Ontogenetic shifts in the social behaviour of pairing coral reef rabbitfishes (Siganidae)

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\textbf{ABSTRACT}

Adult rabbitfishes (Siganidae) differ from most other herbivorous coral reef fishes by forming stable pair bonds throughout their adult lives. However, little is known about the early life stages of rabbitfishes, and no quantitative evidence regarding the ontogeny of pairing behaviour exists to date. This study describes the abundance, distribution and ontogeny of social associations in juvenile rabbitfishes on the mid-shelf reefs around Lizard Island, Great Barrier Reef, Australia. Using underwater visual censuses, we surveyed an area of 5728 m\textsuperscript{2} across three distinct habitat types, revealing that the abundance of juveniles varies significantly among species, size class and exposure level. Furthermore, we demonstrate a pronounced ontogenetic shift in the social associations of juveniles of \textit{Siganus doliatus} and \textit{Siganus corallinus}, changing from primarily solitary individuals in the smallest size class (<50 mm) to predominantly paired individuals in the larger size classes (50–100 mm and 100–150 mm). In this context, we report the presence of several mixed-species pairs of rabbitfishes, providing the first evidence for this behaviour within the family. This supports previous research, which posits that there are strong ecological drivers, rather than a solely reproductive basis, for pairing behaviour in rabbitfishes. Based on our results, we suggest that further exploration of the ecology of early life stages of herbivorous reef fishes will increase our knowledge about ecological processes on coral reefs.

\textbf{KEYWORDS} Herbivory; juvenile reef fish; mixed-species pair; pair formation; rabbitfish; schooling; \textit{Siganus}

\section*{Introduction}

On Indo-Pacific coral reefs, rabbitfishes (Siganidae), together with surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), form the majority of large, mobile, nominally herbivorous coral reef fishes (Choat et al. 2002; Cheal et al. 2012). Rabbitfishes are roughly divided into two major lineages, consisting of brightly coloured, pair-forming species which live in close association with coral reefs, and drab-coloured, schooling species which are commonly associated with reef, mangrove and estuarine habitats (Woodland 1990; Borsa et al. 2007). Species in the former lineage (henceforth called ‘pairing rabbitfishes’) differ from most other reef herbivores in their social behaviour and their foraging strategies. Specifically, these species exhibit morphological traits, such as concave foreheads and pointed snouts (Brandl & Bellwood 2013a), which permit the exploitation of resources within interstitial spaces (such as cracks and crevices) on the reef (Fox & Bellwood 2013; Brandl & Bellwood 2014a, 2016). It has been hypothesized that pair-formation supports this foraging strategy through coordinated vigilance, which could potentially decrease predation risk and/or increase foraging efficiency, suggesting that the purpose of pairing in rabbitfishes goes beyond reproductive factors (Brandl & Bellwood 2013b, 2014b, 2015; Fox & Donelson 2014; Fox et al. 2015).

