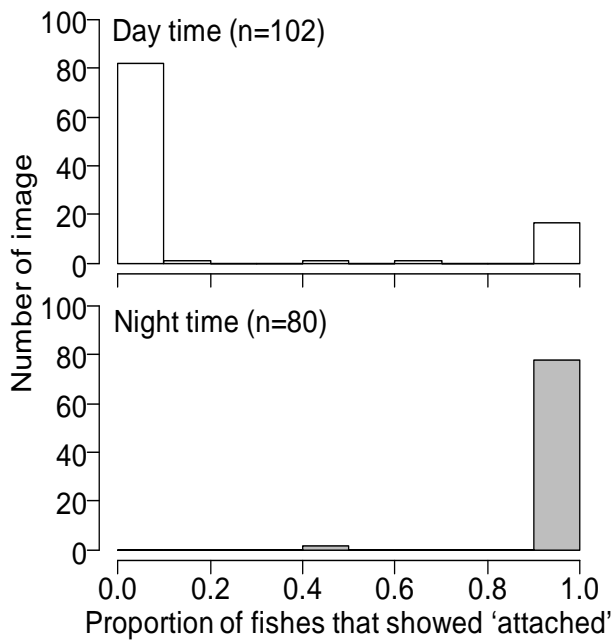


640 Fig. 2. Monitoring system used in our study. A raft was equipped with (a) still and video cameras,
641 (b) a VHF transmitter with float, (c) a drifting GPS buoy, (d) a light logger, (e) a water temperature
642 logger, and (f) a clump of *Sargassum horneri*



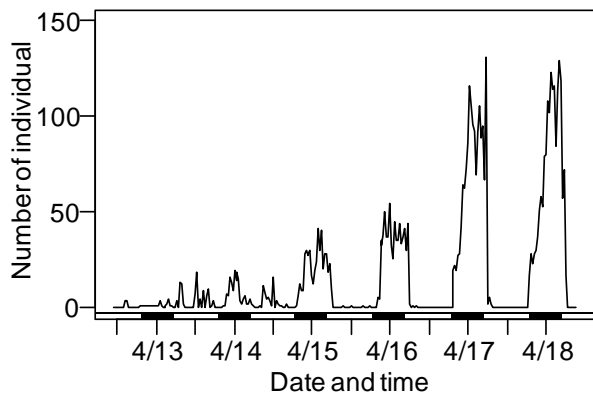
643

644 Fig. 3. *Seriola* spp. Typical still pictures (a) during the daytime (09:00 in 27 May 2014, raft 1) and
645 (b) during the nighttime (04:00 in 26 May 2014, raft 1)



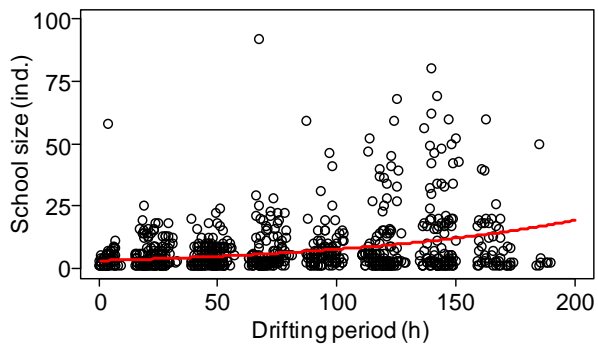
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647 Fig. 4. *Seriola* spp. Typical diel difference of the degree of association with drifting seaweeds (raft 4
 648 in May 2013; categorized into either 'attached' or 'around'). See Fig. S12 in the Supplement for the
 649 data of the other rafts



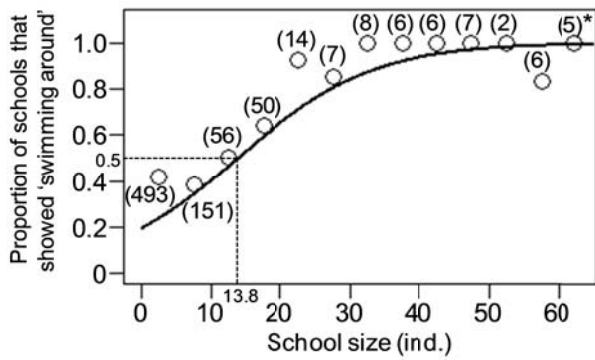
650

651 Fig. 5. *Seriola* spp. Typical change of fish numbers in the still images over time (raft 4 in April
652 2013). Black horizontal bars indicate nighttime (19:30–05:30). See Fig. S11 in the Supplement for
653 the data of the other rafts

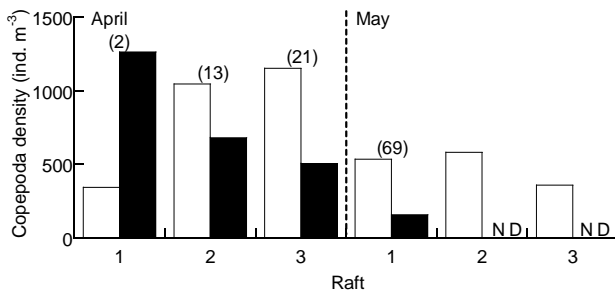


654

655 Fig. 6. *Seriola* spp. The effect of the drifting period (h) on the school size around the rafts,
656 measured from the video images. The red solid line indicates the estimate from the generalized
657 linear mixed model (GLMM). See Fig. S13 for the data of each raft



658
 659 Fig. 7 *Seriola* spp. The effect of school size on the degree of association with drifting seaweeds
 660 (categorized into either 'close proximity' or 'swimming around'). Unfilled circles represent the
 661 proportion of fish schools that exhibit 'swimming around' in every 5-individual-school size class.
 662 The solid line indicates estimate from the generalized linear mixed model (GLMM). Numbers in
 663 parentheses indicate numbers of fish schools examined. Dashed lines represent the school size (13.8
 664 ind.) in which 50 % of schools showed 'swimming around', estimated from the GLMM.
 665 *The number includes all fish schools exceeding 60 individuals



666

667 Fig. 8. Copepoda density of rafts released and retrieved stations, obtained in 2014. ND represents
 668 no data due to the stranding of the rafts. Numbers in parentheses are maximum fish numbers in the
 669 still images during the drifting periods (shown in Table 2)

670 Table 1. *Seriola* spp. Summary of the effect of factors on the maximum fish number

Day	Sample size	Factors ^a			R ²
		Speed	Straightness index	Sea surface temperature	
1	13	++	0.85	NA ^b	0.39
2	13	++	NA ^b	0.32	0.56
3	10	0.30	1.00	0.55	NA ^c
4	9	0.25	0.24	0.42	NA ^c
5	9	0.19	0.28	0.76	NA ^c
6	7	0.95	0.17	0.11	NA ^c

671 ^a; analyzed by the generalized linear model (GLM). + and -; p < 0.05, ++ and --; p < 0.01. Numbers in the column represent p-values

672 ^b; removed factor from analysis because there was a correlation with speed

673 ^c; could not be calculated because no significant effects were found in any variable

674 Table 2. *Seriola* spp. Summary of the statistical analyses on the still images in each raft (continued on next page)

Year	Month	Raft No.	Drifting periods (h)	Maximum fish numbers in each raft		First <i>Seriola</i> spp. occurrence (hours after release)
				(mean \pm SD)		
				Day	Night	
2013	April	1	121.5	8 (0.8 \pm 1.8)	9 (0.9 \pm 1.7)	11.5
		2	118.5	51 (0.7 \pm 4.6)	33 (3.9 \pm 7.3)	11.0
		3	145.5	7 (0.8 \pm 1.4)	6 (0.2 \pm 0.8)	5.0
		4	142.0	18 (1.4 \pm 3.5)	131 (35.3 \pm 36.2)	3.5
	May	1	19.0	8 (0.9 \pm 2.0)	6 (2.9 \pm 1.9)	5.0
		2	190.5	47 (0.5 \pm 3.2)	31 (2.9 \pm 4.3)	5.5
		3	186.0	48 (1.5 \pm 4.8)	25 (6.3 \pm 5.9)	2.0
		4	166.5	11 (1.3 \pm 2.0)	7 (1.2 \pm 1.3)	1.5
2014	April	1	150.0	2 (0.1 \pm 0.3)	1 (0.1 \pm 0.3)	84.5
		2	51.5	12 (4.7 \pm 3.9)	13 (4.6 \pm 4.7)	1.5
		3	169.5	20 (3.3 \pm 5.1)	21 (4.8 \pm 5.8)	12.0
	May	1	161.5	69 (5.1 \pm 11.5)	52 (14.0 \pm 13.6)	0.5
		2	43.5	33 (0.8 \pm 4.6)	6 (1.1 \pm 1.5)	7.5
		3	45.0	165 (10.5 \pm 27.0)	280 (94.9 \pm 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

