

The ecology of *Altrichthys azurelineatus* and *A. curatus*, two damselfishes that lack a pelagic larval phase

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Abstract Out of more than 380 species of damselfish, only three lack a pelagic larval phase, *Acanthochromis polyacanthus*, that ranges from the Philippines to the Great Barrier Reef, and two species in the genus *Altrichthys*, *A. azurelineatus* and *A. curatus*, that are restricted to the Calamian Archipelago (Palawan province) in the Philippines. Therefore in a very restricted geographic area, northern Palawan, Philippines, all three species co-occur. The goal of this study was to fill a knowledge gap about the ecology of *Altrichthys*, where very little is currently known. Using census and behavioral approaches at 14 sites on six islands, we were able to identify adult densities, nest densities, nesting habitat preference, and brood behavior and abundance. We found that densities were very high (more than 17 individuals/100 m² for one species) and *A. azurelineatus* may be displacing *A. curatus* at deeper depths where habitat seems of higher quality. Only one out of 14 surveyed sites contained only one species, *Altrichthys curatus*. Different habitat use and feeding behavior suggest that niche partitioning may play an important role in the life history of these sympatric species.

Keywords *Altrichthys azurelineatus* · *Altrichthys curatus* · *Acanthochromis polyacanthus* · Apelagic fishes

Introduction

Most coral reef fishes exhibit a bipartite lifestyle with a sedentary adult stage and a pelagic larval stage (Leis 1991). Few notable exceptions exist, such as the Banggai cardinalfish, *Pterapogon kauderni*, and the striped eel catfish *Plotosus lineatus*, which lack a pelagic larval stage (apelagic species) (Leis 1991; Vagelli 1999; Vagelli et al. 2009). Parental care increases chances of survival of the offspring (Barlow 1981), yet apelagic lifestyles are more likely to result in smaller distribution ranges, and therefore increase the risks of local extinction (Ree and Smith 2008). Among the more than 380 species of damselfish, only three closely related species are apelagic (Cooper et al. 2009; Bernardi 2011). These include the spiny damselfish, *Acanthochromis polyacanthus*, azure damselfish, *Altrichthys azurelineatus*, and guardian damselfish, *Altrichthys curatus*, (Allen 1999; Bernardi 2011). Much ecological and genetic work has been done on the spiny damselfish, *Acanthochromis polyacanthus*, primarily in the Great Barrier Reef, Australia (Thresher 1985; Doherty et al. 1995; Planes et al. 2001; van Herwerden and Doherty 2006). In contrast, very little is known about *Altrichthys*. All the available information on *Altrichthys* is provided by a single paper that describes *Altrichthys* as a new genus, re-describes *A. azurelineatus* (originally described as *Chromis*

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azurelineatus), describes the new species *A. curatus*, and provides some information about the ecology of this unusual genus (Allen 1999).

Similarly to their close relative *Acanthochromis polyacanthus* (Robertson 1973), *Altrichthys* lay eggs on the substrate and after hatching, parents care for their brood until large enough to escape predation, thus bypassing the pelagic larval phase characteristic of most other coral reef fishes. *Altrichthys* live in a very restricted geographic range, the islands of the Calamian Archipelago in northern Palawan province, Philippines, with an extension for *A. curatus* to the adjacent Cuyo islands (Allen 1999) (Fig. 1). Niche partitioning, character displacement, and sexual selection are likely to have played an important role in the events leading to speciation in *Altrichthys*. However, as mentioned above, very little is known about the ecological similarities and differences between *Altrichthys* species, limiting our abilities to ascertain mechanisms leading to speciation in this genus.