Many studies have described the abundance and distribution of adult herbivorous fishes on coral reefs (cf. Cheal et al. 2012). However, while the settlement patterns and behaviour of larval reef fishes (Jones et al. 1999; Feary et al. 2007) and the distribution of juveniles are relatively well studied in several taxa (e.g. Pomacentridae, Schmitt & Holbrook 2000; Serranidae, Almany 2004; Chaetodontidae, Pratchett et al. 2008), less information is available on juvenile herbivorous reef fishes (but see Doherty 2002; Adams et al. 2006; Mellin et al. 2007; Welsh et al. 2013; Feitosa & Ferreira 2015). The studies conducted on early life-stages of herbivorous reef fishes have revealed that juveniles...
primarily settle into shallow, protected reef habitats after their pelagic larval stage (Bouchon-Navaro & Harmelin-Vivien 1981; Gust et al. 2001; Adams et al. 2006). In parrotfishes, which represent the most thoroughly investigated family, juveniles recruit to the reef over several weeks with only weak recruitment pulses (Green 1998). Subsequently, species such as Chlorurus sordidus (Forsskål, 1775) or Scarus iserti (Bloch, 1789) often assemble into assortative intra- or interspecific schools (Crook 1997a, 1997b, 1999a; Quinn et al. 2012), but can also occur as solitary individuals (Crook 1999b). This behaviour has been linked to benefits in terms of foraging efficiency (Robertson et al. 1976; Crook 1997a, 1999a; Quinn et al. 2012) and predator avoidance (Crook 1997b, 1999a, 1999b), and both size and social behaviour of juvenile parrotfishes have been shown to be variable across sites on Lizard Island (Crook 1999b). In contrast to parrotfishes, no quantitative data on basic aspects of the ecology of juvenile rabbitfishes exist to date. This is particularly interesting, given that in contrast to most surgeon- and parrotfishes, which commonly stay solitary or assemble into schools or harems upon reaching maturity (Barlow 1974; Warner & Robertson 1978; Streelman et al. 2002), rabbitfishes form stable pair bonds that are relatively unique among herbivorous species (Woodland 1990; Brandl & Bellwood 2013b). Preliminary findings suggest that the onset of pairing starts before individuals reach sexual maturity (Woodland 1990; Brandl & Bellwood 2013b) and there is anecdotal evidence that, similar to parrotfishes, juveniles show a transition from shallow lagoonal habitats to deeper habitats on the reef slope (Woodland 1990; Brandl & Bellwood 2013b). Yet, no quantitative evidence for these patterns exists at present.

Therefore, the aim of this study was to provide the first quantitative description of the social associations, abundance and distribution of juvenile rabbitfishes on a mid-shelf reef on the Great Barrier Reef, Australia.

**Materials and methods**

This study was conducted in January and February 2014 on reefs around Lizard Island (14°40’S, 145°28’E), a granitic mid-shelf island in the northern Great Barrier Reef. Three different depth/exposure regimes were chosen and each regime was represented by two sites (Figure 1). The protected reef sites (Pipeline and Loomis Reef) were chosen for their shallow depth (1–2 m) and reduced wave action due to their position on the leeward side of other reefs. The semi-exposed sites (Big Vicki’s and Palfrey Reef) were characterized by a greater depth (2–5 m), and an increase in wave energy relative to the protected sites. The exposed sites (Crest 1 and Crest 2) were located on the windward side of Lizard Island on the reef crest, where the depth was greater (3–8 m) and wave action is typically more pronounced due to the dominance of south-easterly tradewinds. The three types of sites were chosen due to previously suggested ontogenetic shifts in habitat use in rabbitfishes and other taxa (Bouchon-Navaro & Harmelin-Vivien 1981; Woodland 1990), using exposure and depth as a proxy for varying biotic and abiotic conditions; however, there are likely to be several factors characteristic of the respective sites beyond depth and wave exposure, including substrate composition or predation pressure, which may also influence the social behaviour of juvenile fishes (Crook 1997a, 1997b, 1999a, 1999b).

All juvenile (<150 mm total length, TL) rabbitfish species observed on transects were included in the study (Woodland 1990). Although individuals in Siganus doliusus (Guérin-Méneville, 1829–38) have been shown to reach maturity possibly as small as ~130 mm TL (Brandl & Bellwood 2013b), we assumed 150 mm TL to be within the margin of error of size at maturity, thus considering them as juvenile fishes.

