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SHORT COMMUNICATION

Spatial variability in habitat associations of pre- and post-settlement stages of coral reef fishes at Ishigaki Island, Japan

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Abstract Successful settlement of pelagic fish larvae into benthic juvenile habitats may be enhanced by a shortened settlement period, since it limits larval exposure to predation in the new habitat. Because the spatial distribution of marine fish larvae immediately prior to settlement versus during settlement was unknown, field experiments were conducted at Ishigaki Island (Japan) using light trap sampling and underwater visual belt transect surveys to investigate the spatial distribution patterns of selected pre- and post-settlement fishes (Acanthuridae, Pomacentridae, Chaetodonidae and Lethrinidae) among four habitats (seagrass bed, coral rubble, branching coral and tabular coral). The results highlighted two patterns: patterns 1, pre- and post-settlement individuals showing a ubiquitous distribution among the four habitats (Acanthuridae) and pattern 2, pre-settlement individuals distributed in all habitats, but post-settlement individuals restricted to coral (most species of Pomacentridae and Chaetodontidae) or seagrass habitats (Lethrinidae). The first pattern minimizes the transition time between the larval pelagic stage and acquisition of a benthic reef habitat, the latter leading immediately to a juvenile lifestyle. In contrast, the second pattern is characterized by high settlement habitat selectivity by larvae and/or differential mortality immediately after settlement.

Introduction

In coral reef ecosystems, most marine organisms (e.g., fishes, crustaceans and corals) pass through an offshore pelagic larval stage, after which individuals move to reefs and settle into various habitats (e.g., coral areas, seagrass beds and mangroves), where they progress to the benthic juvenile stage (see review by Kritzer and Sale 2006). Such a habitat transition, from a pelagic oceanic environment to a benthic reef environment, during which the relationship between the organism and its environment changes radically is a particularly dangerous phase known as "settlement" (Leis and McCormick 2002). Mortality is high both during and immediately after the settlement event and strong selection pressures exist for a microhabitat choice that will promote post-settlement survival and growth (e.g., Booth and Wellington 1998; Almany and Webster 2006; Bonin et al. 2009). For example, coral reef fish larvae may cross several reef habitats before eventual settlement (Nakamura et al. 2007), the latter occurring in response to substratum/fish-released cues (Sweatman 1988; Lecchini et al. 2005, 2007; Wright et al. 2005; Arvedlund and

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Takemura 2006). Successful settlement may therefore require a shortening of the settlement period, thereby limiting larval exposure to predation in habitats different from the juvenile habitat (Lecchini 2005). However, the degree to which such larvae are distributed just before settlement versus during the settlement stage remains unknown. In the present study, field experiments were conducted at Ishigaki Island (Japan) using light trap sampling and underwater visual belt transect surveys to investigate the spatial distribution patterns of pre- and post-settlement fishes over a fringing reef.

Materials and methods

The study was carried out in the Itona region (24°29′N, 124°13′E) of Ishigaki Island, Japan, where the fringing reef was characterized by four distinct habitats from shoreline to ocean: seagrass bed, coral rubble, branching coral and tabular coral (Fig. 1). The study was conducted on the four most abundant fish families at Ishigaki: Pomacentridae, Chaetodontidae, Lethrinidae and Acanthuridae.

The spatial distribution patterns of pre-settlement fishes (larval stage) were assessed utilizing two light traps (for a diagram of the light trap, see Nakamura et al. 2009) at each habitat, operated on 26 July (new moon), 5 August (first quarter moon), 16 August (last quarter moon) and 25 August (new moon) 2006. The traps were deployed at 1800 hours and retrieved the following morning at 0900 hours. Immediately after collection, the larvae were preserved on ice. Larvae were identified in the laboratory to the lowest possible taxonomic categories (Okiyama 1988; Nakabo 2002) and their total lengths (TL) were measured. For some larvae, reference specimens were permitted to settle in an aquarium (15 × 35 × 20 cm) and, after 1–3 days, identification was possible based on body color patterns.

