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REPORT

Effects of parasites on larval and juvenile stages of the coral reef fish *Pomacentrus moluccensis*

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Abstract The ecological role of parasites in the early life-history stages of coral reef fish is far from clear. Parasitism in larval, recently settled and juvenile stages of a coral reef fish damselfish (Pomacentridae) was therefore investigated by quantifying the ontogenetic change in parasite load and comparing the growth rates of parasitized juvenile fish to those of unparasitized ones. Parasite prevalence in two lunar pulses of *Pomacentrus moluccensis* was 4 and 0% for larval stage fish, 34 and 56% for recently settled fish and 42 and 49% for juveniles. A significant increase in parasite prevalence with age group was found; the most marked increase occurred immediately after larval fish had settled. Standard length did not model prevalence well; as length is a proxy for age, this indicates that the higher prevalence in recently settled and juvenile fish compared with larvae was not a simple result of parasites accumulating with age. In one of three cohorts, there was some evidence that parasitism affected the growth rate of juveniles, as measured by otolith width. The study suggests that settling on the reef exposes young fish to potentially harmful parasites. This supports the idea that the pelagic phase may have the effect of reducing the exposure of young fish to the debilitating effects of parasites.

Keywords Dispersal · Recruitment · Growth · Migration · Settlement transition

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Introduction

Mortality during the larval stage of marine fishes is almost absolute (Leis 1991). Little is known of the agents of this mortality, but it is suggested that most are eaten by predators (Bailey and Houde 1989; Leis and McCormick 2002). For many, predation is likely the ultimate result of a process precipitated by another agent that makes particular individuals more susceptible to predation by lowering larval body condition, growth, or performance (Searcy and Sponaugle 2000; Bergenius et al. 2002; McCormick and Hoey 2004). These agents potentially include starvation, disease, and parasitism. At present, little is known of the prevalence or importance of these agents on the condition of larval marine fishes, or how the prior history of infection may influence the performance and survival in later life stages (Leis and McCormick 2002).

Parasites are well known to affect the behaviour and ecology of adult fishes (see review by Barber et al. 2000). However, it has been predicted that the effect of parasites on fish larvae and juveniles will be greater than that on adults due to low body reserves and high relative metabolism of the small fish (Strathmann et al. 2002).

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Surprisingly, very little research has been done on the identity and load of parasites of fish larvae, and how parasites affect the growth, condition and survival of such fishes. The few studies involving parasites of fish larvae have been mainly descriptive. For instance, Felley et al. (1987) found copepods on post-larval menhaden (0.2%), anchovies (3%), and gobies (4%). Only a few studies have examined the effect of parasites on fish larvae. The prey uptake rate by herring larvae infected with cestodes is 50% lower than for uninfected fish (Heath and Nicoll 1991); indirect parasite-induced mortality in juvenile silversides infected by digenean worms was attributed to weight loss in fish which increased their risk of predation (Faliex and Morand 1994); infected larvae may suffer further stress from hydrodynamic drag as some parasites can be 40% of the length of the fish larva (Felley et al. 1987); anchovy larvae infected with caligids are smaller than uninfected larvae (Herrera 1990); and larval smelt with parasites in their gut eat half as much and are smaller, and as a result suffer higher rates of mortality than unparasitized ones (Sirios and Dobson 2000a, b).

However, not only is almost nothing known about the parasites of the larvae, even less research has been done on the parasites of coral reef fishes during the transition from the pelagic to benthic environment. To our knowledge, the following are the only published reports of parasites of larval and settlement-stage coral reef fishes. In Hawaii, surgeonfish larvae were infected with a hydrozoan (Randall 1961). On the Great Barrier Reef (GBR), caligid copepods infect larvae of gobiid and tripterygiids (Leis et al. 1993). In French Polynesia, Rigby and Dufour (1996) examined settling groupers for internal parasites and found a 4% prevalence of trypanorhynch and phyllobothriid metacestodes. In New Caledonia, settling fish had 13 parasite platyhelminth species with 23% of individuals from 38 species being infected (Cribb et al. 2000). In Mexico, larval reef fishes from 5 families were infected with trematode metacercariae (del Prado-Rosas et al. 2007). Finally, on Lizard Island, GBR, caged *Pomacentrus moluccensis* juveniles, placed on the reef over 4 consecutive time periods to determine if and when they were infected with micropredatory parasites, were found associated with gnathiid and cirolanid isopods at night only, and cirolanids were observed attacking and killing some caged fish (Jones and Grutter 2008); gnathiid isopods also occurred on very young *Acanthochromis polyacanthus* juveniles, a species that does not have a pelagic phase (Penfold et al. 2008).

