

Changing otolith/fish size ratios during settlement in two tropical damselfishes

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Abstract Otolith–fish size (O–L) relationships were analysed in recruits of two damselfish species (*Chrysiptera rollandi* and *Pomacentrus amboinensis*) before and after cohorts had settled onto reefs surrounding Lizard Island in Australia’s Great Barrier Reef. Unexpectedly, O was found to be unrelated to L in pre-settlers of both species. Settlers sampled only 12–15 days later, however, exhibited the expected isometric O–L relationship. This intriguingly rapid change—due to either variable growth, selective mortality or a combination of both—renders otolith increment widths inconsistent proxies for daily somatic growth rates in the pre- versus post-settlement stages of these pomacentrids.

Keywords Otolith microstructure analysis · Settlement · *Chrysiptera rollandi* · *Pomacentrus amboinensis* · Selective mortality

Introduction

Settlement comprises an incisive event in the early life history of many tropical reef fishes. The distinct change from the planktonic larval to the benthic juvenile life requires a suite of physiological and behavioural

adaptations and is typically associated with substantial initial mortalities (e.g. 60% in 24 h, Meekan et al. 2010) in naive settlers (McCormick and Makey 1997; McCormick and Holmes 2006). Mortality may be highly selective for slower or faster growing individuals or favour certain behavioural traits (Gagliano et al. 2007) and is influenced by spatially and temporally varying environmental conditions, particularly by patchy predator assemblages (Villegas-Hernandez et al. 2008; Holmes and McCormick 2010; Meekan et al. 2010). Because of its potential to alter population abundance and characteristics over a very short time period, settlement remains an important research focus of fishery biologists and reef ecologists alike.

Otolith microstructure analysis has been a powerful tool to study settlement dynamics, because it allows reconstruction of past growth on the individual level, which is critical for separating growth from mortality-related processes. The ability to infer previous somatic growth rates from otolith microstructure analysis depends on (a) the daily periodicity of increment formation and (b) the proportionality of otolith and somatic growth. The first is best demonstrated experimentally, while the second is often assumed if an isometric relationship between otolith and fish size can be demonstrated in a specimen sample (e.g. Meekan and Fortier 1996; Wilson and Meekan 2002).

Intriguingly, while analysing otoliths of two pomacentrid fishes from the Great Barrier Reef (GBR), otolith and fish sizes were found to be unrelated in young recruits prior to settlement. In contrast, successful settlers sampled from the same recruitment pulse only few days later showed a strong isometric relationship. The goal of this communication is to demonstrate the sudden change in otolith/fish size ratios during settlement and to discuss the two general, mutually non-exclusive hypotheses that warrant further investigations.

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Materials and methods

Annual peak recruitment pulses of two common Indo–Pacific coral reef fish, i.e., Ambon Damsel (*Pomacentrus amboinensis*, Pomacentridae, Bleeker, 1868) and Roland's demoiselle (*Chrysiptera rollandi*, Pomacentridae, Whitley, 1961), were sampled in November 2005 and December 2007, respectively, on Lizard Island in the northern GBR of Australia (14°41'S, 145°27'E). Newly metamorphosed and ready to settle *C. rollandi* and *P. amboinensis* (hereafter referred to as pre-settlers) were captured by light traps (for trap design see Meekan et al. 2001) deployed at night approximately 1 m below sea surface and 30–50 m outside the reefs surrounding Lizard Island. Pre-settlers collected during the night of the highest catches (peak of the recruitment pulse) were used for analysis. Successful settlers from this pulse were sampled 12–15 days later on the reefs surrounding Lizard Island by divers using SCUBA, hand nets and a mild anaesthetic (ethanol/clove oil mixture 5:1). Light-trapped and reef-collected specimens were immediately preserved in 70% ethanol.

