

Post-settlement growth and body composition in relation to food availability in a juvenile tropical reef fish

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ABSTRACT: *Pomacentrus amboinensis* is an abundant, predominantly planktivorous reef fish which settles into a range of habitats from sheltered lagoons to exposed windward reefs. Recruits are exposed to differences in food availability as a function of the physical dynamics of the habitat. This study examines the effects of a variable food supply on somatic development and the deposition of energy reserves in recently settled fish. Food availability had a complex and significant effect on levels of energy reserves. Trends in lipid content between treatments were similar to those for somatic growth. A 3.5-fold difference in total lipid existed between fully fed and field fish. The lipid content of field fish was similar to starved fish. Trends in the water content of tissues were the inverse of those of total lipid; fish in 'poor' condition and with a slower growth rate had a relatively higher water content. Food availability had no effect on the levels of protein, but elevated levels of protein were detected in field fish compared to all experimental fish. There was a close relationship between feeding history, somatic growth, and levels of energy reserves, principally total lipid concentration.

KEY WORDS: Reef fish · Post-settlement · Lipids · Growth

INTRODUCTION

Somatic growth, levels of energy reserves, and resulting body size in recently settled reef fish have important ramifications for their subsequent survival and length of time to maturity. Variation in these demographic features has the potential to modify recruitment patterns and thereby influence the size structure of the adult reproductive population (Jones 1986, 1991). Reef fish populations are characterised by years of medium to low recruitment, and are only occasionally interrupted by years of extremely high recruitment (Williams 1983, Victor 1986, Doherty & Williams 1988). Doherty & Fowler (1994) demonstrated the transfer of these extreme, high recruitment years through the age classes of a reef fish population (*Pomacentrus moluccensis*) on the central Great Barrier Reef (GBR), Australia. While this pattern clearly demonstrates the effect of unusually high recruitment levels on the dynamics of reef fish populations it does not determine the importance of the more common, but

lower, recruitment pulses. In both high and medium to low recruitment years, post-settlement processes and demographic events in the juvenile phase potentially play a decisive role in the dynamics of adult fish populations (Hixon 1991, Jones 1991).

Initially the importance of post-settlement events in determining adult abundance patterns was judged on whether they significantly modified survivorship patterns of recruits (Doherty 1983, Shulman & Ogden 1987, Doherty & Williams 1988). However, failure to detect an effect on survivorship does not preclude their importance. For example, post-settlement processes can affect juvenile growth rates and subsequent time to reproductive maturity (Jones 1986, Forrester 1990) by influencing food availability (Coates 1980, Koebele 1985). These post-settlement events influence the size structure and growth dynamics of juvenile fish populations and, thus, the absolute density of the reproductive population. Therefore, in size-structured populations, individual growth rates are as important as rates of survivorship in determining population trajectories

(Werner & Gilliam 1984). This realisation has caused a shift in emphasis away from population models based on age to models which are size specific (Werner & Gilliam 1984, Pepin 1991).

Considering the importance of body size, what are the principal factors that drive the growth rates of fish once they settle? The potential for growth in a post-settlement reef fish is intrinsically a product of its genotype, the effects of the individual's presettlement environment (e.g. food availability, temperature regime; McCormick & Molony 1992), and the characteristics of the post-settlement habitat (e.g. food availability, competitive regimes, and risk of predation; Coates 1980, Ochi 1986, Hamner et al. 1988, Hixon 1991) into which they settle. The former 2 factors, combined, determine body size and body chemistry at settlement. Reef fish at settlement are variable in size and nutritional condition (as measured by total lipid, carbohydrate and protein levels). This variability has been shown in 2 recent studies of 2 species of pomacentrids (author's unpubl. data) and 1 species of mullid (McCormick & Molony 1993). However, the specific consequences of variable size, in combination with nutritional condition at settlement, for post-settlement growth and probability of survival are yet to be addressed.