The few studies examining the effect of parasites on young coral reef fish have involved reef-based isopods. On Heron Island, GBR, the mortality of juvenile *Chromis nitida* infected with the cymothoid isopod *Anilocra pomacentri* in the wild was 30% higher than for uninfected fish (Adlard and Lester 1994). Those that survived had retarded growth, lower gonadosomatic indices, and a fecundity that was 88% lower than that of uninfected fish. On Lizard Island, settlement stage or recently settled juveniles of several apogonid fishes infected with *Anilocra apogonae* had decreased growth and increased mortality compared with uninfected fish (Fogelman and Grutter 2008). Similarly, gnathiids decreased the survival of *Dischistodus perspicillatus* settlers but only on the first night of exposure and not after 8 days, while exposure to two gnathiids daily decreased fish growth after 8 days compared with fish exposed to one or no gnathiids (Jones and Grutter 2008). Gnathiids also decreased the survival of settlement stage larvae but not recently settled *Neopomacentrus azysron* (Grutter et al. 2008) and also that of juvenile *A. polyacanthus*, but only in fish <10-mm SL (Penfold et al. 2008). These results highlight the implications that parasite infection may have for young coral reef fish.

The bipartite or two life stage nature of the life cycle of demersal fishes means that individuals are likely to be exposed to different suites of parasites in the larval and juvenile phase (Polyanski 1961; Rigby and Dufour 1996). Indeed, it has been hypothesised that the evolution of dispersal enables terrestrial hosts to avoid debilitating parasites (Clobert et al. 2001). Recent studies proposed that parasitism of fish at the vulnerable larval stage may be a selective force in the evolution of the pelagic phase (Combes 2001; Strathmann et al. 2002). Migration of fish larvae into the water column could break some cycles of parasite transmission through separation of the parents and offspring. It may also lower transmission rates, as larval fish may be less suitable hosts due to their sparse distribution (Strathmann et al. 2002). Despite the potential importance of parasites to the population dynamics of coral reef fishes, little is known of the parasites that infect larval fish and how these change over the transition from larvae to juvenile stages. The few studies on this subject have found that they have nil to low prevalence of parasite infections and that parasite prevalence and diversity generally increases with age, possibly due to changes in habitat, behaviour, diet or increased host size (Rigby and Dufour 1996; Cribb et al. 2000; Sasal 2003).

The present study investigates the types and prevalence of parasites on the larval, recently settled, and juvenile stages of coral reef damselfish (Pomacentridae), and their impact on growth. Specifically, the aim was to: (a) identify and quantify the parasites of larval, recently settled, and juvenile lemon damselfish, *Pomacentrus moluccensis*; and (b) using otolith analysis, examine whether the growth rates of recently settled *P. moluccensis* are influenced by parasitism.

Materials and methods

Ontogenetic changes in parasite prevalence in *Pomacentrus moluccensis*

Host collection

Two lunar fish replenishment events, i.e., input of larvae onto the reef which leads to settlement, were sampled at Lizard Island on the northern GBR, Australia (14°40′S, 145°28′E) between December 2003 and January 2004. Larval samples from the first lunar month (23–28th December 2003) were collected with light traps (Fig. 1 in Meekan et al. 2001) that were moored ~200 m away from the reef, in 8–12 m water over sand. Traps were set out overnight and emptied each morning (0700 h). Larval samples for the second lunar month were collected by dip netting (mouth size: 250 × 500 mm, 1 mm mesh size) around an 8-W waterproof fluorescent light tube between 2130 and 0100 h. This method was selected because it allowed the rapid capture of individual fish, reducing the risk of loss of ectoparasites. Specimens were immediately placed in individual 5-ml vials, euthanized in an ice slurry and fixed with 70% ethanol.