The spatial distribution patterns of post-settlement fishes (newly settled juvenile stage: pomacentrids <3 cm TL, chaetodontids and lethrinids <3.5 cm TL, and acanthurids <4 cm TL) were surveyed in each habitat using underwater visual belt transect surveys on the day (between 1000 and 1600 hours) after each light trap sampling event. For each census, one belt transect (20 × 1 m) was randomly established in the sampling habitat (a total of eight transects on each census day). Newly settled juveniles were identified based on the body size and color patterns by underwater observation: they might have included both individuals that had arrived the previous night and individuals that had experienced a few days of post-settlement.

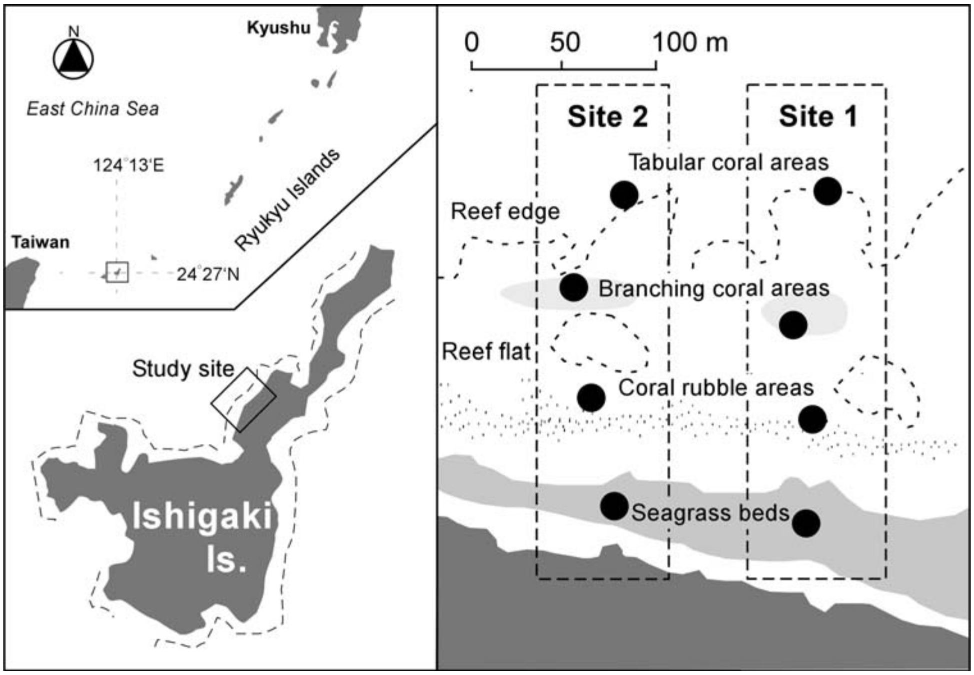

Fig. 1 Map of the fringing reef at Itona, characterized by four distinct habitats from shoreline to ocean. The seagrass bed extends along the coastline between 30 and 100 m from the shore (3.5 ha and 0.5–1 m depth at low tide) and is dominated by *Thalassia hemprichii* (shoot density, 110–130 m^{-2}; leaf height, 8–15 cm). The coral rubble area (3.5 ha; 1 m at low tide) was situated adjacent to the seagrass bed. The branching coral area was located on the reef flat, 60–100 m from the reef edge (0.5–2 ha; 1–3 m at low tide), and was dominated by branching *Acropora* (living coral coverage >80%). The tabular coral area occurred on the outer reef slope (5 ha; 5–15 m at low tide) and was dominated by tabular *Acropora* (living coral coverage >70%), which extended seaward to a sandy floor (ca. 15–20 m deep). *Dashed line* indicates reef margin. *Filled circle* indicates light trap sampling and visual transect survey station

To examine the difference in species richness and the densities of pre- and post-settlement fishes among the four habitats, a one-way analysis of variance (ANOVA) (two sites regarded as habitat replicates) and the post hoc Tukey test were each conducted on 4 sampling days.