Here I examine experimentally the effects of a variable food supply on the deposition of energy reserves and somatic development in recently settled juveniles of the tropical reef fish, *Pomacentrus amboinensis*. *P. amboinensis* is an abundant, predominantly planktivorous reef fish, is highly site attached, and forms loose social groups. Dominance hierarchies have been shown to exist, where adults suppress the growth of subadults (Jones 1987a). This makes it an appropriate model species for analysing the inter-relationships between growth dynamics and nutritional condition, and consequences for survival and successful recruitment into the reproductive population.

METHODS

The relationship between feeding history and post-settlement growth in juvenile *Pomacentrus amboinensis* was determined in an aquarium-based feeding experiment. The experiment was conducted in aquaria to enable the precise manipulation of food and, therefore, permit the testing of a range of feeding regimes. A hierarchical design was employed to test the effects of feeding regime, with 3 replicate tanks nested within feeding treatments. During November 1990 newly settled *P. amboinensis* were captured from a fringing reef at Lizard Island (14° 40' S, 145° 28' E) in the northern section of the GBR. All fish were collected from a

single reef (40 m² area of coral rubble) using a hand net, transported to the laboratory and held in aquaria for 2 d to acclimatise. During the period of acclimation, all fish were fed *Artemia* nauplii.

Fish of a similar size (11 to 13 mm standard length, SL) were randomly allocated to 1 of 3 feeding regimes. Fifteen fish were placed in each of the 3 tanks per feeding treatment. Each 450 l tank (basal area = 0.68 m², height = 0.66 m) contained a bleached coral head (*Pocillopora damicornis*) 40 × 40 × 30 cm high, positioned on a concrete block, to provide shelter. Feeding regimes were chosen to cover a range of potential feeding scenarios, from a constant supply to intermittent pulses of food: Treatment 1, fed 4 times per day (food was always present in the aquaria); Treatment 2, fed once per day; Treatment 3, fed once every second day. Fish were fed to saturation during each feeding episode. On a daily basis, the quantity of food that fish received within each treatment was similar, with the exception of Treatment 3 when fish were starved. *Pomacentrus amboinensis* are predominantly planktivorous but have been observed feeding on algae. Therefore, all tanks were cleaned regularly to prevent the disproportionate growth of algae and the confounding of treatment effects. Food consisted of 36 to 48 h old *Artemia* nauplii (Ocean Star brand) and homogenised green prawn flesh. The proportion of homogenised prawn fed to fish was gradually increased through the course of the experiment, as fish gape increased. When fish were fed, food was dispersed throughout the tank to enable all individuals equal access. Fish were observed feeding in all areas of the tank; therefore, this method reduced the potential monopolisation of point sources by dominant individuals where food was released.

To provide a comparison between the growth dynamics of fish in the field and the laboratory fish, 15 *Pomacentrus amboinensis* of a similar size were placed on each of the 4 patch reefs located 15 m from the main reef on the leeward side of Lizard Island (at 7 m depth, well within this species' natural distribution). Field fish were allowed to feed on naturally available plankton. Patch reefs were 50 × 50 × 50 cm and composed of live and dead *Pocillopora damicornis*. *P. amboinensis* are highly site attached, so once established on patch reefs, they remain. However, to reduce the probability of emigration, fish were released onto reefs in the evening and a 3 mm mesh cage (70 × 70 × 70 cm) was placed over each reef for the first 24 h, then removed. This ensured that the fish remained on the reef until they became familiar with their surroundings. The whole study ran for 53 d.

Morphometrics. All fish were killed at the completion of the study, by chilling. Immediately prior to fixation or freezing, morphometric measurements were

taken to describe the variability in somatic growth of fish between treatments, and in the field: standard length (SL) to the nearest 0.1 mm, body depth at the pectoral fin and the anal fin, blotted wet weight to the nearest mg and wet weight following the removal of otoliths. Otoliths were removed to examine the effect of feeding regime on the deposition and width of daily bands. These data will be presented in a separate publication.