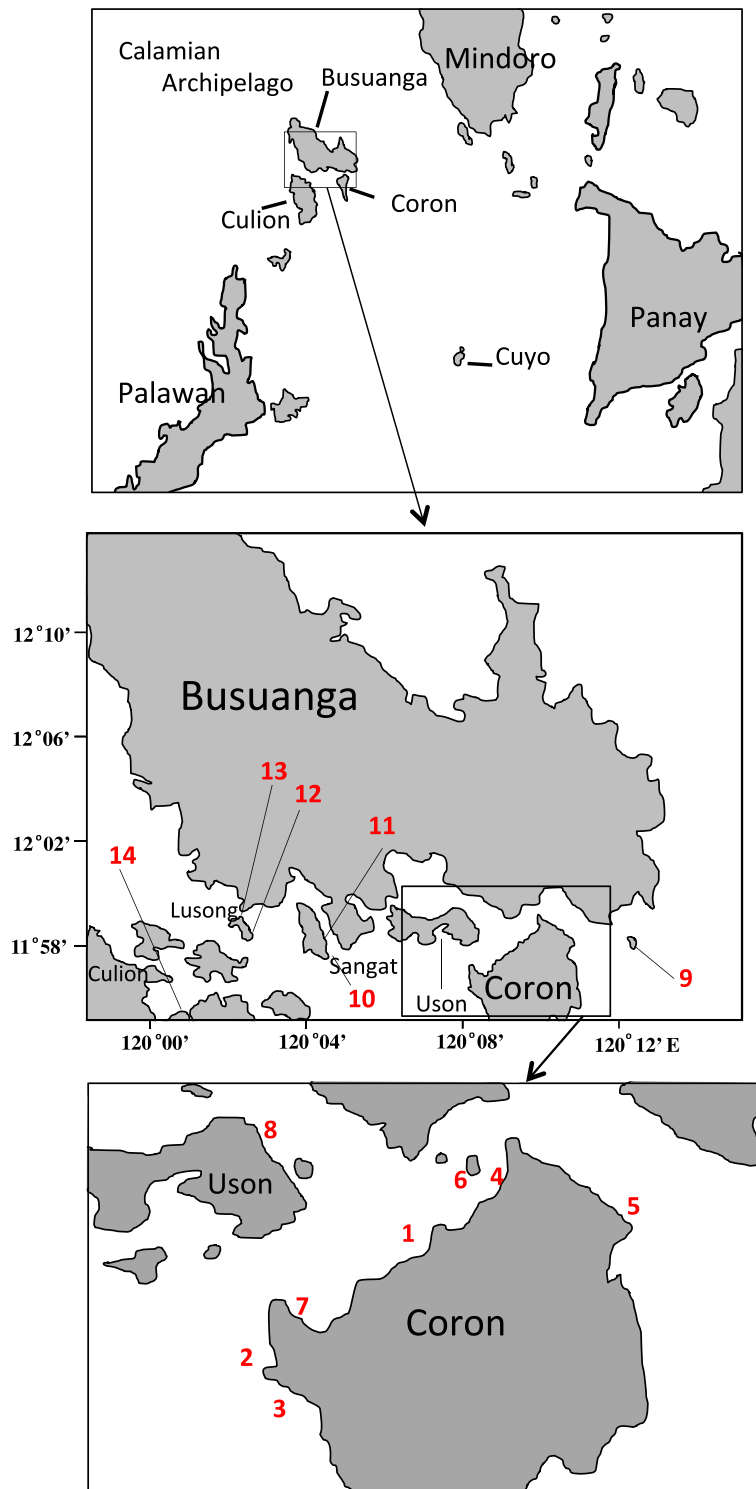
Due to their aggressive and territorial behavior, damselfishes have been used as a model of choice to study spatial organization and habitat partitioning in reef fishes (Sale and Dybdahl 1975; Robertson and Lassig 1980; Waldner and Robertson 1980; Frédérich and Parmentier 2016). Distribution of adult fishes is a combined result of pre-settlement and post-settlement factors. For most damselfishes, which exhibit a pelagic larval phase, the quantity and spatial distribution of recruiting larvae on a given reef often have a strong effect on adult spatial distribution, a phenomenon known as the lottery hypothesis (Sale and Dybdahl 1975; Sale 1977; Sale 1978; Robertson and Lassig 1980; Munday 2004). In the case of apelagic species, pre-settlement factors cannot account for their distribution, leaving open alternative explanations that only involve post-settlement factors to explain their habitat partitioning.

As a first step to estimate potential for niche partitioning, our goal was to assess the ecological characteristics of *Altrichthys azurelineatus* and *A. curatus*, which live sympatrically in the southern Busuanga region. To that effect, we characterized the type of habitat used by nesting parents, the size of the brood, the relative spatial and depth distribution of the nests (Shpigel and Fishelson 1989; Welsh and Perry 1998; Albertson 2008). In addition, since *Acanthochromis polyacanthus* fry have been suggested to feed on their parents mucus (Robertson 1973), a behavior known as glancing (Noakes 1979), we recorded brood feeding mode in *Altrichthys*.