Results

Pomacentridae

We collected 5,457 pre-settlement larvae belonging to 24 species of this family (Table 1). Nine species were distributed in all habitats, three in three habitats, four in two habitats and eight in a single habitat. The greatest species richness and abundance were obtained in tabular and branching coral areas. On two of the four sampling days, we found a significant difference among the four habitats (one-way ANOVA, $P < 0.05$, Fig. 2a). In contrast, newly settled juveniles were almost entirely restricted to tabular and branching coral areas (Fig. 2a). Among 16 species represented by both pre- and post-settlement stages, larvae of 13 species (81.3% of total species numbers) were distributed in non-juvenile habitats (coral rubble areas and seagrass beds) before settlement (Table 1). On the other hand, larvae of *Chrysiptera rex*, *Pomacentrus philippinus* and *P. richardsoni* were restricted to their juvenile habitats (tabular and branching coral areas).

Chaetodontidae

We collected 176 pre-settlement larvae belonging to 11 species of this family (Table 1). Five species were distributed in all habitats, four in two habitats and two in a single habitat. The greatest species richness and abundance were observed in tabular and branching coral areas. However, a significant difference among the four habitats was obtained on only 1 of the 4 sampling days (one-way ANOVA, $P < 0.05$, Fig. 2b). In contrast, newly settled juveniles were restricted to tabular and branching coral areas (Fig. 2b). Among five species represented by both pre- and post-settlement life stages, larvae of *Chaetodon trifasciatus*, *C. plebeius*, and *C. speculum* (60%) were distributed in non-juvenile habitats (coral rubble areas and seagrass beds) before settlement, whereas those of *C. trifascialis* and *C. citrinellus* were restricted to the tabular and branching coral areas (Table 1).

Lethrinidae

We collected 633 pre-settlement larvae belonging to this family. No significant differences were apparent in the numbers of pre-settlement larvae obtained among the four habitats (one-way ANOVA, $P > 0.05$ for each day, Fig. 2c), whereas newly settled juveniles were restricted to the seagrass beds during the study period. Although not all lethrinid larvae in each habitat were identified at the species level in this study, molecular analysis revealed that larvae in the tabular coral areas included *Lethrinus atkinsoni*, *L. nebulosus*, *L. harak*, *L. obsoletus*, *L. genivittatus* and *L. ornatus* (Nakamura, unpublished data), indicating that larvae of all six species (100%) were distributed in non-juvenile habitats before settlement (Table 1).

Acanthuridae

We collected pre-settlement larvae belonging to four species of this family (Table 1). Two species were distributed in all habitats, one in three habitats and one in a single habitat. No significant differences in species richness and abundance of larvae (one-way ANOVA, $P > 0.05$ for each day, Fig. 2d) were found among the habitats. Newly settled acanthurid juveniles occurred in a variety of habitats, such as tabular and branching coral areas, coral rubble areas and seagrass beds. Among the four species represented by both pre- and post-settlement stages, larvae of *Ctenochaetus striatus* and *Naso* spp. (50%) were distributed in non-juvenile habitats (seagrass beds) before settlement (Table 1). On the other hand, larvae of *Acanthurus nigrofuscus* and *Zebrasoma scopas* were restricted to their juvenile habitats (tabular and branching coral areas and coral rubble areas).

Discussion

During the transition from a pelagic oceanic environment to a benthic reef environment, marine larvae that have led a pelagic life for several weeks must adapt to the latter environment without prior experience (Kaufman et al. 1992). Based on the spatial distribution patterns of pre- and post-settlement fishes at Ishigaki Island, two transition patterns were highlighted: pattern 1, the ubiquitous distribution of both pre- and post-settlement fishes among the four habitats (Acanthuridae), and pattern 2, the distribution of pre-settlement individuals in all habitats, but with the restriction of post-settlement individuals to coral (most species of Pomacentridae and Chaetodontidae) or seagrass habitats (Lethrinidae). Patterns of habitat selection by newly settled juveniles are typically inferred from censuses conducted some days after the settlement, but this does not make it possible to distinguish among the effects of habitat selectivity by larvae, mortality immediately after settlement and post-settlement relocation by experienced juveniles on the distribution patterns of newly settled juveniles (Vigliola and Harmelin-Vivien 2001).