In the laboratory, fish were measured for standard length (L, nearest 0.1 mm) using calipers, followed by the extraction of both sagittal otoliths. Choosing randomly left or right, thin transversal sections (following Gagliano et al. 2007) were then produced by grinding otoliths from both the anterior and posterior side with 3- μ m lapping film (PSA 3M). Daily otolith increments were counted along the longest axis of the cross-section, using Image-Pro Plus (V4.5 Media Cybernetics, Inc) and digital multi-frame images taken at different foci with a Nikon Eclipse E400 compound microscope (400 \times magnification) and a SPOT digital camera (Diagnostic Instruments, Inc). Increment counts were checked for consistency, (a) qualitatively against the interpretation of an experienced reader of damselfish otoliths and (b) quantitatively against a random subset ($n = 60$) of blind re-readings that indicated no systematic bias (CV = 5.5%). Otolith increment formation in both species is known to be daily starting at the time of hatch (Pitcher 1988). For this paper, increment counts were mainly used to ascertain that pre-settlers and settlers hatched within the same 20-day interval. Otolith size (O) in settlers and pre-settlers was expressed as the cumulative width of all increments, including the core to first ring distance. All linear regression and correlation analyses were done in PASW Statistics 18 (SPSS, Inc).

Results

C. rollandi

Ages in pre-settlers ranged from 15 to 21 days (mean = 17.4 days) and in settlers from 15 to 34 days

(mean = 22.1 days). Mean \pm SD L of pre-settlers and settlers was 9.7 ± 0.4 mm and 10.5 ± 1.1 mm, respectively. For settlers, a significant linear relationship, with randomly distributed residuals, was detected between O and L ($O = 24.9 * L - 8.9$, $r^2 = 0.83$, $n = 117$, $P < 0.001$, Fig. 1a). In pre-settlers, however, O was unrelated to L (Pearson correlation = 0.16, $n = 37$, $P = 0.36$, Fig. 1a). This discrepancy was not an artefact of the narrower size range in pre-settlers than settlers; if the settler sample was restricted to individuals <10.5 mm (i.e. L of the biggest pre-settler), the linear relationship was still highly significant ($r^2 = 0.63$, $n = 65$, $P < 0.001$). For settlers, O/L ratios plotted against L (Fig. 1c) showed the expected horizontal band of ratios unrelated to L (Pearson correlation = 0.09, $n = 117$, $P = 0.32$), whereas in pre-settlers O/L ratios were significantly and negatively correlated to L (Pearson correlation = -0.64 , $n = 37$, $P < 0.01$). For specimens <9.7 mm L, pre-settler and settler distributions still showed considerable overlap, whereas pre-settlers >9.7 mm L had progressively smaller otoliths than settlers of the same size (Fig. 1c). Age was either unrelated to O/L ratios in pre-settlers (Pearson correlation = 0.29, $n = 37$, $P = 0.09$) or only weakly related to O/L ratios in settlers (Pearson correlation = 0.3, $n = 117$, $P = 0.001$, Fig. 2). This supports the notion that sudden rather than gradual changes caused the shift in the O-L relationship during settlement.

P. amboinensis

Ages in Ambon Damsel pre-settlers ranged from 15 to 22 days (mean = 17.7 days), whereas 15 days later successful settlers were between 30 and 37 days old (mean = 32.8 days). Mean \pm SD L was 12.3 ± 0.6 mm in pre-settlers and 14.8 ± 1.2 mm in settlers. Settlers again exhibited a strong linear O-L relationship with randomly distributed residuals ($O = 21.2 * L + 36.3$, $r^2 = 0.63$, $n = 43$, $P < 0.001$, Fig. 1b), whereas in pre-settlers the O-L relationship was very weak, albeit statistically significant ($O = 6.0 * L + 171.3$, $n = 300$, $r^2 = 0.06$, $P < 0.001$). Consequently, as in *C. rollandi*, there was a clear contrast between length-independent O/L ratios in settlers (Pearson correlation = -0.11 , $n = 43$, $P = 0.49$) but decreasing O/L ratios with length in pre-settlers (Pearson correlation = -0.51 , $n = 300$, $P < 0.001$, Fig. 1d).