675

676 Table 2. (continued)

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

677 ^a; analyzed by the Spearman's rank correlation test (+ and -; $p < 0.05$, ++ and --; $p < 0.01$). Plus and minus represent significant positive and negative
678 correlations, respectively. Numbers in the column represent p-values

679 ^b; could not analysis due to small sample size

680 ^c; percentage of the rafts which have increasing trends or increasing trends at night

681 ^d; analyzed by the generalized linear model (GLM). *; $p < 0.05$, **; $p < 0.01$. Numbers in the column represent p-values

- 682 ^e; with a poisson distribution
- 683 ^f; with a negative binomial distribution
- 684 ^g; could not be calculated because no significant effects were found in any variable
- 685 ^h; could not be analyzed because the algorithm did not converge

686 Table 3. *Seriola* spp. Summary of the statistical analyses on the video images in each raft

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

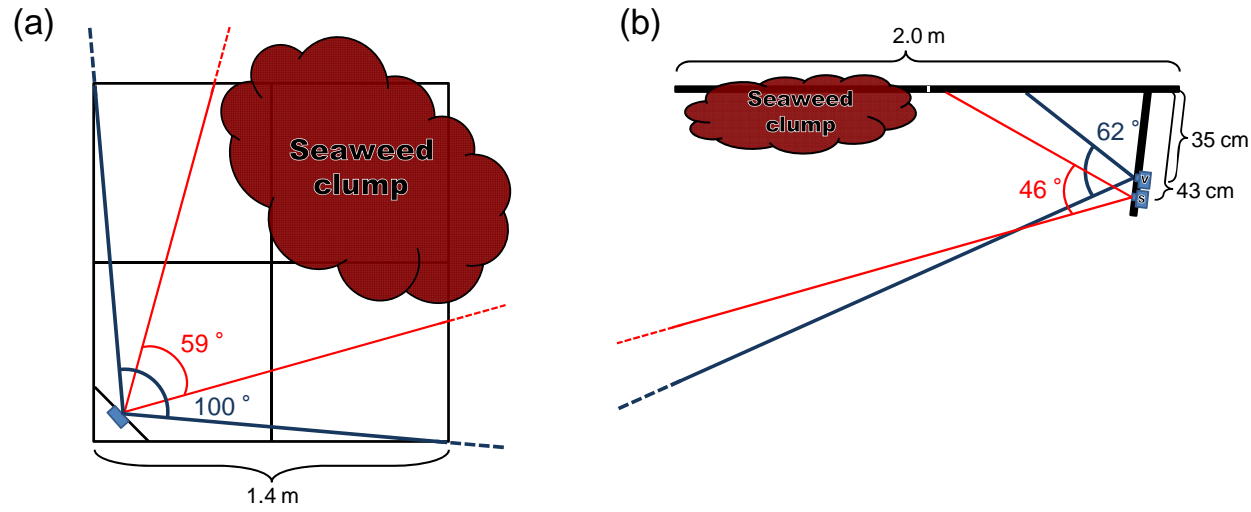
687 ^a; analyzed by the generalized linear model (GLM) (+ and -; $p < 0.05$, ++ and --; $p < 0.01$). Plus and minus represent significant increase and decrease,
 688 respectively. Numbers in the column represent p-values

689 ^b; with a negative binomial distribution

690 ^c; with a poisson distribution

691 ^d; percentage of the rafts which have increasing trends

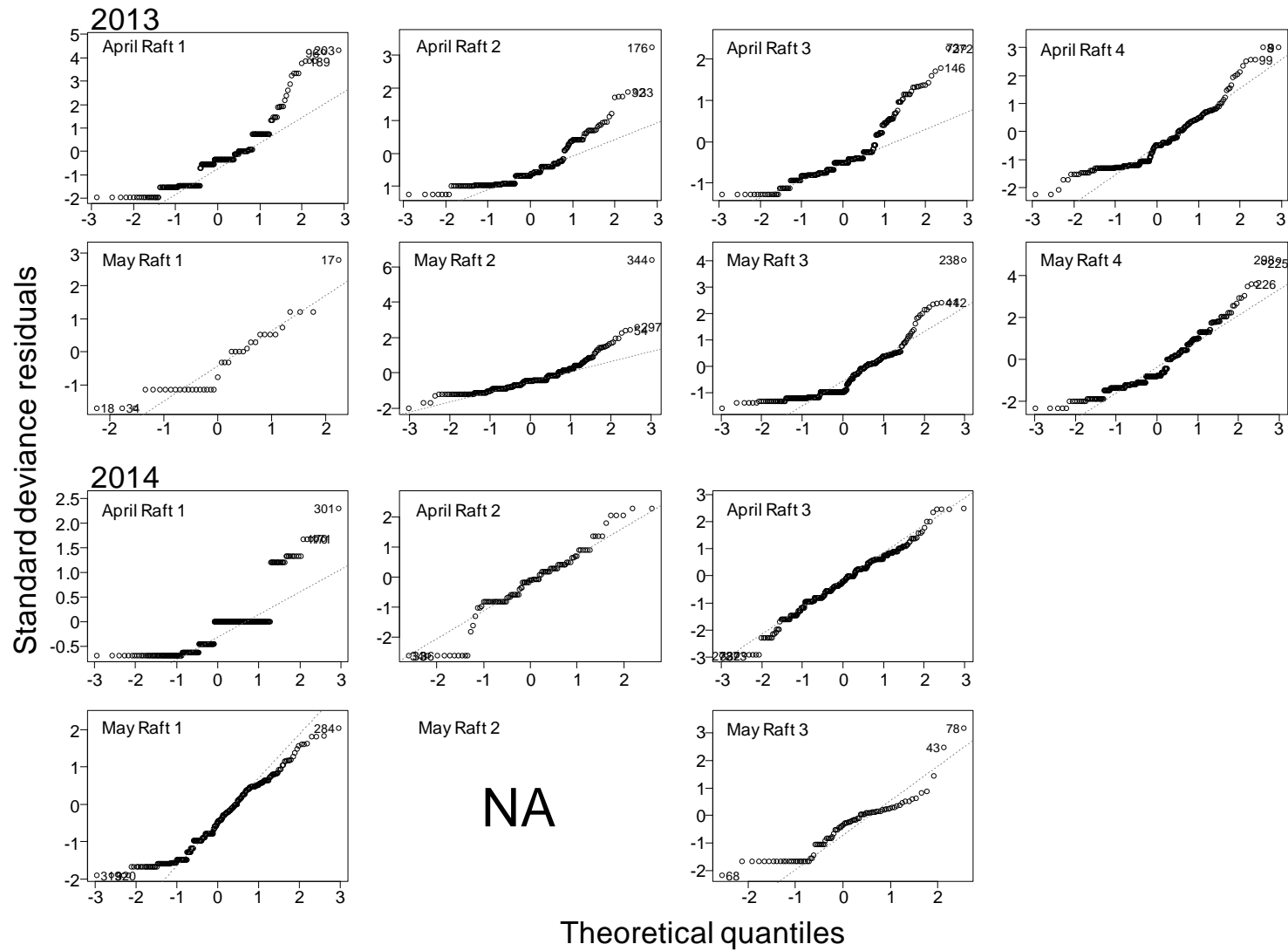
692 ^e; could not be calculated because no significant effects were found in any variable



694

695 Fig. S1. Fields of views of still and video cameras in the monitoring system. (a) Horizontal views and (b) vertical views. Red and blue lines represent

696 edges of the fields of views of still and video cameras, respectively. Video and still cameras were located at 35 cm and 43 cm below the raft