Table 1 Mean numbers (±SD) of individual pre-settlement larvae per light trap sampling and of newly settled juveniles per 20 m^2 in tabular coral areas, branching coral areas, coral rubble areas and seagrass beds

Family/species	Tabular coral		Branching coral		Coral rubble		Seagrass bed		Size range of larvae/juveniles (TL, mm)
	Larvae	Juveniles	Larvae	Juveniles	Larvae	Juveniles	Larvae	Juveniles	
Pomacentridae									
Abudefduf vaigiensis	0.3 ± 0.7	–	1.0 ± 2.4	–	2.6 ± 3.9	–	3.0 ± 6.7	–	15–20/–
Amblyglyphidodon curacao[a]	–	0.3 ± 0.5	–	1.3 ± 2.1	0.1 ± 0.4	–	–	–	10/10–20
Amblyglyphidodon leucogaster	–	2.6 ± 4.8	–	0.1 ± 0.4	–	–	–	–	–/12–20
Cheiloprion labiatus	–	0.1 ± 0.4	–	7.1 ± 5.3	–	–	–	–	–/12–20
Chromis viridis[a]	309 ± 469	3.5 ± 5.1	170 ± 207	42 ± 65	63 ± 43	–	66 ± 96	–	9–10/10
Chromis margaritifer[a]	–	7.6 ± 6.1	–	0.4 ± 0.7	0.3 ± 0.5	–	–	–	8–10/15–25
Chromis lepidolepis	0.3 ± 0.5	–	–	–	–	–	–	–	11/–
Chromis sp.1	0.3 ± 0.5	–	–	–	–	–	–	–	13–17/–
Chrysiptera rex[a]	0.4 ± 0.7	1.5 ± 1.7	0.1 ± 0.4	1.9 ± 1.2	–	–	–	–	18/20–25
Chrysiptera unimaculata	–	–	–	0.1 ± 0.4	–	–	–	–	–/20
Chrysiptera cyanea	0.3 ± 0.5	–	1.5 ± 3.5	–	1.0 ± 1.4	–	0.4 ± 1.1	–	11–15/–
Dascyllus aruanus[a]	2.4 ± 2.1	–	3.9 ± 4.5	0.9 ± 1.1	3.5 ± 3.8	–	5.8 ± 8.7	–	7–10/10–20
Dascyllus trimaculatus	9.8 ± 8.4	–	3.5 ± 5.2	–	0.4 ± 0.7	–	0.4 ± 0.5	–	9–14/–
Dascyllus reticulatus	–	0.1 ± 0.4	–	6.3 ± 9.4	–	–	–	–	–/10–20
Dischistodus prosopotaenia[a]	1.3 ± 2.8	–	0.5 ± 0.8	–	–	0.1 ± 0.4	–	–	12–13/15
Neoglyphidodon nigroris	–	0.1 ± 0.4	–	–	–	–	–	–	–/25
Neoglyphidodon melas	–	–	–	0.4 ± 0.5	–	–	–	–	–/30
Plectroglyphidodon lacrymatus[a]	0.3 ± 0.5	–	0.1 ± 0.4	0.1 ± 0.4	–	–	–	–	11–13/20
Plectroglyphidodon leucozonus	0.5 ± 1.1	–	0.1 ± 0.4	–	0.1 ± 0.4	–	0.1 ± 0.4	–	15–17/–