Body composition. A total of 8 or 9 fish from each tank within the 3 treatments and 25 fish from the 4 patch reefs were placed in Eppendorf tubes and stored in liquid nitrogen for the analysis of total lipids, total carbohydrates, and protein. Fish were freeze dried to a stable weight to derive water content, expressed as mg g^{-1} wet wt. Each fish was then homogenised in 100 mM sodium chloride (NaCl) solution at 0 to 4 °C. Dry weight was used to determine the volume of NaCl required (Hopkins et al. 1984). All analyses were carried out in duplicate, and blanks were run simultaneously. Proteins were measured colorimetrically using the method outlined in Bradford (1976). Total lipids (neutral and polar) were determined using a chloroform:methanol extraction, detailed in Mann & Gallagher (1985). Total carbohydrates were extracted using a modification of the method used by Mann & Gallagher (1985) and outlined in McCormick & Molony (1992).

Muscle development. Five fish from each tank within the 3 treatments, and 3 from each patch reef (field fish) were used to describe the variability in muscle fibre development. A section of the dorsal muscle block (*musculus carinatus dorsalis*) posterior to the first anal fin spine was fixed in formalin acetic acid calcium chloride (FAACC). Sections (6 μm thick) were stained in haematoxylin and eosin. The maximum diameter of 100 fibres within the muscle block were measured. A pilot study showed that there was minimal variability between sections from within a fish, therefore fibres were measured within a single section. Muscle fibres were grouped into 5 μm size classes (0–4.9 μm , 5–9.9 μm , 10–14.9 μm , etc.).

RESULTS

Morphometrics

Somatic growth of juvenile *Pomacentrus amboinensis* was strongly influenced by food availability (Fig. 1). Standard length, and body depth at the pectoral and anal fin all differed significantly among treatments including field fish inhabiting natural patch reefs (Table 1). Growth (expressed as an increase in SL over the course of the experiment, in mm d^{-1}) was greatest

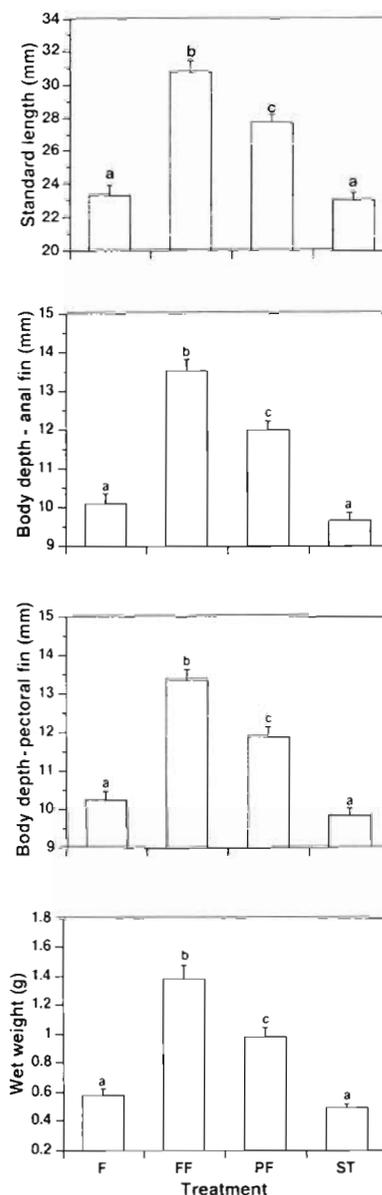


Fig. 1. *Pomacentrus amboinensis*. Changes in the growth of juvenile fish under 3 feeding treatments compared to field fish. Mean standard length, body depth at the anal and pectoral fins, and wet weight. Error bars are standard errors. Feeding treatments: F, field fish; FF, fully fed; PF, partially fed; ST, starved every second day. Means with a common letter are not significantly different at the 0.05 level (Tukey's HSD). Experiment ran for 53 d

in fully fed (FF) fish and least in fish starved every second day (ST) and field fish. ST and field fish displayed very similar growth rates (0.2 ± 0.009 and 0.21 ± 0.015 mm d^{-1} , respectively), suggesting recently settled fish on patch reefs experience food shortages or under such conditions are more physically active. In contrast, fish that were fully fed and partially fed (PF) displayed mean growth rates of 0.35 ± 0.009 and 0.29 ± 0.015 mm d^{-1} , respectively.