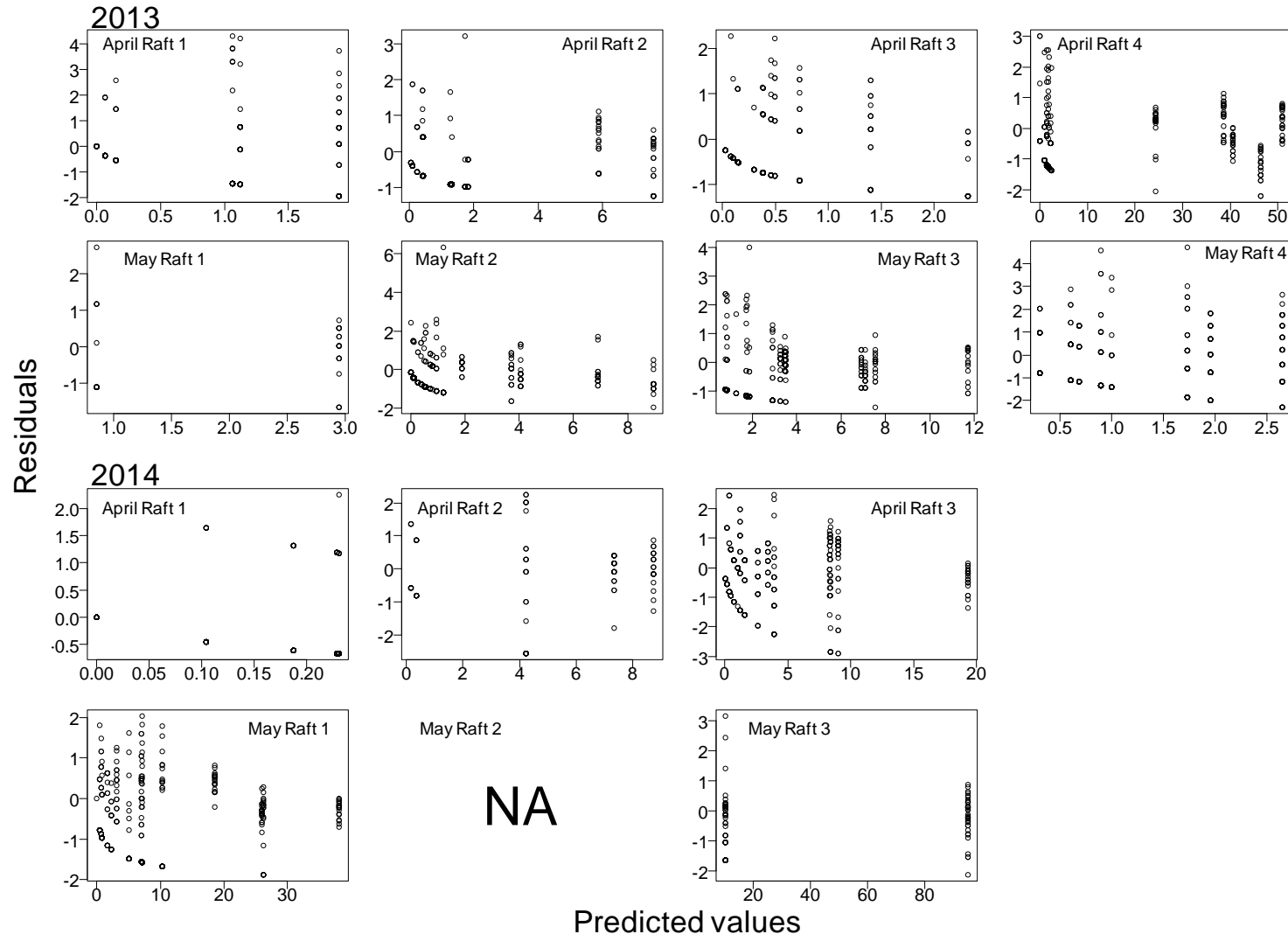


697

698 Fig. S2. Normal quantile-quantile plots for generalized linear models to evaluate the general trend of the change in the fish number over time. NA means

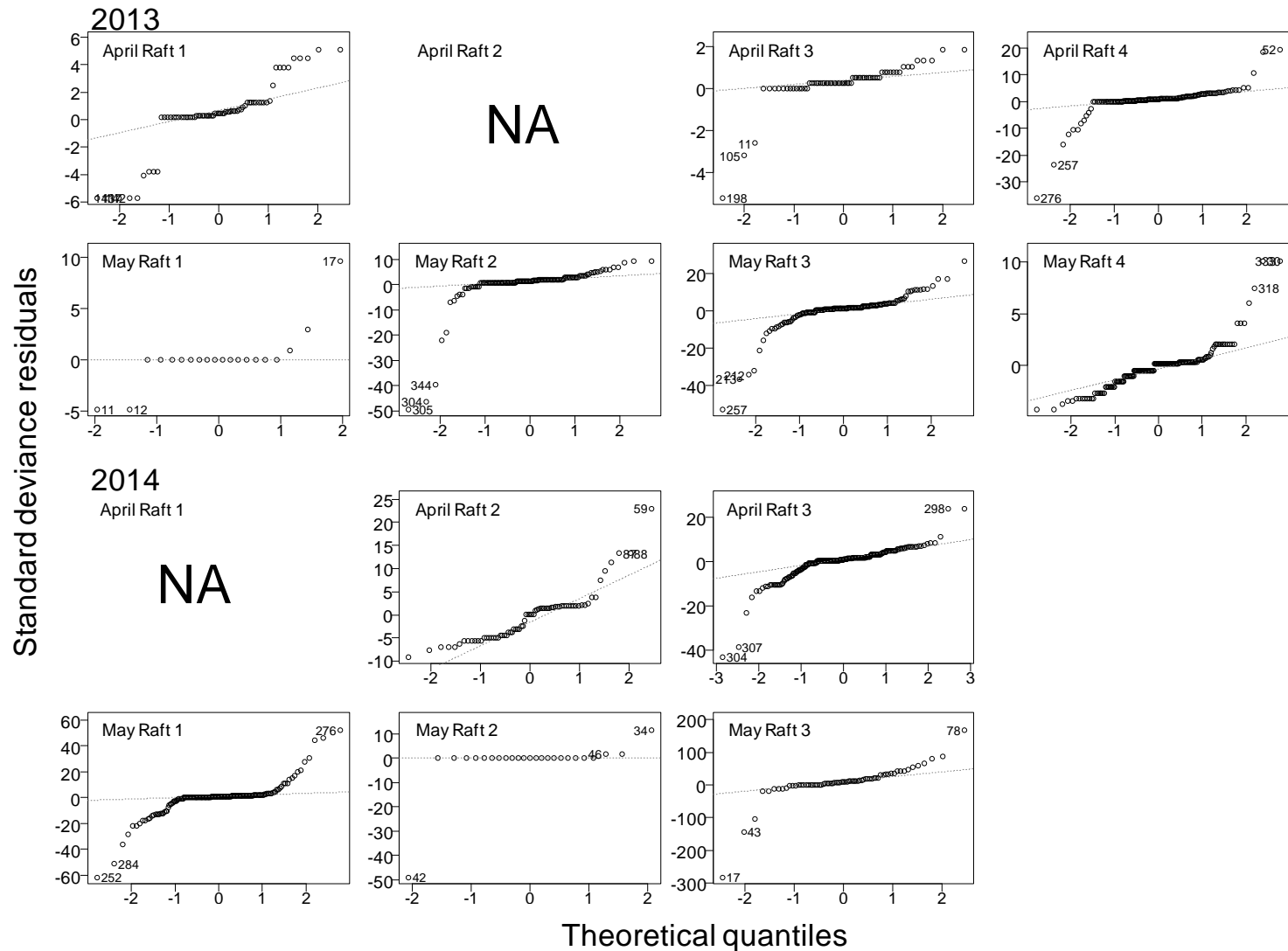
699 the plot could not be calculated because no significant effects were found in any variable. Please note that normal quantile-quantile plots help us detect

700 if the residuals are normally distributed (if the residual is normally distributed, the plot follows straight line), and our models assume poisson or
 701 negative binomial distributions. Therefore, it is natural that the models do not follow straight lines