Pomacentrus moluccensis[a]	0.4 ± 1.1	9.3 ± 11	0.1 ± 0.4	40 ± 11	0.1 ± 0.4	–	0.1 ± 0.4	–	8–13/10-20
Pomacentrus lepidogenys[a]	1.4 ± 2.4	24 ± 4.2	1.5 ± 2.8	2.5 ± 2.6	0.3 ± 0.5	–	–	–	15–20/15–25
Pomacentrus philippinus[a]	0.3 ± 0.7	3.5 ± 2.3	–	0.1 ± 0.4	–	–	–	–	15–16/20–25
Pomacentrus alexanderae[a]	3.9 ± 6.0	–	3.0 ± 4.2	0.4 ± 1.1	0.4 ± 0.7	–	–	–	10–18/15–20
Pomacentrus amboinensis[a]	–	–	0.5 ± 1.1	2.1 ± 3.8	–	–	0.1 ± 0.4	–	13–14/15–20
Pomacentrus bankanensis[a]	6.8 ± 5.0	0.1 ± 0.4	4.5 ± 5.0	0.9 ± 0.8	1.1 ± 2.8	–	1.9 ± 2.9	–	12–20/15–25
Pomacentrus coelestis[a]	0.5 ± 0.5	–	0.4 ± 0.7	2.6 ± 3.2	–	–	–	–	18/20–25
Pomacentrus chrysurus[a]	0.3 ± 0.7	–	0.9 ± 0.8	–	1.0 ± 2.8	0.1 ± 0.4	0.1 ± 0.4	–	15–17/25
Pomachromis richardsoni[a]	0.5 ± 0.8	21 ± 30	–	–	–	–	–	–	14–18/20
Pomacentrus adelus	–	–	–	4.4 ± 3.5	–	–	–	–	–/15–25
Pomachromis sp.1	–	–	0.1 ± 0.4	–	–	–	–	–	16/–
Pomachromis sp.2	0.1 ± 0.4	–	0.4 ± 0.8	–	0.3 ± 0.7	–	–	–	12–18/–
Chaetodontidae									
Chaetodon trifascialis[a]	0.1 ± 0.4	0.1 ± 0.4	0.1 ± 0.4	0.5 ± 0.9	–	–	–	–	12–13/12–30
Chaetodon citrinellus[a]	0.1 ± 0.4	0.1 ± 0.4	–	–	–	–	–	–	30/30
Chaetodon trifasciatus[a]	2.5 ± 1.8	0.3 ± 0.7	1.8 ± 3.2	2.5 ± 1.4	0.5 ± 0.8	–	0.1 ± 0.4	–	15–18/15–35
Chaetodon plebeius[a]	4.6 ± 6.4	–	2.8 ± 4.7	0.4 ± 0.7	1.1 ± 1.4	–	0.4 ± 0.7	–	11–17/25–30
Chaetodon speculum[a]	0.6 ± 0.7	–	0.5 ± 1.1	0.3 ± 0.5	0.3 ± 0.5	–	0.1 ± 0.4	–	11–13/30–35
Chaetodon melannotus	0.1 ± 0.4	–	0.3 ± 0.5	–	0.1 ± 0.4	–	0.1 ± 0.4	–	18–22/–
Chaetodon kleini	–	–	–	0.1 ± 0.4	–	–	–	–	–/30
Chaetodon argentatus	–	–	–	0.1 ± 0.4	–	–	–	–	–/35
Chaetodon auriga	1.9 ± 2.3	–	1.1 ± 1.6	–	0.5 ± 0.8	–	0.3 ± 0.5	–	18–23/–
Chaetodon vagabundus	0.3 ± 0.7	–	0.1 ± 0.4	–	–	–	–	–	18–22/–