Table 1. *Pomacentrus amboinensis*. Summary of ANOVA on the 4 variables measured to determine the effects of feeding treatment and tanks on the growth of juvenile *P. amboinensis*. Residual analysis was used to check assumptions of ANOVA (Snedecor & Cochran 1980). Data are not transformed

Variable	Source	df	MS	Pr > F
Standard length	Treatment	3	502.38	0.0001
	Tank (treatment)	9	19.65	0.1084
	Residual	155	11.96	
Body depth				
	Pectoral fin			
	Treatment	3	95.82	0.0001
Tank (treatment)	9	3.78	0.0880	
Residual	155	2.19		
Anal fin	Treatment	3	117.96	0.0001
	Tank (treatment)	9	4.35	0.0538
	Residual	155	2.27	
Wet weight	Treatment	3	6.15	0.0001
	Tank (treatment)	9	0.24	0.1209
	Residual	155	0.15	

d⁻¹, respectively. FF fish grew approximately 1.7 times faster than the field and ST fish. Similarly, marked differences in weight among treatments were recorded.

Dominant individuals attempted to monopolise access to food despite its uniform distribution throughout the tank. Aggressive interactions were observed between larger, dominant individuals and the smaller, subordinate juveniles within 14 d of the experiment starting. As a consequence of these aggressive interac-

Table 2. *Pomacentrus amboinensis*. Summary of ANOVA on all 4 biochemical variables measured, to determine the effects of feeding treatment and tanks on the body chemistry of juvenile *P. amboinensis*. Residual analysis was used to check assumptions of ANOVA (Snedecor & Cochran 1980). Data are not transformed

Variable	Source	df	MS	Pr > F
Water	Treatment	3	32670.19	0.0001
	Tank (treatment)	9	304.84	0.1904
	Residual	89	214.25	
Carbohydrate	Treatment	3	48.98	0.0001
	Tank (treatment)	9	1.64	0.0514
	Residual	89	13.51	
Lipid	Treatment	3	5864.68	0.0001
	Tank (treatment)	9	44.52	0.5596
	Residual	89	51.49	
Protein	Treatment	3	180.94	0.0255
	Tank (treatment)	9	35.92	0.2239
	Residual	89	26.64	

tions the dominant fish in each tank obtained a greater size by the completion of the experiment. FF fish had a mean weight of 1.38 g, 0.8 to 0.89 g greater than ST and field fish. Size hierarchies were observed in all tanks. The greatest variability in standard length occurred in the FF treatment (mean % coefficient of variation of 64.05). Variability in the PF (% CV of 42.13) and ST (% CV of 31.41) treatments were very similar.

Body composition

Feeding regime had a more complex effect on the levels of energy reserves than on somatic growth. Significant treatment effects were detected for all biochemical constituents (Table 2). Variability among treatments was most accentuated in total lipid content (Fig. 2). A 3.5-fold difference in total lipid existed between FF fish (43.87 mg g⁻¹) and field fish (12.37 mg g⁻¹). Furthermore, fish from the PF treatment contained 2.5 times as much total lipid as ST fish. Trends in lipid content between treatments were similar to those for somatic growth. The lipid content of field fish did not differ significantly from ST fish (Fig. 2, Tukey's HSD).

Trends in the water content of tissues were the inverse of those of total lipid. Fish in 'poor' condition had a relatively higher water content. Significant differences were detected among all treatments (Table 2, Fig. 2). Field fish had the highest mean water content (764.25 mg g⁻¹), FF fish the lowest (686.35 mg g⁻¹).

In contrast to total lipid and water content, the carbohydrate levels within juvenile *Pomacentrus amboinensis* did not display the same patterns in relation to treatment. FF and PF fish had significantly higher carbohydrate levels than fish from the ST treatment, but were not significantly different from one another (Fig. 2, Tukey's HSD).

Protein levels did not differ significantly among experimental treatments (Fig. 2). Starved fish showed a relative increase in levels of protein compared to FF and PF fish. Higher levels were detected in field fish from the leeward patch reefs, than experimental fish (Fig. 2, Tukey's HSD) with a 1.1-fold difference in protein concentration.