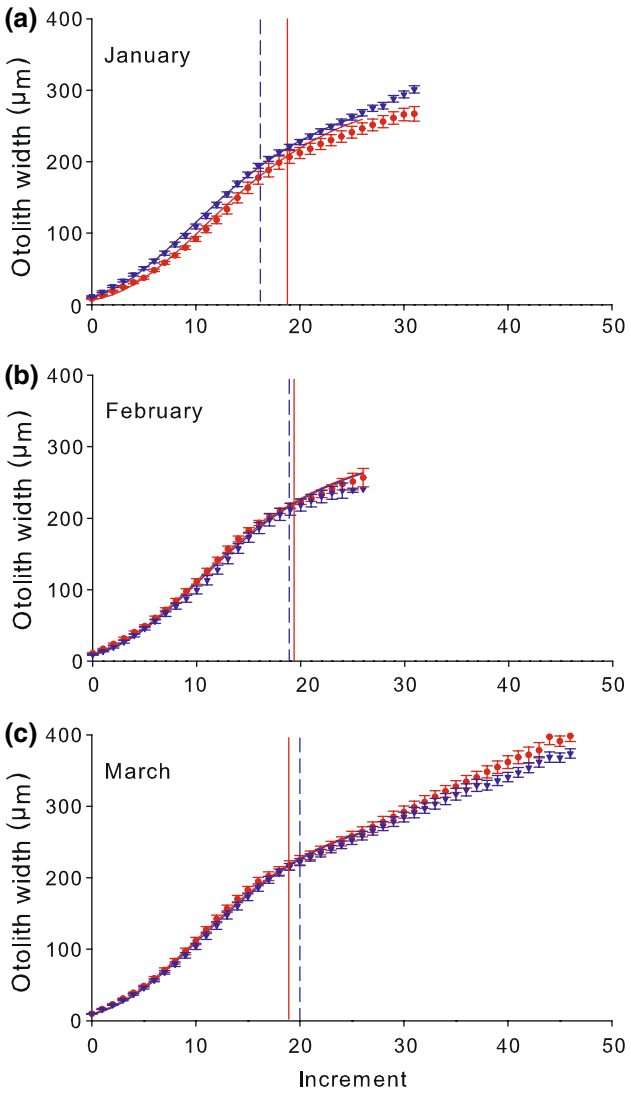

Fig. 1 Growth, since hatching, of *Pomacentrus moluccensis* juveniles collected from the Lizard Island backreef. Mean otolith width (microns) as a function of increment number or days since hatching for parasitized (*red circle symbols*) and unparasitized (*blue triangle symbols*) juveniles in January (**a**), February (**b**), and March (**c**). The best fit Gompertz curve is shown for parasitized (*solid red line*) and unparasitized (*dashed blue line*) juvenile growth over the first 26 increments, the number being used to ensure compatibility with the February data, for which only 26 intervals were available. *Vertical lines* represent the mean age at settlement for parasitized (*solid red*) and unparasitized (*dashed blue*) fish

During January, February and March 2004, recently settled and juvenile fish were collected by handnet from shallow reef habitats. No anaesthetic was used to reduce loss of ectoparasites during the capture process. Fish were transferred individually into click-sealing plastic bags (50 × 75 mm) and transported back to the research station on ice. Specimens were preserved in 70% ethanol in individual 5-ml vials. The contents of the plastic bags were rinsed with seawater and examined for parasites under a dissection microscope (20×). Parasites were placed in individual 5-ml vials and fixed with 10% formalin in seawater for identification. The parasites of these fish were compared with those of adult *P. moluccensis* collected previously (Grutter 1996 and this study).

Parasite identification

Both external and internal parasites were identified to species where possible. The body and fins and gills of the fish were examined at 40× magnification. The gut was removed and examined for endoparasites; the body tissues were examined also by tearing the tissue apart with fine forceps. Standard lengths (SL) of each fish were measured with callipers (±0.5 mm) before dissection.

Sections of some gills were prepared for microscopic examination by dehydrating the tissue using an ascending series of absolute ethanol (70, 90, 100, 100%) for 30 min each, followed by two changes of the clearing agent Xylene for an hour at 45°C, and two changes of Paraffin wax at 45°C for one hour each; the second change of wax being in a 58°C vacuum oven. A series of sections (6 µm) were taken of the gills and stained with haematoxylin and eosin.

The proportion of parasitized and unparasitized fish for each age group (larval, recently settled, juvenile and adult), standard lengths and collection date were compared using binary logistic regression (BLR) analysis with the software *MINITAB 14* with the response variable being the presence or absence of infection.

Parasite presence and size, growth, and settlement age of fish

Otolith analysis

Sagittal otoliths were dissected from a subsample of randomly selected infected and non-infected recently settled and juvenile fish, cleaned of endolymph tissue, rinsed in ethanol, dried, stored individually in containers and processed as described by Wilson and McCormick (1997). One sagitta was randomly selected from each fish. Fish age (days) was estimated by counting the number of increments starting from the nucleus. The dark bands under transmitted light were counted as the end of the increments. Daily formation of increments have been validated for *P. moluccensis* (Pitcher 1988). Otolith growth was used as a proxy for fish growth rate under the assumption that there was a direct correspondence between otolith and somatic growth. A previous study showed that there was a close relationship between radius of the sagitta and SL in this species ($r^2 = 0.93$, $p < 0.001$, $n = 156$, Brunton and Booth 2003). Sagittal otolith sections were photographed on a compound microscope (1000× magnification). Otolith growth rate was then quantified by measuring the width of each increment (daily ring) along the longest axis from the nucleus to the margin using image analysis software (Optimas 6.5).