Table 1 continued

Family/species	Tabular coral		Branching coral		Coral rubble		Seagrass bed		Size range of larvae/ juveniles (TL, mm)
	Larvae	Juveniles	Larvae	Juveniles	Larvae	Juveniles	Larvae	Juveniles	
Chaetodon ephippium	0.4 ± 0.7	–	–	–	–	–	0.1 ± 0.4	–	17–20/–
Chaetodon auripes	0.5 ± 1.4	–	–	–	–	–	–	–	17–18/–
Chaetodon sp.l	0.3 ± 0.7	–	–	–	–	–	0.4 ± 1.1	–	20–22/–
Lethrinidae									
Lethrinus atkinsoni	–	–	–	–	–	–	–	2.4 ± 1.3	–/20–35
Lethrinus nebulosus	–	–	–	–	–	–	–	0.1 ± 0.4	–/30
Lethrinus ornatus	–	–	–	–	–	–	–	0.3 ± 0.5	–/30
Lethrinus obsoletus	–	–	–	–	–	–	–	0.3 ± 0.7	–/27–35
Lethrinus genivittatus	–	–	–	–	–	–	–	0.1 ± 0.4	–/35
Lethrinus harak	–	–	–	–	–	–	–	0.1 ± 0.4	–/35
Lethrinus spp.	22 ± 23	–	21 ± 13	–	18 ± 20	–	18 ± 27	–	16–29/–
Acanthuridae									
Acanthurus nigrofuscus[a]	0.6 ± 0.9	0.1 ± 0.4	0.8 ± 2.1	0.8 ± 0.9	0.3 ± 0.7	0.3 ± 0.5	–	–	30–43/30–40
Acanthurus nigricans	–	–	–	0.1 ± 0.4	–	–	–	–	–/40
Acanthurus blochii	–	–	–	–	–	0.9 ± 1.6	–	–	–/30–35
Acanthurus mata	–	–	–	–	–	–	–	0.1 ± 0.4	–/40
Ctenochaetus striatus[a]	0.6 ± 1.1	0.1 ± 0.4	1.1 ± 2.1	0.5 ± 0.8	0.3 ± 0.7	0.1 ± 0.4	0.5 ± 0.8	–	31–36/35–40
Naso spp.[a]	0.3 ± 0.5	–	1.4 ± 3.2	0.3 ± 0.5	0.1 ± 0.4	0.1 ± 0.4	0.3 ± 0.5	–	33–40/30–40
Zebrasoma scopas[a]	–	0.1 ± 0.4	0.1 ± 0.4	0.6 ± 0.5	–	–	–	–	18/30–40

Data pooled across sampling periods and sites ($N = 8$ for each)