A total of 60 five-minute timed swims to a maximum length of 50 m were performed along a transect tape on scuba or snorkel. The area one metre on each side of the transect line was surveyed for (a maximum) transect area of 100 m². Total transect area was factored into the analysis to avoid bias when conditions or high densities of juvenile fishes did not allow the full 50 m of a transect to be surveyed, thus resulting in a smaller surveyed area. Individuals were recorded as the transect tape was deployed in order to reduce effects of diver disturbance (Dickens et al. 2011). Each transect was separated by a minimum of 10 m in order to avoid pseudo-replication. Individuals were assigned to species, placed in one of three size classes (0–50 mm, 50–100 mm, 100–150 mm), and their social association was determined, distinguishing between solitary, paired and schooling individuals. The species affiliation of associated individuals was recorded for all species in pairs or schools. All transects were performed during the daytime low tide hours. Due to the presence of zero counts in the contingency tables, the data on ontogenetic changes in social behaviour were analysed using an extension of Fisher’s Exact test for r × c contingency tables with the FORTRAN subroutine FEXACT (Mehta & Patel 1986; Clarkson et al. 1993). All P-values were computed using Monte Carlo simulations with 9999 permutations (Agresti 2002).
Results

A total of 216 individual juvenile rabbitfishes (<150 mm; Woodland 1990), from five different species, *Siganus corallinus* (Valenciennes, 1835); *S. doliatus*; *S. puellus* (Schlegel, 1852); *S. punctatus* (Schneider & Forster, 1801); *S. vulpinus* (Schlegel & Müller, 1845), were recorded in a total area of 5728 m$^2$, equating to an average abundance of $4.2 \pm 0.55$ (SE) individuals per 100 m$^2$. Only two species (*S. doliatus* and *S. corallinus*) were abundant enough to permit analyses of ontogenetic changes in their social associations. Social associations of juvenile *S. doliatus* in the three size classes differed significantly from the null hypothesis of independence (Fisher’s Exact test with simulated $P$-value: $P < 0.0001$), with the proportional prevalence of paired individuals strongly increasing with size, while solitary individuals became less prevalent in larger size classes (Figure 2a). For *S. corallinus*, a similar trend was visible (Figure 2b), but results were non-significant (Fisher’s Exact test with simulated $P$-value: $P = 0.116$).

The distribution of juvenile rabbitfishes in the three size classes also appeared to differ across sites. Specifically, based on the graphical representation, average density of juveniles appeared highest at the two shallow, sheltered sites (Loomis and Pipeline Reef), and lowest at the deepest, exposed sites (Bird and South), with the two semi-exposed sites occupying intermediate positions (Figure S1a, supplementary material). Similarly, the proportional frequency of solitary individuals was high at Loomis, Pipeline and Palfrey Reef, while being markedly lower at Big Vicki’s Reef, Bird Islets and South Island (Figure S1b).

Finally, of all juvenile rabbitfishes recorded during this study, eight individuals (3.7%) were found in mixed-species pairs (Figure 3). Specifically, on three occasions, we recorded a juvenile *S. doliatus* in a pair with a juvenile *S. punctatus*, and on one occasion, we recorded a pair formed between a juvenile *S. doliatus* and *S. corallinus*. Three of these mixed-species pairs were among individuals in the smallest size class (<50 mm), while one pair of *S. doliatus* and *S. punctatus* was in the medium size class (50–100 mm).

Discussion

A clear pattern emerging from our findings is the difference in social associations over the course of juvenile rabbitfish’s ontogeny. There was a marked increase in the frequency of paired individuals in the larger size...
Figure 2. Proportional frequency of individuals in different size classes across social associations for *Siganus doliatus* (a) and *S. corallinus* (b). Small <50 mm TL; Medium = 50–100 mm TL; Large = 100–150 mm TL.