The otolith growth was compared between *P. moluccensis* that, after being surveyed for parasites, showed no sign of being parasitized at the time they were euthanized and fish that had external or internal parasites. Comparisons of otolith growth between parasitized (internal plus external) and non-parasitized fish were made for each month (sample size with internal, external, internal plus external parasites/no parasitises) of collection (January (6,0,0/21), February (4,10,2/6) and March (5,3,0/14)). Gompertz growth curves were fitted to the otolith growth data for each individual *P. moluccensis* juvenile, using the functions "SSGompertz" and "nls" in R version 2.6.1 (R Development Core Team 2007). The function is shown in Eq. 1, where $W(t)$ is the cumulative otolith width at time t, W_∞ is the asymptotic width and b_2 and b_3 are growth parameters.

$$W(t) = W_\infty \exp\left(-b_2 b_3^t\right) \quad (1)$$

The growth series in the months of March and January were truncated to 26 intervals to ensure compatibility with the February data, for which only 26 intervals were available. Values of the estimated parameters were compared between months and between parasitized and unparasitized larvae using linear models.

Age at settlement was assumed to be represented by a substantial decrease in the width of increment. One-way ANOVAs were used to test for equality of the first increment width (otolith nucleus), age at settlement, and otolith width at settlement between parasitized and non-parasitized fish. Assumptions of homogeneity of variance and normality were examined using residual analysis. Growth of otoliths was also analysed as a function of days post settlement. As the relationship between otolith width and time since settlement was linear, a linear mixed effects "random slopes" model (Pinheiro and Bates 2000) was used, fitted with maximum likelihood, implemented using the function "lmer" in R package "lme4" (Bates et al. 2008).

Results

Ontogenetic changes in parasite prevalence in *Pomacentrus moluccensis*

Parasite prevalence in two lunar pulses of *P. moluccensis* was 4 and 0% for larval stage fish, 34 and 56% for recently settled fish and 42 and 49% for juveniles (Table 1). Of the adults, 74% were parasitized. Representatives from four groups of parasites: Trematoda, Turbellaria, Cestoda and Copepoda were found on or in *P. moluccensis* (Table 2). No protozoan, bacterial or viral infections were visible. Only two individuals from the larval group had parasites (Table 2). One hosted a digenean trematode, *Tergestia* sp. (Fellodistomidae), in the gut and the other an unidentified digenean metacercaria in the gill cavity. Fifty-five percent of larval fish collected in January had unidentified cyst-like structures that had deformed the gill filaments. We found no evidence that these were produced by parasites.

Turbellarians varied in prevalence among post-settlement stages: 17.8% (recently settled), 5.1% (juveniles), and 20.7% (adults) (Table 2). Turbellarians were unidentifiable beyond class due to the lack of any apparent internal features. The copepods also could not be identified because they were only at the copepodite stage. Prevalences of copepodites were 7.9% for recently settled and 25.3% for juveniles, ranging from 1 to 3 per host (Table 2). Copepod prevalences on adult *P. moluccensis* ranged between 2.4% (Copepod sp. b) and 52.4% (Copepod sp. a), with a range of 1–8 per host fish.

Endoparasites were present at prevalences of between 5.9 (recently settled) and 12.1% (juveniles) for the digenean *Aponurus laguncula* (Lecithasteridae) that was found in the gut (Table 2). Digenean metacercariae were also found in the gill cavity or gut with prevalences of between 0.9 and 9.9% (Table 2). While most metacercariae could not be identified, bucephalid metacercariae were identifiable by the mouth and pharynx being positioned in the middle of the body. Only one metacercaria was identifiable to genus; *Dollfustrema* sp. was identified based on the

Table 1 Parasite prevalence in four age groups of *Pomacentrus moluccensis* from Lizard Island, Great Barrier Reef

Age group	Collection date	Mean SL (mm)	±SE	*n*	Parasite prevalence (%)
Larval	23rd–28th December 2003	11.47	0.10	50	4
	20–25th January 2004	10.80	0.11	60	0
Recently-settled	6–12th January 2004[a]	14.81	0.21	50	34
	1st–4th February 2004[a]	11.99	0.15	50	56
Juvenile	7–10th February 2004[a]	16.61	1.72	49	49
	11–15th March 2004[a]	18.77	0.29	50	42
Adult[b]	19–30th October 1993	37.64	0.50	164	74

SL standard length; *n* number of fish examined

[a] A subsample of these fish were the "January", "February", and "March" fish used in the growth analyses (See Figs. 1, 2)

[b] Adult data is from Grutter (1996) and this study

Table 2 Parasites of larval, recently settled, juvenile and adult stage *Pomacentrus moluccensis* from Lizard Island