Materials and methods

All three species of brooding damselfishes are present in the Calamian Archipelago (Fig. 1). The three species are easily distinguishable by the observers, *Acanthochromis polyacanthus* is a much larger fish that is entirely black (in this locality), *Altrichthys azurelineatus* is bluish with trailing edges of dorsal, anal, and caudal fin, with black margins, and *A. curatus* is solid grey and lacks the trailing edges on fins. While our study was specifically designed to gather information about the ecology of *Altrichthys*, data were also recorded for *Acanthochromis polyacanthus*, when present. Basic information about *Altrichthys* is poorly known (Allen 1999), we therefore addressed issues of presence/absence, adult density, nesting substrate, number and size of brood, and their feeding. We sampled sites in the Calamian Archipelago including 14 sites on six islands (Fig. 1, Table 1). Surveys were done by scuba and free diving to ascertain the presence of *Altrichthys* at a given site. Adult density was estimated using band transects that were 30 m long and 4 m wide (2 m on each side of the transect). Nests were studied using the same band transects. The position of each nest was recorded by its coordinate on the transect line (x axis) and its position relative to the transect (y axis) with negative values to the left of the transect and positive ones to the right, as we swam along the transect, which allowed to later graph the precise position and Euclidean distance of each nest relative to each other. At each nest, we identified the substrate (identifying corals to genus level), the guarding species, and any other comment that was relevant to the specific nest (e.g. brood feeding in water column). The size and number of fry was recorded. A subset of fry ranging in sizes was collected and measured in the lab to allow proper estimation of size by divers, and pictures of broods were taken. Size and numbers were then estimated by eye after one week of training. Within a clutch, fry sizes are remarkably similar. We assumed the presence of two clutches when two size classes were obviously present, although it is not possible to eliminate the possibility that the identification of a single clutch was in fact a mix of two or more clutches of similar sizes. In order not to miss any rare type of nests, we also swam haphazardly and recorded the same information on all nests encountered. Most *Altrichthys* are found within 10 m depth (Allen 1999), we therefore performed a stratified survey, with transects at three fixed depths: 3, 6 and 9 m, when possible. We also searched nests at deeper depths, up to

Fig. 1 Geographic distribution of *Altrichthys* and sampling locations (see also Table 1)



30 m, to ascertain that we were not missing any unique habitat or behavior. For proper examination of feeding

behavior of adults and juveniles, we also video recorded nests by placing a camera (GoPro, San Mateo,

Table 1 Surveyed sites for *Altrichthys azurelineatus*, *Altrichthys curatus*, and *Acanthochromis polyacanthus*. Columns from left to right correspond to: site number (as used in Fig. 1), site name given in this study, local site name, number of transects at 3, 6, and 9 m

depth for adult individuals and for broods (numbers in parentheses); presence or absence is denoted by an “x” if all three species are present, or by the species present at a site [*Altrichthys curatus* (ACU)]; and the GPS coordinates of the sites

#	Site	Local name	Transects			Presence	Coordinates	
			3 m	6 m	9 m			
1	Coron 1	Twin peaks	2 (4)	2 (4)	2 (5)	x	N 11° 57.601	E 120° 13.098
2	Coron 2	Skeleton Reef				x	N 11° 56.428	E 120° 11.559
3	Coron 3					x	N 11° 55.924	E 120° 11.760
4	Coron 4	Dima's Beach	3 (3)	2 (3)	3 (3)	x	N 11° 59.156	E 120° 14.727
5	Coron 5					x	N 11° 58.243	E 120° 16.164
6	Coron 6	Alcatraz Island				x	N 11° 58.891	E 120° 14.236
7	Coron 7	Cap's Point	3 (3)	2 (3)	4 (3)	x	N 11° 57.071	E 120° 11.754
8	Uson 1	Dive Link		(1)		x	N 11° 59.556	E 120° 11.105
9	Dibatuc 1					ACU	N 11° 58.076,	E 120° 18.874
10	Sangat 1	Malpandon				x	N 11° 57.494	E 120° 05.109
11	Sangat 2			(1)		x	N 11° 57.848	E 120° 04.930
12	Lusong 1	Gunboat		(1)		x	N 11° 58.249	E 120° 01.389
13	Lusong 2	Coral Gardens		(1)		x	N 11° 58.366	E 120° 01.267
14	Culion 1		2 (2)	3 (3)	3 (3)	x	N 11° 53.593	E 120° 01.532

California) in front of nests and leaving the area to avoid further disturbance. We found that behavior seemed to return to normal in the presence of a camera after approximately two minutes. We therefore let the camera record the nest for a minimum of three minutes and a maximum of 15 min.

Results

Presence / absence

We surveyed six islands and 14 sites (Fig. 1, Table 1). These islands are all surrounded by fringing reefs that provide the main general habitat of *Acanthochromis* and the two *Altrichthys* spp. All three species were found at all sites except Dibatuc Island (site 9, Fig. 1), where only *Altrichthys curatus* was present (Table 1). At Dibatuc Island, we found that most of the habitat consisted of *Porites attenuata*, which may be preferred by *A. curatus*.

Adult abundance

We performed 31 band transects, with 10 transects at 3 m, 9 transects at 6 m, and 12 transects at 9 m depth

(Table 1). We counted a total of 1386 adult individuals. These included 681 (49.1%) *Altrichthys azurelineatus*, 213 (15.4%) *A. curatus*, and 492 (35.5%) *Acanthochromis polyacanthus*. When only considering the two *Altrichthys* species, 76.1% of individuals were *A. azurelineatus*, which is approximately three times as many as *A. curatus* (23.9%) individuals (681 v.s 213 individuals, chi square test 190.9, df = 1, $p < 0.001$). These numbers, however, were different with depth. In shallow water, at 3 m, the two *Altrichthys* species were almost equally abundant (55.6% for *A. azurelineatus*, 44.4% for *A. curatus*, (109 vs. 87 individuals, chi square test 1.24, df = 1, $p = 0.13$), while in deeper water *A. azurelineatus* was considerably more abundant than *A. curatus* (85% of individuals at 6 m and 82% of individuals at 9 m, 256 vs. 45 individuals chi square test 84.87, df = 1, $p < 0.0001$, and 288 vs. 63 individuals, chi square test 80.28, df = 1, $p < 0.0001$, respectively). The abundance of *Acanthochromis polyacanthus* did not seem to differ with depth, it accounted for 38.0%, 34.3% and 34.9% of all individuals at 3, 6 and 9 m respectively.