Discussion

The present findings suggest that an isometric otolith-fish size relationship in these pomacentrids is only established after recruits have settled into their benthic reef habitat. While ontogenetic changes in otolith versus somatic

Fig. 1 **a, b** Relationship between otolith size (O) and standard length (L) in pre-settlers (black dots, lines) and settlers (grey circles, lines) *C. rollandi* (a) and *P. amboinensis* (b), two common damselfish from the Great Barrier Reef, Australia. Only significant ($P < 0.05$) linear regression lines are shown. **c, d** Relationship between O/L ratios and L in pre-settlers versus settlers of both damselfish species. Lines depict the 10th and 90th percentiles of L-dependent cumulative probability distributions of O/L ratios calculated using locally weighted, non-parametric density estimators with varying bandwidths (0.18–0.36 mm). The non-parametric method is described in detail, e.g., in Pepin et al. (1999) or Evans (2000)

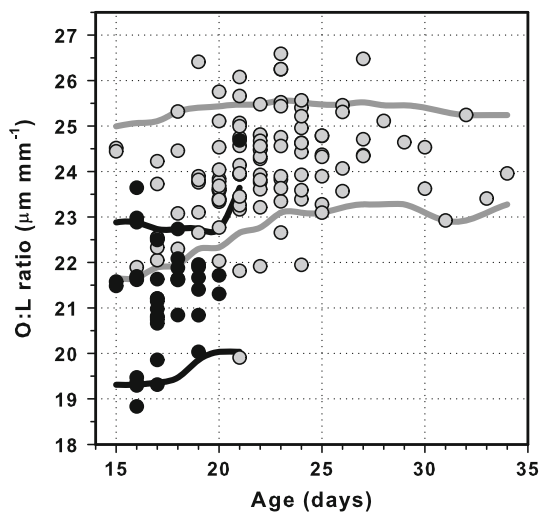
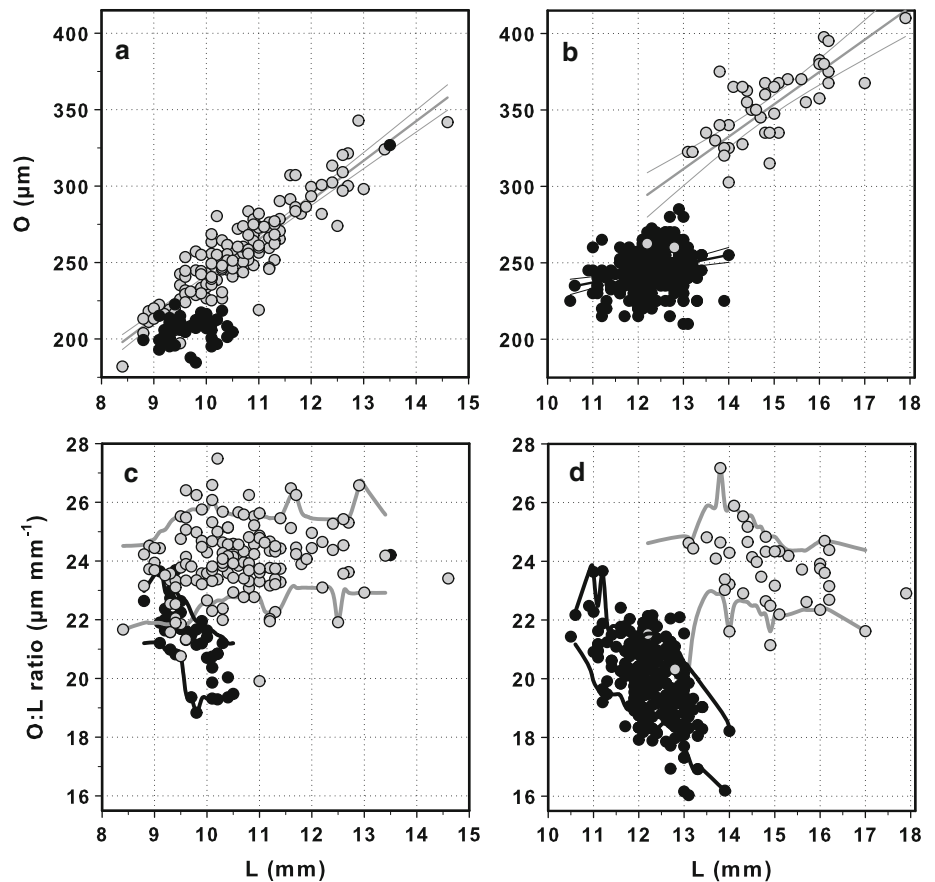