[a] Species collected at both pre- and post-settlement life stages

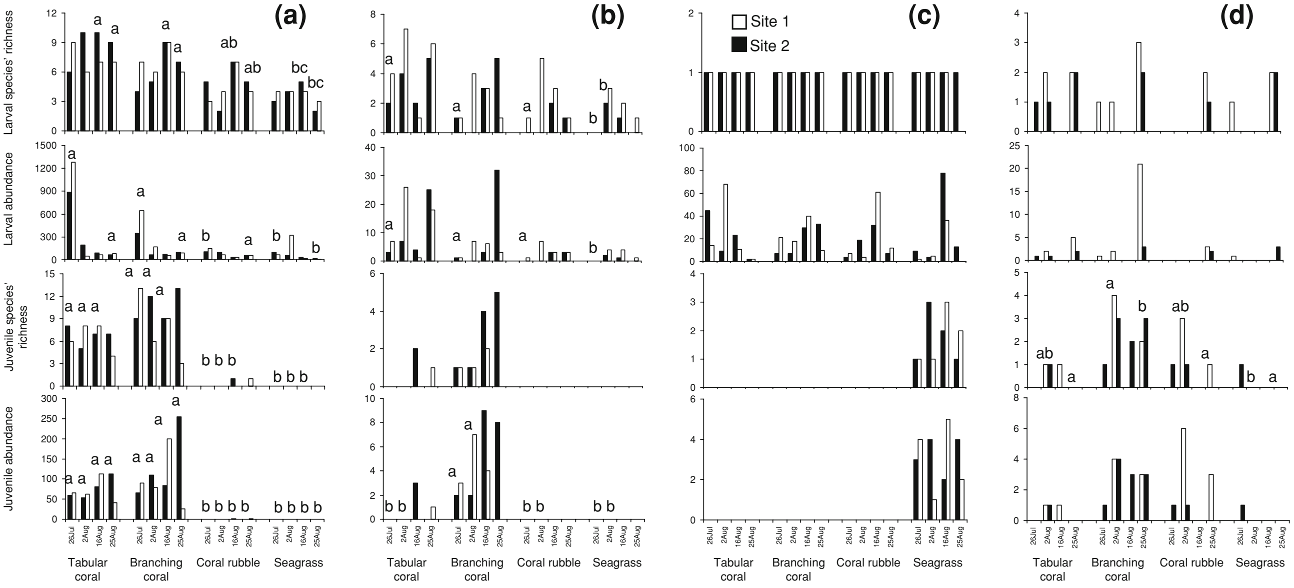

Fig. 2 Species richness and abundance of pre-settlement larvae collected by light traps (one night) and newly settled juveniles recorded by visual transect survey (20 m^2) in the four habitats. **a** Pomacentridae, **b** Chaetodontidae, **c** Lethrinidae and **d** Acanthuridae. Significant difference among the four habitats (Tukey post hoc test) coded by *a*, *b*, and *c* ($P < 0.05$). All lethrinid larvae samples were treated as a single catch-all taxon in the present study

In the present study, the spatial distribution patterns of newly settled juveniles were determined immediately after larval sampling to minimize the effects of post-settlement relocation by experienced juveniles. Pattern 1 (same habitat shared by pre- and post-settlement fish) enabled a minimal transition time between a pelagic lifestyle and life on the reef: i.e., the larvae moved directly to a benthic habitat without specific selectivity and immediately acquired the lifestyle of juveniles (Sancho et al. 1997). Indeed, McCormick (1999) showed that *A. triostegus* larvae adapted to a juvenile-style benthic life within 24 h. The relatively large body size of acanthurid larvae at their arrival in the reef (30–40 mm TL) compared to those of larvae from other families (Table 1) may enable them to adopt such a recruitment strategy, which may be accompanied by a reduced risk of predation because of the short transition period. For pattern 2 (pre- and post-settlement fish having different habitats), on the other hand, more than 60% of larval species were not observed in their non-benthic juvenile habitats within 12 h after each light trap sampling event. Other studies demonstrated that predation may lead to removal of between 30 and 90% of new settlers within the 1st weeks of settlement, the losses in some species possibly being as high as 60% on the first night of arrival (see review by Doherty 2002). Since the body size of Pomacentridae, Chaetodontidae and Lethrinidae larvae at settlement is small (10–30 mm TL, Table 1), predation may have influenced the settlement patterns recorded, with higher mortalities in non-juvenile habitats (Webster 2002). However, because the present surveys were conducted immediately after the larval sampling events, it is probable that other factors had also affected the spatial patterns of post-settlement fishes. Some studies demonstrated that larvae of the latter families exhibited strong habitat selection at settlement, including selection for particular substrata, which will promote post-settlement survival (Booth and Wellington 1998). Therefore, pattern 2 might be explained by strong habitat selectivity by larvae and/or differential mortality immediately after settlement according to the habitat.

The settlement process of fish larvae has been difficult to evaluate because the recruiting larvae are minute and difficult to track and settlement often occurs at night (Holbrook and Schmitt 1997; Irisson and Lecchini 2008). The present study is one of the first to explore the spatial distribution of coral reef fishes in various habitats just before and immediately after the settlement process. The two patterns highlighted at Ishigaki Island showed that spatial patterns of newly settled juveniles resulted from the effects of lower habitat selectivity by larvae (pattern 1) or strong habitat selectivity by larvae and/or differential mortality immediately after settlement according to the habitat (pattern 2). Further study is now required to assess spatiotemporal variability (consistency of the two settlement patterns with different spatial scale reefs) to better understand the settlement process of marine fish.