Density was high, with an average of 17.2 *Altrichthys azurelineatus*, 5.4 *A. curatus*, and 12.4 *Acanthochromis polyacanthus* individuals over an area of 100 m².

Nest abundance

We counted a total of 391 nests. Of those, 230 (58.8%) were guarded by *Altrichthys azurelineatus*, 114 (29.2%) by *A. curatus*, and 47 (12.0%) by *Acanthochromis polyacanthus*. The relative abundance of the two *Altrichthys* species was consistent with the abundance of adults with *Altrichthys azurelineatus* nests being more abundant than *A. curatus* ones (66.9% vs. 33.1% respectively). The relative abundance of nests for *Acanthochromis polyacanthus* was lower than the relative abundance of adults (12% vs. 35.5%).

Brood characteristics

To evaluate brood characteristics, we performed 47 band transects (Table 1). We counted a total of 308 broods containing 10,989 juveniles (defined as fish within a brood). Juvenile abundance reflected the adult abundance. Juveniles of *Altrichthys azurelinatus* were the most abundant (184 broods, 5704 juveniles, 51.9%), followed by *A. curatus* (77 broods, 2756 juveniles, 25.1%) and *A. polyacanthus* (47 broods, 2528 juveniles, 23.0%).

The maximum number of fry we found in one brood was 80 individuals for both species of *Altrichthys* and 140 for *Acanthochromis* (Table 2). We observed fry as small as 1 mm and as large as 30 mm in *Altrichthys curatus* and up to 45 mm in *Altrichthys azurelineatus* and *Acanthochromis polyacanthus*. Relationships were estimated between the number of individuals in a brood and the size of the fry contained in that brood (Table 2). The overall trend was an expected negative relationship, as the fry increase in size with time fewer individuals are found in the brood presumably due to mortality (not shown). That relationship was statistically significant in *A. azurelineatus* and *A. polyacanthus* but not in

A. curatus (Table 2), suggesting that in that species, the number of individuals in a brood did not significantly decrease with time. We were not able, however, to follow specific clutches over time to estimate mortality of a given clutch.

In general individuals in a brood all had very similar sizes, indicating that they likely belonged to a single cohort. In addition, we observed 26 *A. azurelineatus* and one *A. curatus* nest where more than one cohort was present. Cohorts could easily be distinguished because the average difference in size between cohorts was 11.0 mm (st.dev 6.9 mm). In most of these nests two cohorts were present (19 nests). In some cases three or four cohorts were present (6 and 1 nest, respectively). In some cases, juvenile individuals were loosely associated with nests as well, but it was difficult to precisely quantify their presence. We did not see any *Acanthochromis* nests with more than one cohort.

Nesting characteristics

We recorded substrate use for 391 nests. Guarding parents were seen using ten different types of habitat as primary substrate for their nests (Table 3). The use of primary substrate was neither random nor used equally by different species. The most commonly used nesting substrate (45.5% of all nests) was corals of the genus *Porites* (mostly *Porites cylindrica*). *Acropora* was the second most commonly used substrate (17.6% of the nests), and was preferentially associated with *A. azurelineatus* (61 of 69 nests). Several substrates were exclusively associated with a single species, however these substrates were uncommon. For example, *Echinopora horrida* was found exclusively as a substrate for *Altrichthys azurelineatus*, but only in eight nests. The alga *Padina*, the coral *Agaricia*, rubble habitat, and sponges were only used by *A. curatus* in eight,

Table 2 Brood characteristics of *Altrichthys azurelineatus*, *Altrichthys curatus*, and *Acanthochromis polyacanthus*. Starting from the left, columns correspond to: number of broods (nbr), number of fry (nfr), the next three columns are sizes of individuals (fry) within a brood in millimeters (with standard deviations in

parentheses), the next three columns are the number of individuals per brood, the last three columns describes the relationships between size and number of individuals per brood with the parameters R^2 , F ratio and p value

	nbr.	nfr.	Size			Number			R ²	df	F ratio	p
			min	max	average	min	max	average				
Aa	184	5704	1	45	12.9 (8.5)	2	80	31.0 (17.4)	0.049	1, 182	8.8816	0.0033
Ac	77	2756	1	30	10.3 (6.1)	5	80	35.8 (14.0)	0.013	1, 75	0.8128	0.3709
Ap	47	2528	3	45	20.5 (11.5)	6	140	53.8 (30.0)	0.139	1, 45	7.2924	0.0097