Figure 3. A mixed-species pair of juvenile rabbitfish, consisting of *Siganus corallinus* (left) and *Siganus doliatus* (right).
classes, indicating that juveniles begin to pair shortly before or after reaching 50 mm, and that the majority are in pairs by the time they reach 100 mm. This suggests that the importance of pairing becomes more critical as individuals get closer to maturity, a trend often associated with a reproductive role of pairing (Pratchett et al. 2006). However, the onset of pair formation at ~50 mm TL, and therefore well before adulthood (~150 mm TL, Brandl & Bellwood 2013b), brings into question a purely reproductive role of pairing (Brandl & Bellwood 2013b, 2014b). This is further supported by the occurrence of eight individuals arranged in mixed-species pairs, including Siganus doliatus with S. corallinus and S. doliatus with S. punctatus. Mixed-species pairs have been reported for few other reef fish species (Whiteman & Côté 2004; Allen et al. 2003; Brandl & Bellwood 2014b), but have not yet been observed in rabbitfishes. The presence of such pairs strengthens the hypothesis that the pair bond in rabbitfishes is not solely due to reproductive advantages (Brandl & Bellwood 2013b; Fox et al. 2015), as these fishes are probably neither sexually mature (Brandl & Bellwood 2013b), nor reproduc-tively compatible. Yet, the lack of these pairs in the largest size class suggests that individuals then reshuffle into intraspecies pairs, possibly due to an increasing importance of securing a reproductive partner (but see Fox et al. 2015). Overall, the presence of mixed-species pairs in juvenile rabbitfishes and the lack thereof in adults suggests that this behaviour is restricted to sexually immature individuals, and reinforces the potential ecological importance of pairing in rabbitfishes (Brandl & Bellwood 2015).

In terms of the size-specific distribution of juvenile rabbitfishes across sites, the data from the present study corroborate Woodland’s (1990) anecdotal observations regarding the settlement and the following ontogenetic shift in habitat use for reef-associated rabbitfishes. The smallest individuals (newly settled recruits) are predominantly found solitarily or in schools in shallow, protected habitats. They then appear to move progressively into more exposed and deeper habitats. A similar trend has been observed in the juveniles of other herbivorous coral reef fish species, such as Acanthurus triostegus (Linnaeus, 1758) (Acanthuridae) and Chlorurus spilurus (Valenciennes, 1840) (Lecchini & Galzin 2005), and distinct site-specific differences in the size of juvenile C. spilurus on Lizard Island have been reported (Crook 1999b). While depth and exposure have previously been cited as determinants of juvenile rabbitfish abundance and distribution (Woodland 1990), both factors are likely to be correlated with a range of different biotic and abiotic factors, which may influence juvenile fish settlement and survival (e.g. habitat composition, predation pressure, food resources or larval supply; Crook 1997a, 1997b, 1999a, 1999b). As our study was conducted over a limited timeframe, we are unable to attribute the size-specific distribution patterns to any particular factor, also precluding us from determining the ultimate cause of the demonstrated patterns (settlement preferences and subsequent movement, or differences in post-settlement mortality). Although previous research on other species of coral reef fishes demonstrates high post-settlement mortality (Connell & Jones 1991; McCormick & Hoey 2004), other results point towards successive movement of individuals between habitats (Lecchini & Galzin 2005) or a substantial increase in home-range size (Welsh et al. 2013). Based on our data, we suggest a potential decline in mortality rates or an increase in mobility after juveniles reach 50 mm TL, as the two larger size classes (50–100 mm TL and 100–150 mm TL) did not display distinct distribution patterns. However, more research is needed to determine the factors underpinning the size-specific distribution patterns and the correlated social associations demonstrated in the present study. For example, interspecific competition with damsel-fishes (Pomacentridae) has been shown to influence the distribution of juvenile parrotfishes (Feitosa & Ferreira 2015), and is known to affect the foraging behaviour of adult rabbitfishes (Casey et al. 2014).

Overall, the present study leads to two important questions. First, our results raise the question of why juvenile rabbitfishes are pairing. Strong pairing behaviour in sexually immature individuals and taxonomic mismatches indicate that the drivers of pairing behaviour in rabbitfishes reach beyond sexual reproduction, although increasing prevalence of pair bonding in older individuals connotes that the latter is likely to play a role. Second, the movements and/or mortality rates of juvenile rabbitfishes over the course of their ontogeny warrant examination in order to reveal the reason for the observed size-specific distribution. Answering these questions will shed light on factors that underpin the unique ecological strategy of pairing rabbitfishes, and help elucidate the processes governing the abundances and distribution of adult fishes.

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