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References

Almany GR, Webster MS (2006) The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25:19–22. doi:10.1007/s00338-005-0044-y

Arvedlund M, Takemura A (2006) The importance of chemical environmental cues for juvenile *Lethrinus nebulosus* Forsskål (Lethrinidae, Teleostei) when settling into their first benthic habitat. J Exp Mar Biol Ecol 338:112–122. doi:10.1016/j.jembe.2006.07.001

Bonin MC, Srinivasan M, Almany GR, Jones GP (2009) Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. Coral Reefs 28:265–274. doi:10.1007/s00338-008-0451-y

Booth DJ, Wellington G (1998) Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. Aust J Ecol 23:274–279. doi:10.1111/j.1442-9993.1998.tb00731.x

Doherty (2002) Variable replenishment and the density of reef fish populations. In: Sale PF (ed) Coral reef fishes. Academic Press, New York, pp 327–355

Holbrook SJ, Schmitt RJ (1997) Settlement patterns and process in a coral reef damselfish: in situ nocturnal observation using infrared video. Proc 8th Int Coral Reef Symp 2:1143–1148

Irisson JO, Lecchini D (2008) In situ observation of settlement behaviour in larvae of coral reef fishes at night. J Fish Biol 72:2707–2713. doi:10.1111/j.1095-8649.2008.01868.x

Kaufman L, Ebersole J, Beets J, McIvor CC (1992) A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Env Biol Fish 34:109–118. doi:10.1007/BF00002386

Kritzer JP, Sale PF (2006) Marine metapopulations. Academic Press, New York

Lecchini D (2005) Spatial and behavioural patterns of reef habitat settlement by fish larvae. Mar Ecol Prog Ser 301:247–252. doi:10.3354/meps301247

Lecchini D, Shima J, Banaigs B, Galzin R (2005) Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. Oecologia 143:326–334. doi:10.1007/s00442-004-1805-y

Lecchini D, Osenberg CW, Shima JS, St Mary CM, Galzin R (2007) Ontogenetic changes in habitat selection during settlement in a coral reef fish: ecological determinants and sensory mechanisms. Coral Reefs 26:423–432. doi:10.1007/s00338-007-0212-3

Leis JM, McCormick MI (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed) Coral reef fishes. Academic Press, New York, pp 171–199

McCormick MI (1999) Delayed metamorphosis of a tropical reef fish (*Acanthrus triostegus*): a field experiment. Mar Ecol Prog Ser 176:25–38. doi:10.3354/meps176025

Nakabo T (2002) Fishes of Japan with pictorial keys to the species. Tokai University Press, Tokyo

Nakamura Y, Kawasaki H, Sano M (2007) Experimental analysis of recruitment patterns of coral reef fishes in seagrass beds: effects of substrate type, shape, and rigidity. Estuar Coast Shelf Sci 71:559–568. doi:10.1016/j.ecss.2006.09.005

Nakamura Y, Shibuno T, Lecchini D, Watanabe Y (2009) Habitat selection by emperor fish larvae. Aquat Biol 6:61–65. doi:10.3354/ab00169

Okiyama M (ed) (1988) An atlas of the early stage fishes in Japan. Tokai University Press, Tokyo

Sancho G, Ma D, Lobel PS (1997) Behavioral observations of an up-current reef colonization event by larval surgeonfish *Ctenochaetus strigosus* (Acanthuridae). Mar Ecol Prog Ser 153:311–315. doi:10.3354/meps153311

Sweatman H (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J Exp Mar Biol Ecol 124:163–174. doi:10.1016/0022-0981(88)90170-0

Vigliola L, Harmelin-Vivien M (2001) Post-settlement ontogeny in three Mediterranean reef fish species of the genus *Diplodus*. Bull Mar Sci 68:271–286

Webster MS (2002) Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia 131:52–60. doi:10.1007/s00442-001-0860-x

Wright KJ, Higgs DM, Belanger AJ, Leis JM (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). Mar Biol 147:1425–1434. doi:10.1007/s00227-005-0028-z