Table 3 Nesting substrate for *Altrichthys azurelineatus* (*A. a*), *A. curatus* (*A. a*), and *Acanthochromis polyacanthus* (*A. p*). each species is arranged in three columns. The first column corresponds to the number of nests that were found in that substrate for a given species. The second column corresponds to the proportion of usage for that species. The third column is the proportion of usage

of a given substrate among the three species. The last two columns are the total number of observations for a given substrate and their percentage. For example: 129 nests of *A. azurelineatus* were found in *Porites*, this number corresponds to 58.4% of the *A. azurelineatus* nests. As a substrate, *Porites* is used 72.5% of the time by *A. azurelineatus*

Substrate	<i>A. a</i>	%	%tot	<i>A. c</i>	%	%tot	<i>A. p</i>	%	%tot	Total	%
<i>Porites</i>	129	58.4	72.5	40	40.5	22.5	9	25.0	5.0	178	50.0
<i>Acropora</i>	61	27.6	88.4	6	6.1	8.7	2	5.6	2.9	69	19.4
<i>Seriatopora</i>	15	6.8	38.5	24	24.2	61.5	0	0.0	0.0	39	10.9
Rock Cave	0	0.0	0.0	2	2.0	8.0	23	63.9	92	25	7.0
<i>Isopora</i>	8	3.6	72.7	1	1.0	9.1	2	5.6	18.2	11	3.1
<i>Echinopora</i>	8	3.6	100.0	0	0.0	0.0	0	0.0	0.0	8	2.2
<i>Padina</i>	0	0.0	0.0	8	8.1	100.0	0	0.0	0.0	8	2.2
Sponge	0	0.0	0.0	8	8.1	100.0	0	0.0	0.0	8	2.2
Rubble	0	0.0	0.0	7	7.1	100.0	0	0.0	0.0	7	2.0
<i>Agaricia</i>	0	0.0	0.0	3	3.0	100.0	0	0.0	0.0	3	0.8
Total	221	100	62.1	99	100	27.8	36	100	10.1	356	100.0

eight, seven, and three nests, respectively. Rock caves were mostly used by *Acanthochromis polyacanthus* (23 of 25 nests). Some nests were adjacent to specific types of corals, such as *Oxypora lacera*, *Mycedium elephantotus*, and often *Hydnophora rigida*, but this use was not quantified.

Nest distribution

We recorded the position of each encountered nest along transects, thus allowing to establish the distance between each nest. Overall, we analyzed the spatial distribution of 270 nests. The average distance between any two nests was 3.9 m, the average distance between nests of the same species was 5.1 m (Fig. 2). Distances between *Altrichthys azurelineatus* and other nests of any species was the smallest (3.5 m), and their distance to other *A. azurelineatus* nests was also the smallest (4.8 m). In contrast, distances between *Acanthochromis polyacanthus* and other nests of any species was the largest (5.0 m), and their distance to other *A. azurelineatus* nests was also the largest (6.0 m). *Altrichthys curatus* showed intermediate values of 5.4 m and 4.0 m, respectively. The observations reported above seemed consistent across depth except for *A. curatus* where nests in shallow water were seen further apart than deeper ones, while individuals were

found at higher densities as noted above, suggesting an active avoidance of nest proximity.

Brood feeding

When very young, the brood tends to be very compact (a sphere of approximately 10 cm) and tightly cluster around the nesting substrate. As the fry grow, they tend to form looser feeding aggregations, venturing as far as 60 cm from their original nesting area, that only come back in tighter balls if parents signal a threat. It has been suggested that *Acanthochromis polyacanthus* brood may feed on the body mucus of the parents, a behavior called “glancing” (Robertson 1973), and that *Altrichthys* brood may be exhibiting the same behavior (Allen 1999). We directly observed broods of all species and filmed *Altrichthys azurelineatus* and *A. curatus* broods for a total of 93 min 18 s (mean observation time per brood 8 min 10 s), and 88 min 48 s (mean observation time per brood 6 min 20 s), respectively. All observations were done during the daytime, and involved all type of nesting substrate previously identified. We never observed any fry feeding directly on the skin of the parents. In one instance, some fry swam close to the parents and some mucus could possibly have sloughed off the skin and then eaten by the fry. It is very difficult to be certain that this was the case, and did not look like the “glancing” behavior where fry swim to the body of