702

703 Fig. S3. Distribution of residuals of generalized linear models to evaluate the general trend of the change in the fish number over time. NA means that
704 the plot could not be calculated because no significant effects were found in any variable. Please note that the residuals vs predicted plots can help us
705 examine whether the residuals are unbiased and/or homoscedastic, and poisson and negative binomial distributions (used in the models) are naturally
706 heteroscedastic

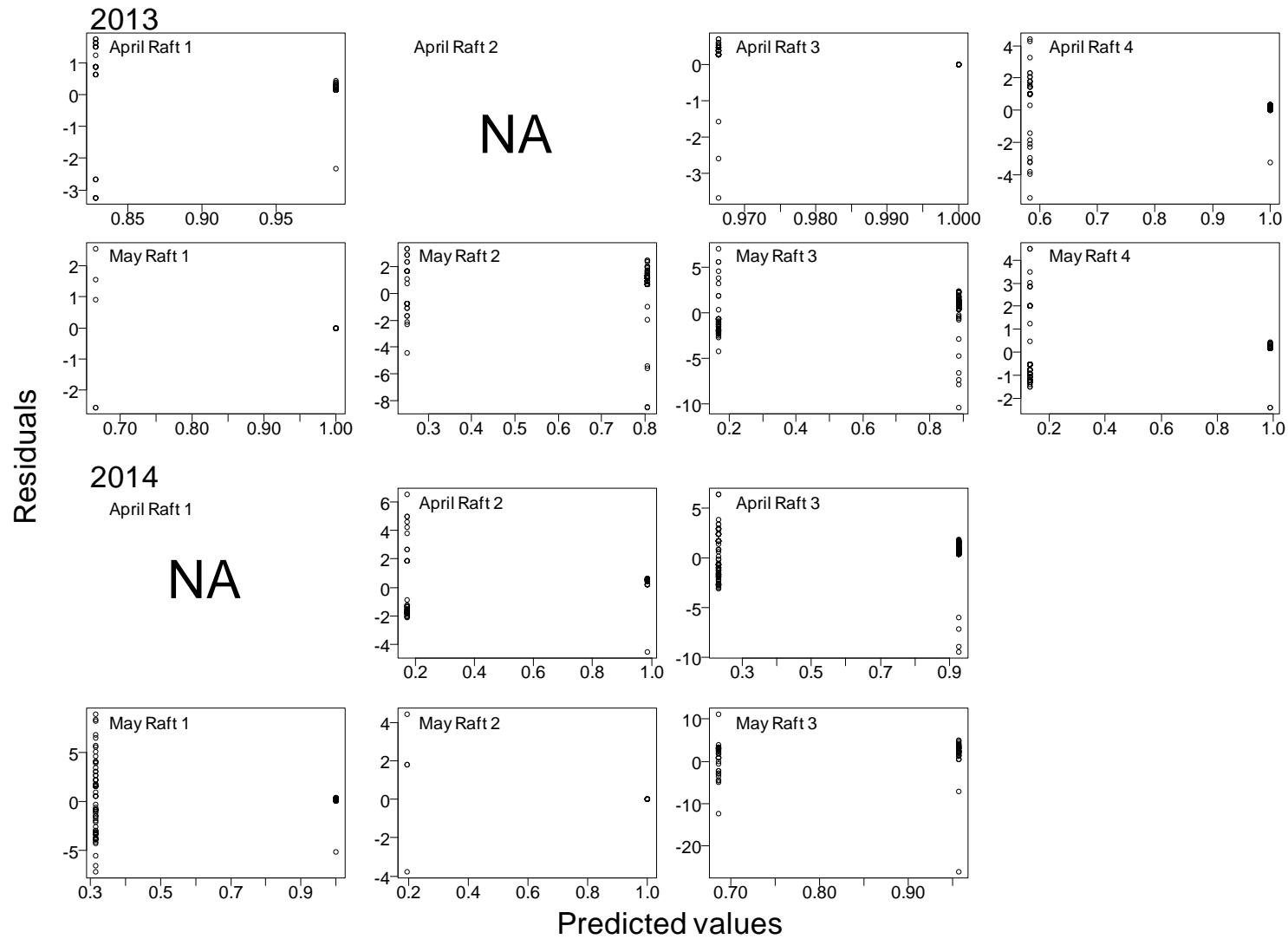


707

708 Fig. S4. Normal quantile-quantile plots for generalized linear models to assess the behavioral difference between the day and night. NA means that the

709 plot could not be calculated because no significant effects were found in any variable. Please note that normal quantile-quantile plots help us detect if

710 the residuals are normally distributed (if the residual is normally distributed, the plot follows straight line), and our models assume binomial
711 distributions. Therefore, it is natural that the models do not follow straight lines

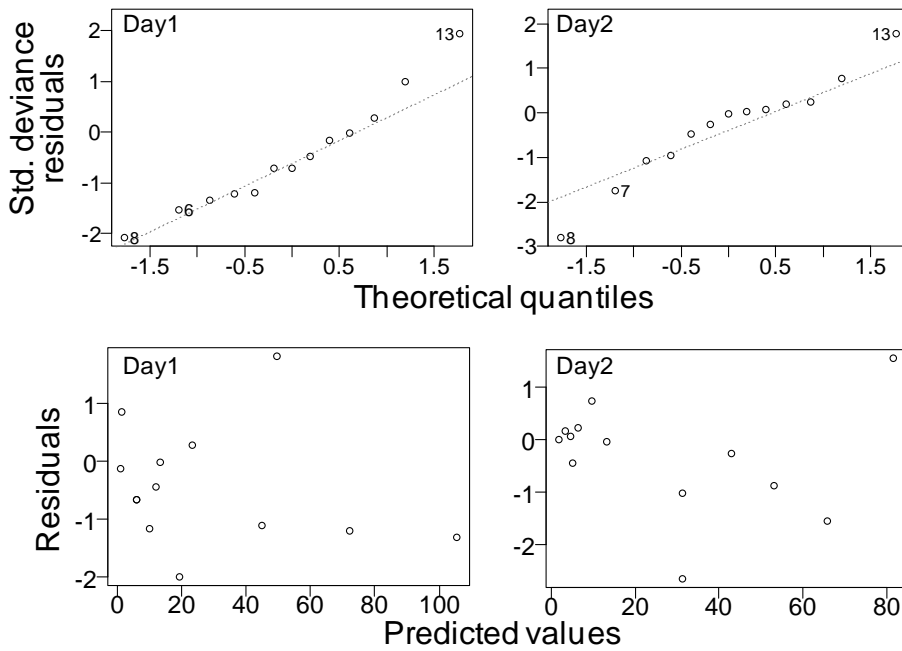


712

713 Fig. S5. Distribution of residuals of generalized linear models to assess the behavioral difference between the day and night. NA denotes that the plot

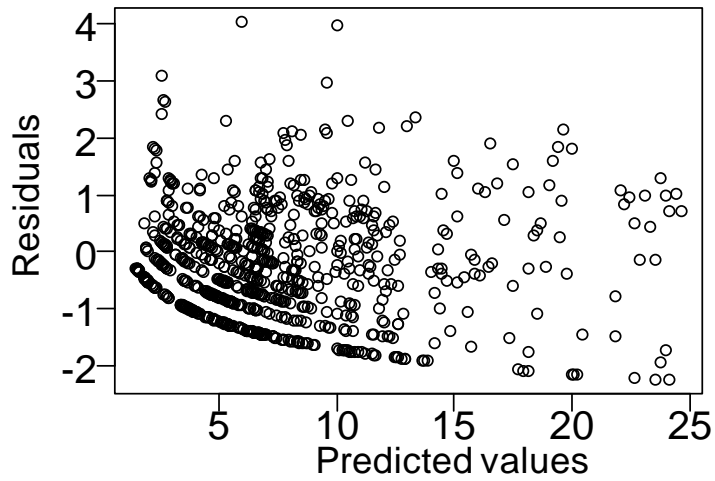
714 could not be calculated because no significant effects were found in any variable. Please note that the residuals vs predicted plots can help us examine

715 whether the residuals are unbiased and/or homoscedastic, and binomial distributions (used in the models) are naturally heteroscedastic