Parasite	Larval fish $n = 110$		Recently settled fish $n = 100$		Juvenile fish $n = 99$		Adult fish[a] $n = 164$	
	%	(Range)	%	(Range)	%	(Range)	%	(Range)
Copepoda								
Hatschekia crenulatus							3.1	(1–2)
Copepod sp. a					3	(1)	52.4	(1–8)
Copepod sp. b							2.4	(1)
Copepod sp. c							9.8	(1–2)
Copepodite			7.9	(1–2)	25.3	(1–3)		
Platyhelminthes								
Cestode larvae			1	(1)	1	(1)	1.2	(1)
Turbellaria			17.8	(1–3)	5.1	(1–2)	20.7	(1–4)
Digenea								
Transversotrema licinum							2.4	(1)
Aponurus laguncula			5.9	(1)	12.1	(1)		
Tergestia sp.	0.9	(1)						
Bucephalid Metacercaria			1	(1)				
Dollfustrema sp.? Metacercaria			1	(1)				
Other Metacercaria	0.9	(1)	9.9	(1–2)	6.1	(1)		
Other Digenean							1.8	(1)
Cysts								
Gill cyst			1	(1)	2	(1)	25.5	(1–5)
Gut cyst			5	(1)				
Tissue cyst			4.9	(1)	9.1	(1–2)	5.5	(1–3)
Other					1	(1)	1.2	(1)

Parasite prevalence (%), and range of parasites per infected host given

n Total number of fish examined

? Signifies a tentative identification

[a] Adult ectoparasite data is from Grutter (1996) and this study; endoparasites were not recorded in Grutter (1996)

rhynchus having three to four circlets of short spines and the mouth positioned in the posterior half of the body. An unidentifiable cyst was also found to vary in occurrence within the body tissue (4.9–9.1%), gills (1–25.5%) and gut (5%) in all four age groups (Table 2). Digeneans were the only parasite group observed in all life stages of

P. moluccensis, ranging from between 1 and 2 per host fish and prevalences of between 0.9 and 12.1% (Table 2).

Relationship between host age class and parasite prevalence

Parasites were present in *P. moluccensis* from all four age groups and both cohorts, except for the larval age group of the January cohort (Table 1). As any individual parasite taxon was present at low prevalence and mean intensity of infection was also low (Table 2), fish were simply classified as either "parasitized" or "unparasitized" for analysis. There was no evidence that, within age groups, collection date affected parasite presence. Parasite prevalence differed significantly among age groups (larval, recently settled, juvenile, and adult) (Δdev = 83.07, $df = 3$, $P < 0.0001$) with prevalence in adults (74%) being significantly higher than in all other age classes. Prevalence did not differ between juvenile and recently settled fish but was significantly lower in larvae (Wald statistic = −4.375, $P < 0.0001$).

Table 3 shows results of logistic modelling of parasite prevalence as a function of month of collection, standard length and life history stage, for the dataset collected during 2003–2004. Prevalence was significantly lower in larvae than in recently settled and juvenile fish pooled, but models including all three life history stages did not perform better. Standard length did not model prevalence well, either when it was fitted on its own or in addition to life-history stage. As length is a proxy for age, this indicates that the higher prevalence in recently settled and juvenile fish compared with larvae was not a simple result of parasites accumulating with age. Month of collection was a poor predictor on its own, but explained some variation within life history category.

Parasite presence and size, growth, and settlement age of fish

Linear models, including interactions, were used to compare estimated Gompertz growth function parameters between months and between parasitized and unparasitized fish. These analyses showed no indication of significant effects for the asymptotic width of the otolith W_∞ or for the growth parameter b_3. However, the model for the growth parameter b_2 was significant overall ($F_{5,65} = 2.63$, $P = 0.03$). This was due to a highly significant interaction between the collection month and infection status ($F_{2,65} = 5.82$, $P = 0.004$). Further, a model including all 3 months performed no better than one contrasting the collection month of January with the other 2 months. Thus, the effect of parasitism on the otolith growth rate was different in January than in the other 2 months (which did not differ from each other). Inspection of Fig. 1 shows that, in January, parasitized fish had slower otolith growth rates than unparasitized fish, but this was not the case in February and March when the growth curves were almost identical between parasitized and unparasitized larvae. Growth curve shapes were similar in all months. The growth departed from the Gompertz curve towards the end of the data series in all 3 months, which is an evidence of some polyphasic growth at this time.

Interestingly, there was a difference in the width of the otolith nucleus (i.e., $t = 0$) between parasitized and non-parasitized fish in January, with fish that had internal parasites having smaller otoliths at hatching ($F_{1,20} = 7.363$, $P = 0.013$). These fish were between 28 and 31 days old at the time of capture. There was also a difference in age at settlement between parasitized and non-parasitized fish in January, with fish that had internal parasites being older (mean ± SE, 18.8 ± 0.9 days) than unparasitized fish

Table 3 Logistic modelling of prevalence of infection as a function of month of collection, standard length and life history stage, for *P mollucensis* collected from Lizard Island between 2003 and 2004