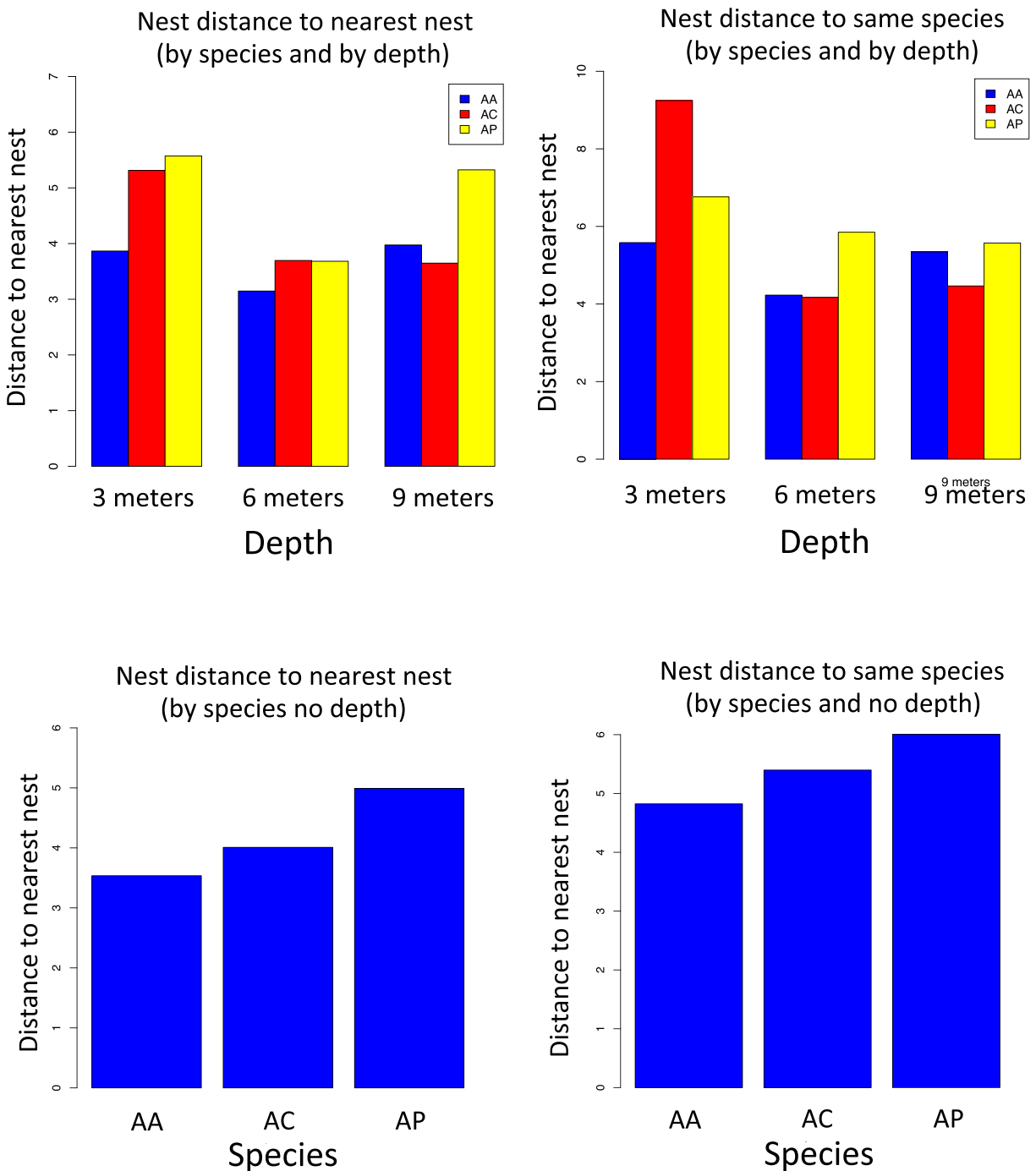


Fig. 2 Distances between nests of *Altrichthys*. Left panels show distances between any two nests regardless of species, right panels show distances between any two nests of each species. Top panels

show distances separated by depth (3, 6, and 9 m), bottom panels show distances regardless of depth. All distances are given in meters

the parents and bounce off of it after taking in some mucus. Therefore while we cannot entirely rule out the possibility of mucus feeding in *Altrichthys*, the behavior

is not common or easy to observe. In contrast, our videos and observations suggest that the fry and adult feed on plankton and other floating particles.

Nest protection and aggression

We did not observe aggressive interactions between males, or active courtship displays. However, we qualitatively observed that *Altrichthys* aggressively defend their nests against potential predators. Indeed, when we separated the guarding parents from their brood, we observed several predation events on defenseless fry by serranids (*Cephalopholis microprion*), wrasses (*Halichoeres leucurus*, *Oxycheilinus celebicus*) and pomacentrids (*Amblyglyphidodon batunai* and adult *Altrichthys* individuals). In addition to the species that were seen actively preying on broods, we also observed aggressive behavior against *Thalassoma lunare*, *Amblyglyphidodon curacao*, and *A. ternatensis*. *Altrichthys* tend to also be very aggressive towards conspecifics, congeners, and smaller damselfish that occupy their habitat such as *Chrysiptera springeri*.