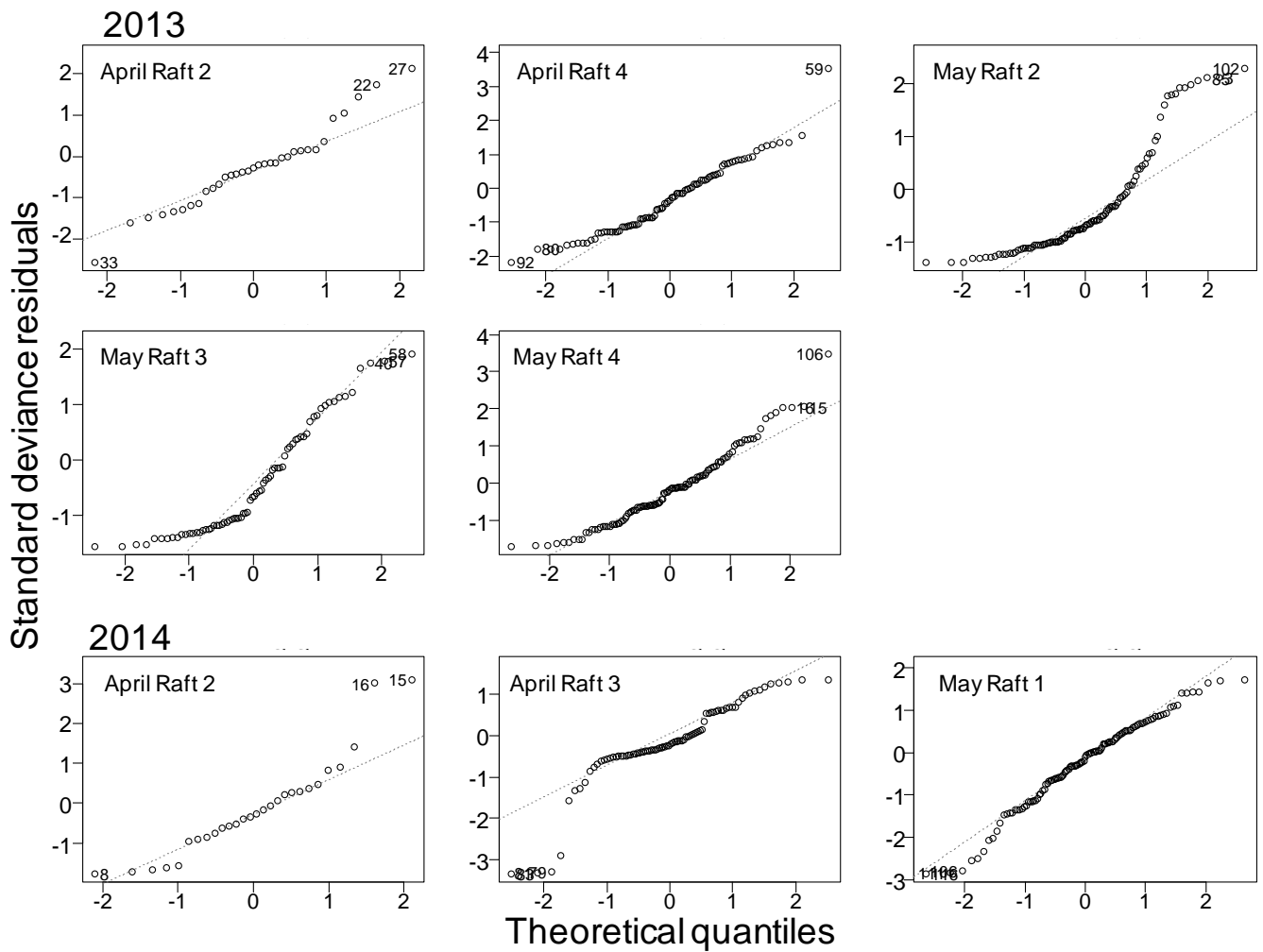
717

718 Fig. S6. Normal quantile-quantile plots (above) and distribution of residuals (below) for generalized
 719 linear models to investigate the factors affecting the aggregation process of *Seriola* spp. juveniles.
 720 Day 3 to 6 were omitted, because the plots could not be calculated due to no significant effects in
 721 any variable. Please note that normal quantile-quantile plots help us detect if the residuals are
 722 normally distributed (if the residual is normally distributed, the plot follows straight line), and our
 723 models assume negative binomial distributions. Therefore, it is natural that the models do not
 724 follow straight lines. Please also note that the residuals vs predicted plots can help us examine
 725 whether the residuals are unbiased and/or homoscedastic, and negative binomial distributions are
 726 naturally heteroscedastic



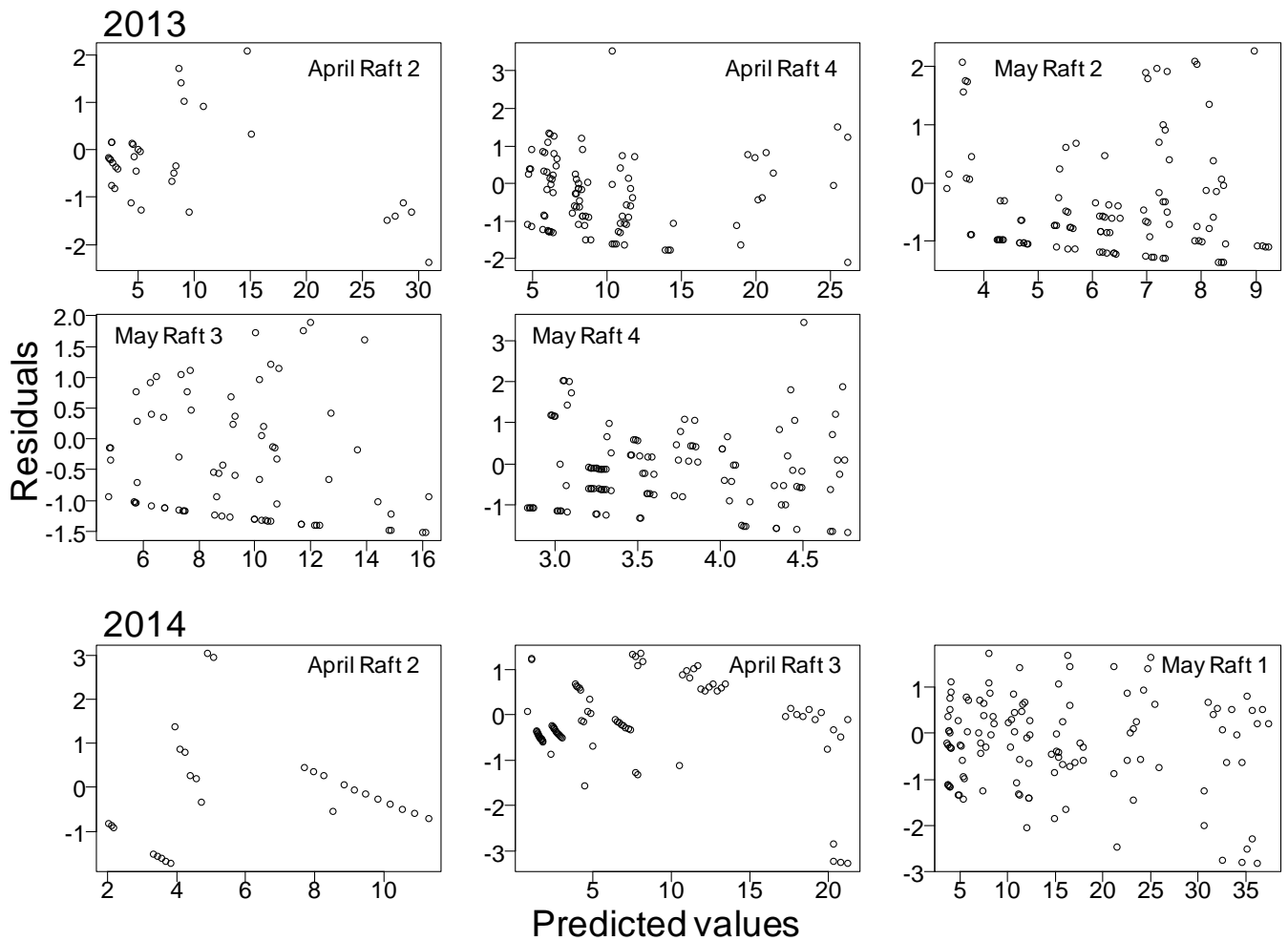
727

728 Fig. S7. Distribution of residuals for generalized linear mixed model to evaluate the effect of time
729 after release (h) on the school size. Please note that the residuals vs predicted plots can help us
730 examine whether the residuals are unbiased and/or homoscedastic, and the negative binomial
731 distribution (used in the model) is naturally heteroscedastic