Fig. 2 *C. rollandi*. Relationship between O/L ratio and age. Lines depict the 10th and 90th percentiles of age-dependent cumulative probability distributions of O/L ratios calculated using locally weighted, non-parametric density estimators with a bandwidth of 2.5 days (Pepin et al. 1999; Evans 2000)

growth appear to be common in fish (Wright et al. 1990; Hare and Cowen 1995; Otterlei et al. 2002; Reglero et al. 2007), the present case highlights how quickly such shifts

can indeed occur in nature. Thus, settling tropical damselfish may comprise a particularly interesting group for studying whether those shifts are primarily caused by highly flexible growth patterns, strong selective mortality or a combination of both.

The growth hypothesis is supported by evidence that damselfish recruits settle over a range of different sizes and ages (Wilson and McCormick 1997) with energy allocation, and thus otolith and somatic growth still being highly flexible around their transition from pelagic to benthic life. Hence, individuals that settle at large sizes and with otoliths smaller than their already settled, same size conspecifics would be able to accelerate otolith relative to somatic growth and thereby eventually ‘catch up’ with the isometric relationship observed in successful settlers. There is evidence for flexible growth being indeed critical to survival in *P. amboinensis* (Gagliano and McCormick 2007). In addition, otolith and somatic growth are known slow down during settlement in many tropical reef fishes (Wilson and McCormick 1997), which potentially results in a temporary decoupling of both growth processes (Molony and Choat 1990; Baumann et al. 2005). Slower growing fish also exhibit generally larger otoliths than faster growing individuals of the same size (Secor and Dean 1989; Wilson et al. 2009). However, if flexible

growth would be the major explanation, one should expect to find settlers with transitional O/L ratios, particularly if sampling occurred within short periods of days to few weeks. In the present two cases, however, there was very weak evidence for such transitional stages.

Alternatively, individuals with otoliths ‘too small’ for their size might be selectively removed during the initial days of settlement; a period that inflicts particularly severe mortalities on naïve recruits (McCormick and Holmes 2006) and can thus quickly alter previously established patterns of size- and growth distributions (Schmitt and Holbrook 1999; Gagliano and McCormick 2007). Selection against low O/L ratios may simply be a by-product of selection against ‘too fast’ growers. Gagliano et al. (2007) and Meekan et al. (2010) showed that slower growing, newly settled *P. amboinensis* survived preferentially over fast growing phenotypes of the same size, arguably because the latter took higher foraging risks and hence suffered from higher vulnerabilities to predation. Fast growing fish tend to have low O/L ratios (Secor and Dean 1989; Francis et al. 1993; Wilson et al. 2009). Selection might also operate more directly, perhaps because individuals with smaller otoliths at size can navigate the 3-dimensional landscape of the new reef habitat less successfully and are thus more vulnerable to predators than conspecifics with bigger otoliths. Teleosts use otoliths to aid both hearing and orientation, and even small perturbations in symmetry or size may have functional consequences, as shown, e.g., for the ability of young pomacentrids to detect suitable reef habitat for settlement (Gagliano et al. 2008).

Our paper documented a consistent change in O/L ratios around settlement in two common, pomacentrid fishes from the GBR and discussed the two alternative but mutually non-exclusive mechanisms responsible for these patterns. Whether they are of general or just local importance depends on further empirical support from different species, years and regions. Advanced understanding may come from future studies trying to disentangle the two processes by contrasting field with parallel laboratory longitudinal observations of otolith versus somatic growth across settling cohorts. Until then, settler versus pre-settler comparisons of otolith-based somatic growth rates should be made with caution, since ‘increment width’ appears to be a different growth proxy prior and after settlement.

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