We observed an event where a very large number of pomacentrids (*Pomacentrus smithi*) recruited at once on *Altrichthys* habitat. In that case, guarding parents were overwhelmed by hundreds of invading recruits, and did not attempt to fend off the new intruders. No sign of aggression was observed until a few days later when the number of recruits had naturally dwindled down and become more manageable by parents that became aggressive again.

Discussion

Habitat partitioning

Habitat partitioning in coral reef fishes results from an interaction between larval dynamics and adult competition (Sale and Dybdahl 1975; Sale 1978; Robertson and Lassig 1980; Sale 1991; Munday 2004). In general, coral reef fishes exhibit two main spawning modes, broadcast spawning and demersal spawning with different parental investment (low and high respectively) (Barlow 1981). For demersal spawners, strong competition for limited substrate has been suggested as the primary driver of post-settlement competition (Jan 1997; Jan 2000). Therefore, adult distribution of fishes on coral reefs is the result of a complex dynamic that takes into account pre-settlement and post-settlement factors.

Altrichthys are unusual fish that brood their young and entirely bypass the pelagic larval phase commonly observed in most other coral reef fish. Like their close

relative, the spiny damselfish *Acanthochromis polyacanthus*, both parents aggressively guard a brood until fry reach a size of approximately 35 to 45 mm. *Altrichthys* therefore offer a simplified model to understand spatial distribution of fishes on reefs. The spatial distribution of *Altrichthys* is likely to be greatly influenced by adult interactions and competition for nesting substrate, without having to take into account complex pre-settlement dynamics.

Unlike previous studies on damselfishes, where aggressive adult interactions between species were recorded and species could be directly categorized into dominant and submissive, and in turn potentially explaining the distribution of individuals on the reefs (Robertson and Lassig 1980; Jan 1997), we did not observe strong intra- or inter-specific interactions between *Altrichthys* individuals.

Partitioning according to nesting substrate

The distance between *Altrichthys* nests was relatively uniform, approximately 4 m. The presence of adequate nesting substrate between nesting sites suggests that some aggressive behavior between nesting parents is present (Jan 1997). *Altrichthys* also showed evidence of partition according to nesting substrate. This was not an absolute partition, but some substrates were exclusively used by one species or another. In addition, the two most common substrates, *Porites* and *Acropora*, were preferentially used by *A. azurelineatus*. Indeed, out of 236 nests that were observed on these two coral types, 190 were guarded by *A. azurelineatus* and only 46 by *A. curatus*. This is consistent with *A. azurelineatus* being a stronger competitor, although again we neither have direct evidence of aggression, nor an estimate for higher fitness achieved by using this substrate. We did not record the nesting substrate of other damselfish species (except for *Acanthochromis polyacanthus*) in the area, we therefore cannot comment on the interaction between *Altrichthys* and other species.

Acanthochromis polyacanthus is a much larger species that usually spawns in rock crevices throughout its range (Robertson 1973). At our sampling sites, *A. polyacanthus* was seen either guarding nests (mostly in rock crevices) or out at the edge of the reef over drop offs, feeding in the water column in very large aggregations. Such feeding was never observed in *Altrichthys*

curatus, because this species always stayed very close to the substrate. Occasionally *A. azurelineatus* was seen hovering over the reef, more so than *A. curatus*, but never as high up in the water column as *Acanthochromis polyacanthus*. This behavior probably allows *A. azurelineatus* to access food that is unavailable to *A. curatus*.

Brood ecology and interactions

Most individuals within a clutch had very similar sizes. The presence of different size-classes within a nest (when present, approximately 11 mm on average) is suggestive of the presence of multiple age-classes guarded by a pair of adults. Similarly to some cichlid species, such as *Neolamprologus brichardi* (Taborsky 1984), our observations were consistent with a possible helping behavior by *Altrichthys* juveniles to raise confamilial broods.

Brood feeding on the mucus of the parents has been described in many species of fish (Noakes 1979), most notably in the cichlid *Symphysodon discus* (Buckley et al. 2010). Robertson suggested that this behavior is also present in *Acanthochromis polyacanthus* (Robertson 1973). Yet, while we specifically searched for this behavior, we never observed any fry feeding directly on the skin of the parents. We cannot exclude that this behavior could be furtive, hidden, or rare.

Conclusions

By lacking a pelagic larval phase, *Altrichthys* offer a unique opportunity to study the dynamics of habitat partitioning in a very simplified context. Here we show the substrate preferences and interactions between the two recognized species of *Altrichthys*, *A. curatus* and *A. azurelineatus*, as well as their closely related species *Acanthochromis polyacanthus*. Unlike *Acanthochromis*, which ranges from the Philippines to the Great Barrier Reef, the geographic range of *Altrichthys* is very restricted, yet within this range they are very abundant, with more than 20 individuals per 100 m². It is therefore remarkable that within a very small geographic range, all three species of brooding damselfishes are found, including the two congeneric *Altrichthys*.