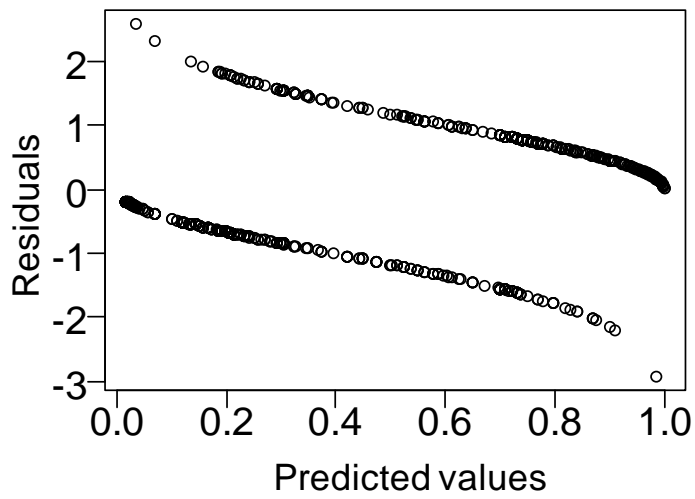
732

733 Fig. S8. Normal quantile-quantile plots for generalized linear models to understand the change of
 734 school size over time in each raft. Raft 1 and Raft 3 in April and Raft 1 in May 2013, and Raft 1 in
 735 April and Raft 2 and Raft 3 in May 2014 were omitted, since the plots could not be calculated due
 736 to no significant effects in any variable. Please note that normal quantile-quantile plots help us
 737 detect if the residuals are normally distributed (if the residual is normally distributed, the plot
 738 follows straight line), and our models assume poisson or negative binomial distributions. Therefore,
 739 it is natural that the models do not follow straight lines



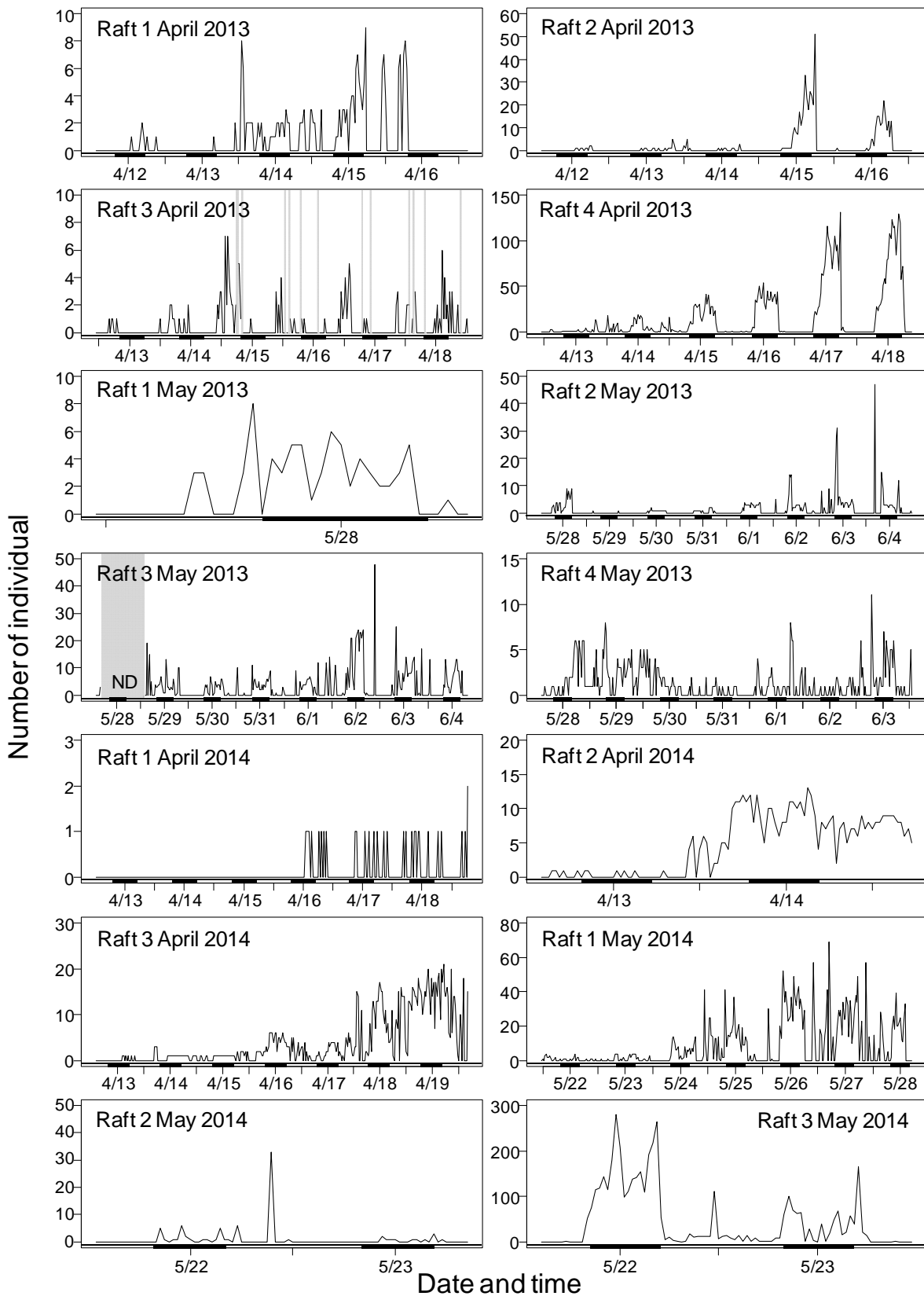
740

741 Fig. S9. Distribution of residuals of generalized linear models to understand the change of school
 742 size over time in each raft. Raft 1 and Raft 3 in April and Raft 1 in May 2013, and Raft 1 in April
 743 and Raft 2 and Raft 3 in May 2014 were omitted, since they could not be calculated due to no
 744 significant effects in any variable. Please note that the residuals vs predicted plots can help us
 745 examine whether the residuals are unbiased and/or homoscedastic, and poisson or negative binomial
 746 distributions (used in the models) are naturally heteroscedastic



747

748 Fig. S10. Distribution of residuals for generalized linear mixed model to evaluate the effect of
749 school size on the degree of association. Please note that the residuals vs predicted plots can help us
750 examine whether the residuals are unbiased and/or homoscedastic, and the binomial distribution
751 (used in the model) is naturally heteroscedastic