Model number	Model terms	AIC	*D df* from model 1	*D* deviance from model 1	*P*
1	Larva	292.35	–	–	
2	Larva + month	290.12	3	8.23	0.041
3	Stage	294.32	1	−0.028	0.867
4	Larva + SL	294.33	1	−0.017	0.897
5	Larva * SL	295.91	2	−0.439	0.803
6	Month	316.89	2	20.533	
7	SL	346.49	0	54.14	
8	–	369.94	1	79.59	~0.00

Models with differences in Akaike Information Criterion (AIC) values of less than two are similar in their ability to describe the data, while differences in AIC values of greater than two indicate that one model is considerably better supported by the data (Burnham 2002). "Larva" is a binary variable contrasting larval fish with the other life history stages, whereas "stage" compares all three life-history stages. *P* tests as H_0 the model with "larva" alone versus other models. The operator * includes interactions

(16.3 ± 0.4 days) ($F_{1,25} = 6.782$, $P = 0.015$) (Fig. 1a). Otolith width at settlement, however, did not differ with parasite presence in January. Otolith nucleus and age and otolith width at settlement did not differ with parasite presence in February and March (Fig. 1b, c).

Otolith width increased linearly as a function of days since settlement for each of the January, February and March cohorts (Fig. 2). As a likelihood ratio test showed that the effect of parasitism on otolith growth differed between the cohorts ($\chi^2 = 8.39$, 2 *df*, $P = 0.01$), the effect of parasitism on growth since settlement was analysed separately for each cohort. The increase in otolith width after settlement was greater in unparasitized fish than in parasitized fish in the January cohort (likelihood ratio test: $\chi^2 = 6.59$, 1 *df*, $P = 0.01$). There was, however, no evidence of a similar effect in either the February cohort ($\chi^2 = 0.96$, 1 *df*, $P = 0.32$) or in the March cohort ($\chi^2 = 0.54$, 1 *df*, $P = 0.46$).

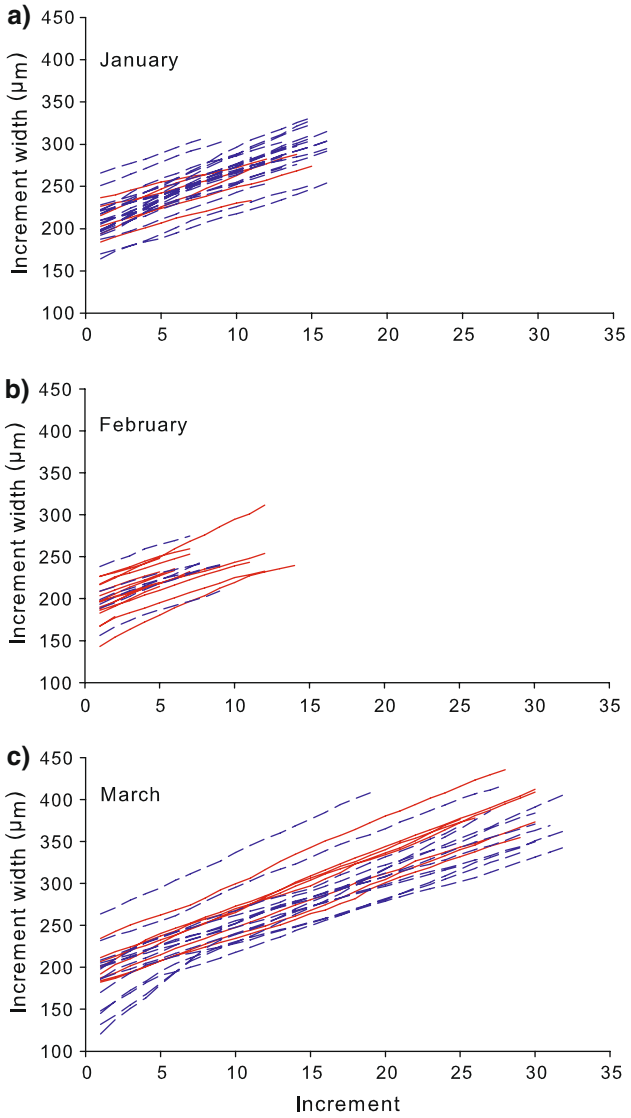

Fig. 2 Growth, since settlement, of *Pomacentrus moluccensis* juveniles collected from the Lizard Island backreef. Mean otolith width (microns) as a function of increment number or days since settlement for parasitized (*solid red*) and unparasitized (*dashed blue*) juveniles in January (**a**), February (**b**), and March (**c**)