Further work is warranted for understanding partitioning in *Altrichthys*, where additional ecological data and proper assessment of the

distribution of the species are necessary to fully understand the mechanisms involved in the divergence of these species.

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References

- Albertson RC (2008) Morphological divergence predicts habitat partitioning in a Lake Malawi cichlid species complex. *Copeia* 2008:689–698
- Allen GR (1999) *Altrichthys*, a new genus of damselfish (Pomacentridae) from Philippine seas with description of a new species. *Rev Fr d' Aquariol* 26:23–28
- Barlow GW (1981) Patterns of parental investment, dispersal and size among coral-reef fishes. *Environ Biol Fish* 6:65–85
- Bernardi G (2011) Monophyletic origin of brood care in damselfishes. *Mol Phylogenet Evol* 59:245–248
- Buckley J, Maunder RJ, Foey A et al (2010) Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid. *J Exp Biol* 213:3787–3795
- Cooper WJ, Smith LL, Westneat MW (2009) Exploring the radiation of a diverse reef fish family: phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. *Mol Phylogenet Evol* 52:1–16
- Doherty PJ, Planes S, Mather P (1995) Gene flow and larval duration in seven species of fish from the great barrier reef. *Ecology* 76:2373–2391
- Frédérich B, Parmentier E (2016) Biology of damselfishes. CRC Press, Boca Raton
- Jan RQ (1997) Sympatric spawning of the damselfishes *Chromis fumea* and *Pomacentrus coelestis* on the northern coast of Taiwan. *Zool Stud* 36:26–32
- Jan RQ (2000) Resource limitation underlying reproductive strategies of coral reef fishes: a hypothesis. *Zool Stud* 39:266–274
- Leis JM (1991) The pelagic stage of reef fishes. In: Sale P (ed) *Ecol. Fishes coral reefs*. Academic Press Inc., San Diego, CA, pp. 182–229
- Munday PL (2004) Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. *Ecology* 85:623–628
- Noakes DLG (1979) Parent-touching behavior by young fishes: incidence, function and causation. *Environ Biol Fish* 4:389–400
- Planes S, Doherty PJ, Bernardi G (2001) Strong genetic divergence among populations of a marine fish with limited dispersal, *Acanthochromis polyacanthus*, within the great barrier reef and the Coral Sea. *Evolution (N Y)* 55:2263–2273
- Ree RH, Smith SA (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction,

- and cladogenesis. *Syst Biol* 57:4–14. doi:[10.1080/10635150701883881](https://doi.org/10.1080/10635150701883881)
- Robertson DR (1973) Field observations on the reproductive behaviour of a pomacentrid fish, *Acanthochromis polyacanthus*. *Z Tierpsychol* 32:319–324
- Robertson DR, Lassig B (1980) Spatial distribution patterns and damselfishes from the great barrier reef. *Bull Mar Sci* 30: 187–203
- Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *Am Nat* 111:337–359
- Sale PF (1978) Coexistence of coral reef fishes - a lottery for living space. *Environ Biol Fish* 3:85–102
- Sale PF (1991) Reef fish communities: open nonequilibrium systems. In: Sale PF (ed) *Ecol. Fishes coral reefs*. Academic Press, New York, pp. 564–598
- Sale PF, Dybdahl R (1975) Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56: 1343–1355
- Shpigiel M, Fishelson L (1989) Habitat partitioning between species of the genus *Cephalopholis* (Pisces, Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea). *Mar Ecol Prog Ser* 58:17–22
- Taborsky M (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Anim Behav* 32:1236–1252
- Thresher RE (1985) Distribution, abundance, and reproductive success in the coral reef fish *Acanthochromis polyacanthus*. *Ecology* 1985:1139–1150
- Vagelli A (1999) The reproductive biology and early ontogeny of the mouthbrooding Banggai cardinalfish, *Pterapogon kauderni* (Perciformes, Apogonidae). *Environ Biol Fish* 56:79–92
- Vagelli A, Burford M, Bernardi G (2009) Fine scale dispersal in Banggai cardinalfish, *Pterapogon kauderni*, a coral reef species lacking a pelagic larval phase. *Mar Genomics* 1:129–134. doi:[10.1016/j.margen.2009.01.001](https://doi.org/10.1016/j.margen.2009.01.001)
- van Herwerden L, Doherty PJ (2006) Contrasting genetic structures across two hybrid zones of a tropical reef fish, *Acanthochromis polyacanthus* (Bleeker 1855). *J Evol Biol* 19:239–252. doi:[10.1111/j.1420-9101.2005.00969.x](https://doi.org/10.1111/j.1420-9101.2005.00969.x)
- Waldner RE, Robertson DR (1980) Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bull Mar Sci* 30:171–186
- Welsh SA, Perry SA (1998) Habitat partitioning in a community of darters in the Elk River, West Virginia. *Environ Biol Fish* 51: 411–419