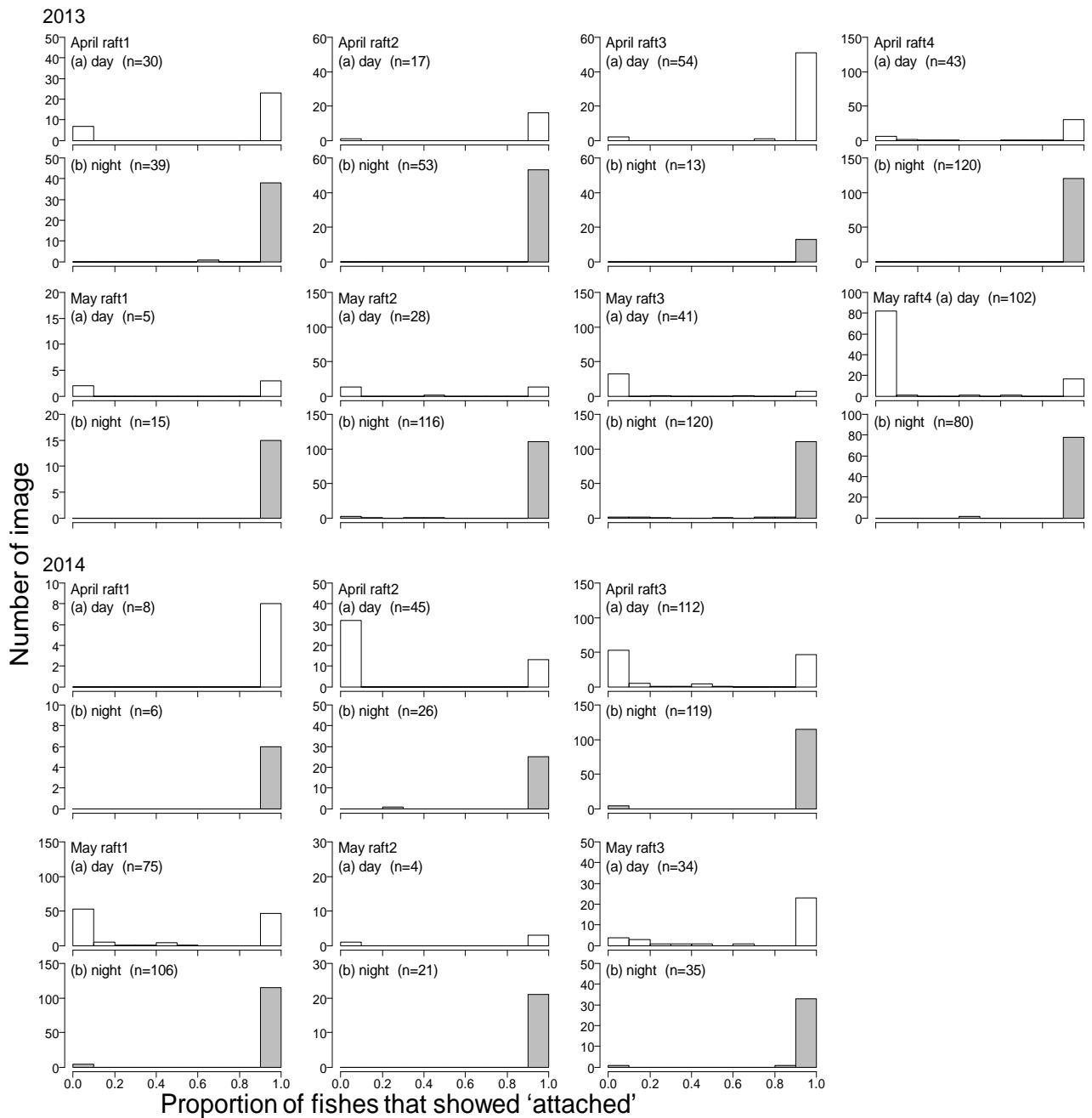


752

753 Fig. S11. *Seriola* spp. The change of the fish number (still images) in each raft over time. The black

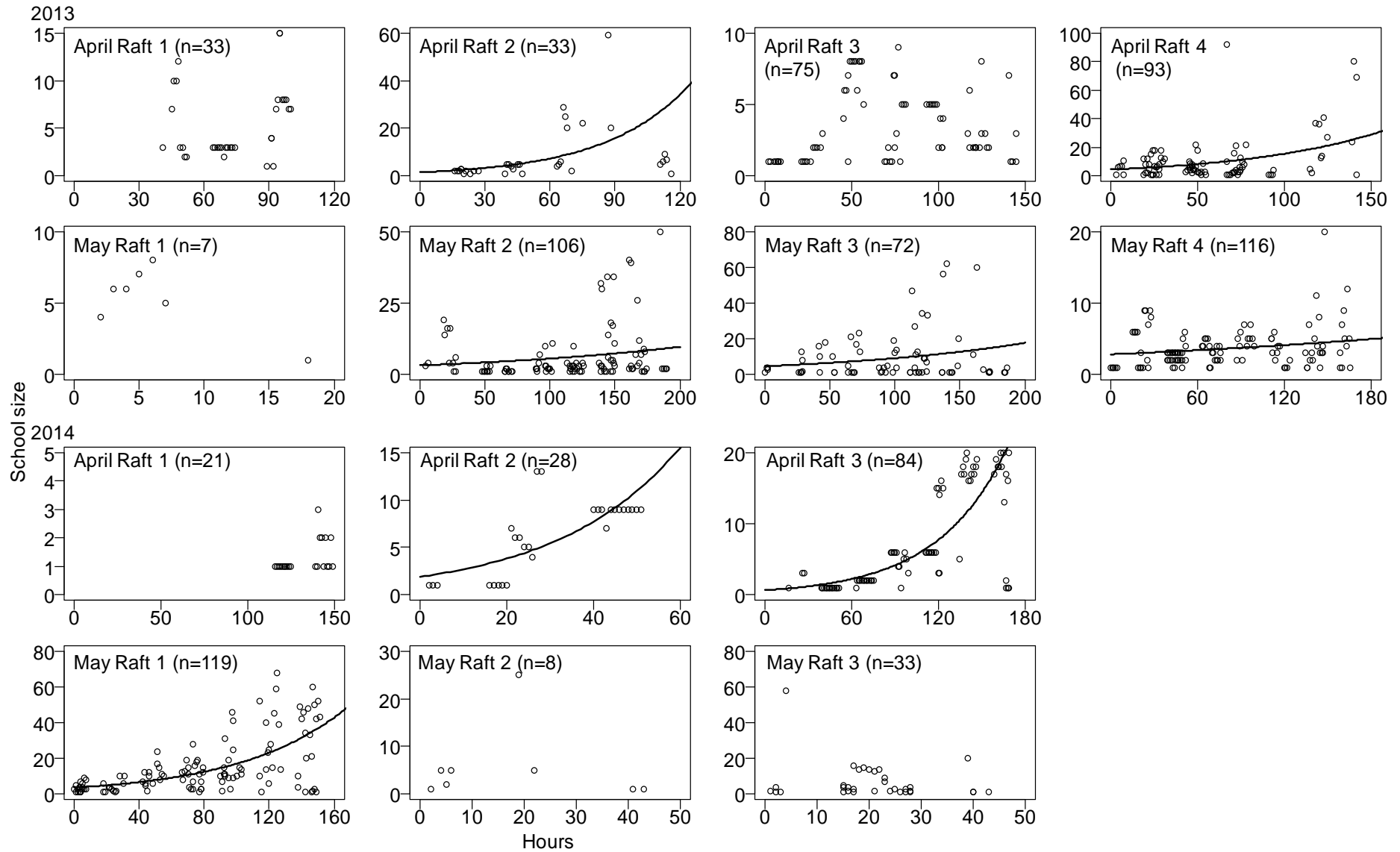
754 horizontal bars at the bottom of each graph indicate nighttime (April; 19:30–05:30, May; 20:00–

755 04:30). Shaded areas indicate no available data (ND)



756

757 Fig. S12. *Seriola* spp. The diel difference of the degree of association with drifting seaweeds in each
 758 raft in 2013 and 2014 (categorized into either 'attached' or 'around'). (a) is the daytime and (b) is
 759 the nighttime for each raft



763

764 Fig. S13. *Seriola* spp. The change of the school size in each raft over time. Solid lines indicate estimates from the generalized linear model (GLM)

765 Table S1. Summary of the models and variables for each analysis

Image type	Objective	Response variable	Explanatory variables			Model (random effect)	Error distribution	Link function
Still	Patterns in diel association	Number of individuals	Diel period	Days after release		GLM	Poisson / Negative binomial	Log
	Diel behavioral difference	Degree of association	Diel period			GLM	Binomial	Logit
	Factors affecting the aggregation process	Maximum fish number	Raft speed	Straightness index	Sea surface temperature	GLM	Negative binomial	Log
Video	Change of school size over time	School size	Hours after release			GLMM (raft)	Negative binomial	Log
	Change of school size over time in each raft	School size	Hours after release			GLM	Poisson / Negative binomial	Log
	Effect of school size on degree of association	Degree of association	School size			GLMM (raft)	Binomial	Logit

766

767 Table S2. Occurrence frequency F (%) and mean observed number of fishes and cephalopoda in still images during our study period (continued on next
768 page)