Discussion

The results are consistent with the hypothesis that the pelagic larval stages of the damselfish *P. moluccensis* have less exposure to parasitism than do post-settlement stages. Parasite prevalence in *P. moluccensis* increased dramatically from a maximum of 4% for the larval pelagic stage to a maximum of 56% for the recently settled demersal stage. Parasite species richness also increased from two to eight. Although larval fish were collected with light traps in December 2003, then by dip netting in January 2004 to prevent potential losses of external parasites in light traps, only internal parasites were found on fish and these were in fish that had been sampled with light traps. Most of the increase in parasite prevalence upon settlement found here can be attributed to infection by ectoparasitic copepods and turbellarians. Although 165 adult individuals of *P. moluccensis* were examined for this study, they were not examined for gastrointestinal parasites. It is noteworthy that elsewhere *P. moluccensis* has been shown to have a rich fauna of adult trematodes. Six species of trematodes were recovered from a sample of 20 individuals examined at Heron Island on the southern Great Barrier Reef (Barker et al. 1994; Bray et al. 1993). Although the trematode fauna of the northern and southern GBR are by no means identical (e.g., Nolan and Cribb 2006a, b), it can be expected that most of these species, and perhaps some others, will also occur at Lizard Island. Thus, the overall parasite richness in adult *P. moluccensis* is likely to exceed that of the larvae and juveniles by even more than has been revealed here. Similarly, Sasal (2003) found that grunts were not infected with monogeneans when they settled on the reef, only acquiring them at 40 mm SL.

This increase in infection prevalence and parasite diversity after settlement presumably reflects the shift in habitat, increased transmission associated with greater host density, or changes in host susceptibility to infection with ontogeny. Reef environments are more structurally complex than the pelagic environment, thus they likely provide more habitats for a greater diversity and density of parasite species. Furthermore, susceptibility to ectoparasites may be directly proportional to fish size. The small size of larval *P. moluccensis,* such as those that were sampled (10.8–11.5 mm), may impede attachment by ectoparasites (such as copepods) to gills or appendages because their hooks may be too large to fasten to tissue successfully. In

Caribbean French grunts 14–96 mm SL, only juveniles >40 mm SL (90 days old) were infected with monogenean worms (Sasal 2003).

An alternative explanation for a lower prevalence of parasites in larval stages is that direct or indirect mortality as a result of parasitism may be greater in larval stages than in post-settlement stages, resulting in fewer infected individuals surviving to be collected. Thus, the low parasite prevalence observed in larval fish may be a result of parasitized individuals being removed from the population through predation. This hypothesis requires greater efficiency of predation of larval fishes in open waters than of juvenile fishes on reefs; we see no reason to predict that this would occur.

Although many studies have found that hosts generally acquire and keep parasites over time (Rohde 1993), the distinction in prevalence of parasites between larval and juvenile fish does not appear to be explicable by reference to a model of parasite accumulation with age. Fish standard length, a proxy for age, did not explain the variation in parasite prevalence well. Thus, the higher prevalence of parasites in recently settled and juvenile fish compared with larvae was not a simple result of parasites accumulating with age.

The observation of very few parasite infections (up to 4%) in larval *P. moluccensis* is similar to that reported in Mexico where 5% of fish, which were sampled with a plankton net in the reef edge lagoon, were infected with metacercariae (del Prado-Rosas et al. 2007). Our results, however, are in contrast to the high prevalence of parasite infection in a study of parasites of recruiting coral reef fish in New Caledonia (Cribb et al. 2000). Recruits collected from crest nets were found with infection levels of up to 71% (Scorpaenidae), 65% (Labridae) and 32% (*Thalassoma* sp., Labridae) (Cribb et al. 2000). Indeed, the infection levels of scorpaenid and labrid recruits were higher than the ones we found in recently settled fish. A partial explanation for this difference may be that nets on the reef crest will collect fish exposed to a more concentrated array of plankters or benthic parasites than samples collected by our light traps or dipnets, which were placed or used, respectively, over sand, some distance from the reef itself or by plankton nets away from the reef edge in Mexico (del Prado-Rosas et al. 2007). This difference in prevalence of infections between studies may also be due to differences in the pelagic larval duration (PLD) of the fishes examined, as species with a longer pelagic phase would have a greater chance of encountering a parasite before settlement. *P. moluccensis* has a relatively short PLD of between 15 and 23 days (Wellington and Victor 1989; Wilson and McCormick 1999), whereas the fish families sampled by Cribb et al. (2000) have larval durations of between 24 and 54 days (Wilson and McCormick 1999). However, it should be noted that relatively low parasite prevalences (3–12%) were found for honeycomb grouper, *Epinephelus merra* (Serranidae) recruits from French Polynesia (Rigby and Dufour 1996). Larval duration for a closely related species, *Epinephelus corallicola,* is 41 days (Wilson and McCormick 1999). Whether these differences in parasite prevalence are instead due to phylogenetic differences needs to be determined. A comparison of more species and of species that have a variable pelagic larval duration, while accounting for phylogeny, is necessary to understand whether PLD influences parasite infection. Alternatively, the differences in parasite prevalence observed among the studies may simply be due to geographic variation in parasites, a common occurrence in adult coral reef fishes (Grutter 1994; Rigby et al. 1997).