Year	2013															
Month	April								May							
Raft No.	Raft1		Raft2		Raft3		Raft4		Raft1		Raft2		Raft3		Raft4	
Sample size	244		238		280		285		39		382		329		334	
Category	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean
<i>Seriola</i> spp.	28	2.96	29	7.23	24	2.19	57	28.58	51	3.55	38	3.72	49	6.81	54	2.35
<i>Naucrates ductor</i>	0		0		0		0		0		0		0		0	
<i>Oplegnathus punctatus</i>	0		0		0		0		0		0		16	1.00	0	
Girellidae/Kyphosidae	0		0		0		5	1.00	8	1.00	17	1.20	6	1.00	16	1.55
<i>Petroscirtes breviceps</i>	0		0	1.00	0		16	1.85	0		0		0		0	
<i>Psenes cyanophrys</i>	0		1	1.00	16	1.20	0	1.00	8	1.00	11	1.77	20	2.87	21	1.99
<i>Hyperoglyphe japonica</i>	0		0		0		0		8	1.00	9	4.34	26	8.64	4	1.50
<i>Abudefduf vaigiensis</i>	0		0		0		0	1.00	0		7	1.72	6	1.15	15	1.14
<i>Sebastes thompsoni</i>	10	1.48	0		0		0		0		0		0		0	
Tetraodontiformes	0		0		0		0		5	1.00	30	1.06	2	1.20	42	4.01
<i>Coryphaena hippurus</i>	0		0		0		0		0		2	1.33	4	1.42	5	1.31
<i>Lobotes surinamensis</i>	0		0		0		0		0		6	1.00	0		0	
Belonidae	0		0		0		0		0		0		0		0	
Exocoetidae	0		0		0		0		0		0		0		0	
<i>Mola</i> spp.	0		0		0		0		0		0		0		0	
Decapodiformes	6	1.20	0		0		1	1.00	0		0		5	1.06	1	1.00
Others	5	2.33	3	2.86	6	1.18	12	1.21	38	1.27	34	2.19	18	3.97	36	1.81

769

770 Table S2. (continued)

Year	2014													
Month	April						May							
Raft No.	Raft1		Raft2		Raft3		Raft1		Raft2		Raft3		Summary	
Sample size	301		104		340		324		88		91			
Category	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean
<i>Seriola</i> spp.	10	1.03	68	6.82	68	5.84	56	16.6	28	3.16	76	57.90	44	11.03
<i>Naucrates ductor</i>	0		0		0		0		5	1.00	0		0	1.00
<i>Oplegnathus punctatus</i>	0		0		14	1.00	6	1.00	0		0		4	1.00
Girellidae/Kyphosidae	0		0		0		0		0		0		5	1.27
<i>Petroscirtes breviceps</i>	0		0		0		0		0		0		1	1.83
<i>Psenes cyanophrys</i>	0		0		1	1.00	0		0		3	2.33	7	2.01
<i>Hyperoglyphe japonica</i>	0		0		0		0		0		0		4	6.68
<i>Abudefduf vaigiensis</i>	0		0		0		0		0		0		3	1.29
<i>Sebastes thompsoni</i>	9	1.44	0		0		5	2.00	0		0		2	1.58
Tetraodontiformes	0		0		0		2	1.00	0		0		8	2.62
<i>Coryphaena hippurus</i>	0		0		1	1.00	1	1.50	1	1.00	2	1.00	1	1.31
<i>Lobotes surinamensis</i>	0		0		0		0		0		0		1	1.00
Belonidae	0		0		0		0		0		0		0	
Exocoetidae	0		0		0		1	1.00	0		0		0	1.00
<i>Mola</i> spp.	0		0		0		0	1.00	0		0		0	1.00
Decapodiformes	0		0		0		0		0		0		1	1.11
Others	53	2.89	51	1.00	43	1.85	48	3.70	89	6.14	37	1.47	30	2.70

771

772 Table S3. Occurrence frequency F (%) and mean observed number of fishes and cephalopoda in video images during our study period (continued on
 773 next page)

Year	2013															
Month	April								May							
Raft No.	Raft1		Raft2		Raft3		Raft4		Raft1		Raft2		Raft3		Raft4	
Sample size	67		64		80		76		9		109		95		97	
Category	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean
<i>Seriola</i> spp.	46	5.10	50	8.31	84	3.90	76	16.59	78	5.29	70	8.82	61	11.71	95	4.65
<i>Naucrates ductor</i>	0		0		0		0		0		0		0		0	
<i>Oplegnathus punctatus</i>	0		0		0		0		0		0		78	1.00	0	
Girellidae/Kyphosidae	0		0		0		20	1.00	0		74	1.89	16	1.20	91	2.05
<i>Petroscirtes breviceps</i>	0		2	1.00	0		57	1.95	0		0		0		0	
<i>Psenes cyanophrys</i>	0		0		68	1.87	0		11	1.00	28	2.13	38	3.50	54	3.62
<i>Hyperoglyphe japonica</i>	0		0		0		0		11	1.00	20	7.05	60	9.39	19	2.22
<i>Abudefduf vaigiensis</i>	0		0		0		16	1.00	11	6.00	39	2.17	39	1.76	80	1.72
<i>Sebastes thompsoni</i>	33	1.41	0		0		4	1.00	0		0		0		0	
Tetraodontiformes	0		0		0		0		0		74	1.49	36	2.38	65	3.41
<i>Coryphaena hippurus</i>	0		0		0		1	1.00	22	1.50	29	1.91	23	1.59	39	2.11
<i>Lobotes surinamensis</i>	0		0		0		0		11	1.00	19	1.00	0		0	
Belonidae	0		0		0		0		0		0		0		0	
Exocoetidae	0		0		0		0		0		0		0		0	
<i>Mola</i> spp.	0		0		0		0		0		0		1	1.00	0	
Decapodiformes	15	1.90	2	1.00	0		3	1.00	0		0		7	1.00	1	2.00
Others	1	1.00	30	1.05	1	1.00	38	1.38	100	1.11	94	4.97	29	2.79	15	1.13

774

775 Table S3. (continued)

Year	2014													
Month	April						May							
Raft No.	Raft1		Raft2		Raft3		Raft1		Raft2		Raft3		Summary	
Sample size	84		30		93		92		24		25			
Category	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean	F (%)	Mean
<i>Seriola</i> spp.	39	1.27	93	6.18	84	8.33	88	22.10	33	5.63	84	10.95	71	9.54
<i>Naucrates ductor</i>	0		0		0		0		8	1.00	0		0	1.00
<i>Oplegnathus punctatus</i>	0		0		59	1.00	77	1.00	0		0		21	1.00
Girellidae/Kyphosidae	0		0		0		0		0		0		21	1.84
<i>Petroscirtes breviceps</i>	0		0		0		0		0		0		5	1.93
<i>Psenes cyanophrys</i>	0		0		0		0		0		12	2.33	19	2.77
<i>Hyperoglyphe japonica</i>	0		0		0		0		0		0		10	7.46
<i>Abudefduf vaigiensis</i>	0		0		0		0		0		0		18	1.81
<i>Sebastes thompsoni</i>	87	1.77	0		0		29	3.04	0		0		13	1.96
Tetraodontiformes	0		0		0		26	1.25	0		0		21	2.21
<i>Coryphaena hippurus</i>	6	1.60	3	1.00	28	1.19	33	2.60	4	1.00	8	1.00	17	1.88
<i>Lobotes surinamensis</i>	0		0		0		0		0		0		2	1.00
Belonidae	0		0		4	1.00	0		0		0		0	1.00
Exocoetidae	0		0		0		1	1.00	0		0		0	1.00
<i>Mola</i> spp.	0		0		0		1	1.00	0		0		0	1.00
Decapodiformes	0		0		0		0		8	1.00	0		3	1.32
Others	98	5.71	80	1.00	52	1.54	70	5.48	96	8.30	88	2.32	50	3.93

776

777 Video S1. *Seriola* spp. Typical video image during the daytime (a part of the file recorded during
778 12:00–12:02 in 26 May 2014, raft 1)

779

780 Video S2. *Seriola* spp. The behavioral transition from the nighttime dense aggregation pattern to the
781 daytime swimming pattern (a part of the file recorded during 05:05–05:10 in 23 May 2014, raft 3)

782

783 Video S3. *Seriola* spp. Two schools met each other to form a larger school (a part of the file
784 recorded during 10:00–10:02 in 13 April 2013, raft 4)

785

786 Video S4. *Seriola* spp. One fish (around the center of the frame) escaped into the seaweed when
787 *Coryphaena hippurus* appeared (a part of the file recorded during 08:00–08:02 in 22 May 2014, raft
788 3)