Representatives of the Digenea were found throughout all life stages of *P. moluccensis,* including larval fish. The digenean metacercaria found in the gill cavity of a larval individual had the potential to develop into an adult digenean if a definitive host, such as an adult fish or bird consumed the host (Rohde 1993). Such parasitism of larval fish is thought to be of greater importance to the dispersal of parasites to new reef environments than infected adults, which are site-attached, or the free stages of parasites that do not have sufficient longevity to successfully disperse (Rigby and Dufour 1996; Cribb et al. 2000). Previous studies of recruiting and recently settled reef fish have concluded they mainly have parasites with pelagic life cycles which would not be transferred to adults of the same populations (Rigby and Dufour 1996; Cribb et al. 2000).

Parasite presence and size, growth, and settlement age of fish

There was some evidence that the growth, as measured by otolith width, of recently settled juvenile *P. moluccensis* was influenced by the presence of internal parasites but only in one (January) out of three cohorts. Here, fish with internal parasites had lower larval growth than those without parasites when growth rates were estimated from hatching or from after settlement. However, inspection of Figs. 1 and 2 shows that the difference in growth was relatively small and the growth curves were almost identical for infected and uninfected fish in the other months. Also, in January only, parasitized fish were older than unparasitized fish at time of settlement, however, otolith radius to the settlement mark, a proxy for fish size at settlement (Wilson and McCormick 1999) did not differ with parasite infection. This supports our finding that parasitized fish grew more slowly in January, as slower growing fish would have required more time to grow to the same size as unparasitized fish at settlement. Comparisons of otolith growth rate parameters between months require some caution as differing cohorts of larval

fish may have different relationships between otolith growth and somatic growth rates (Campana and Jones 1992). This means that the main effects of month on the growth rate parameters may not be a meaningful representation of differences in somatic growth rates between months. However, the significance of the month–parasitism interaction term on the rate parameter b_2 can be interpreted as indicating that the effect of parasitism on this component of the growth rate differed between collection months. Similarly, the significant interaction between growth rate after settlement, parasitism, and cohort indicates that the effect of parasitism on the growth rate post settlement differed between collection months. These findings are consistent with two explanations, either: (1) parasites have infected all fish regardless of growth history, but the fastest growers have subsequently died; or (2) parasites preferentially infect fish that have a history of low growth. However, there is mounting evidence for tropical fishes that larval growth history influences larval and juvenile survival. In keeping with the growth-mortality hypothesis (Anderson 1988), many studies have found that high larval growth leads to higher survival (Bergenius et al. 2002; Hoey and McCormick 2004; McCormick and Hoey 2004; Raventos and Macpherson 2005). In contrast, a recent study has shown that selection on growth during the larval phase of a tropical damselfish was generally against fast growers, suggesting that slow growth, whether the cause is intrinsic or parasite-related, may be advantageous to larval survival (Gagliano et al. 2007). The behavioural correlates of slow growth, such as low metabolism and activity (e.g., Biro et al. 2007), may have made fish with slow growth more susceptible to infection by internal parasites. Thus, it was not possible to differentiate between the first two scenarios based on present data. Because there were few fish with the same parasite type, it was not possible to test for differences in the effect of parasites on growth among parasite types. Smaller sample sizes in February and March and more variation in the types of parasites compared with the January samples (internal only) may explain the differences among months. The relatively small sample size for parasitized fish in January means that the power of the analysis to detect differences in the growth rates is rather low. Herrera (1990) found that the lengths of anchovy larvae infected with copepod larvae were below the average growth function for non-parasitized fish; however, their growth rates from time of hatching are unknown, and the infections were considered to be accidental as fish were too small for copepods to fully develop. Rigby and Dufour (1996), in contrast, found no difference in length between larval fish with and without internal parasites. We acknowledge, however, that the growth results may be spurious ones due to the small sample sizes involved. Larger sample sizes of fish for parasite surveys and manipulative experiments are needed to examine the effect of different types of parasite infection on young coral reef fish.

In contrast to results of previous studies in the Pacific (Rigby and Dufour 1996; Cribb et al. 2000), the parasite fauna of larval fishes at Lizard Island was depauperate. This was despite the fact that the exterior surface of fish, the gills, and the gut cavity were all surveyed for parasites, unlike Rigby and Dufour (1996) that only surveyed internal parasites. The basis for such differences needs further exploration, specifically whether it is due to methodological, geographic, or phylogenetic factors.

In conclusion, the parasite fauna of reef fish develops very rapidly in abundance and diversity immediately after settlement onto the reef. These findings highlight the ecological importance of parasitism on early stage coral reef fish, and support the idea that the pelagic phase may allow young fish to avoid reef-based parasites (Strathmann et al. 2002).

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