Muscle development

Feeding regime influenced the growth and development of muscle fibres in juvenile *Pomacentrus amboinensis*. Fish in the field had a bimodal normal frequency distribution with peaks at 15 to 25 µm and 35 to 45 µm, and a maximum fibre diameter of 60 µm

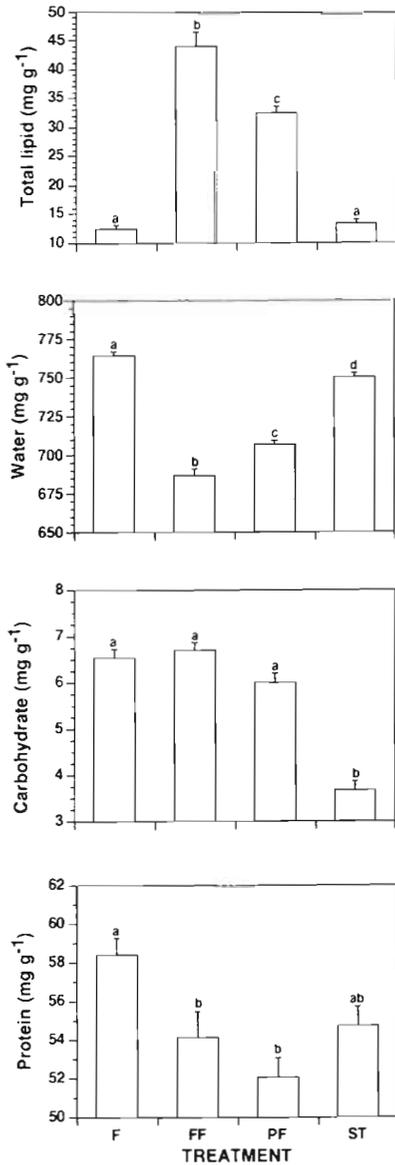


Fig. 2. *Pomacentrus amboinensis*. Changes in the body chemistry of juvenile fish under 3 feeding treatments compared to field fish. Concentration of total lipid, water, total carbohydrate, and protein in mg g⁻¹ wet weight (symbols and treatment codes as for Fig. 1). Experiment ran for 53 d

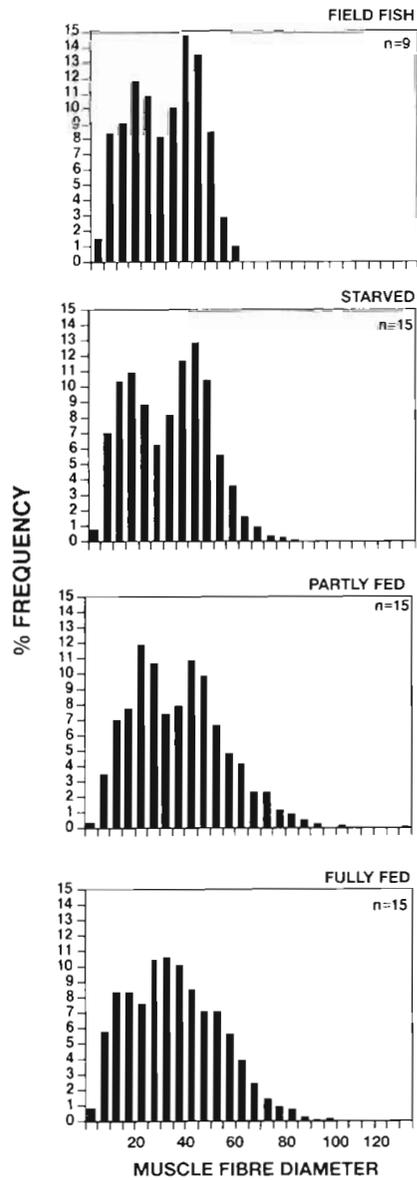


Fig. 3. *Pomacentrus amboinensis*. Size-frequency distributions of muscle fibres (in 5 µm size classes) from juvenile fish, from each feeding treatment and the field. Experiment ran for 53 d

(Fig. 3). Muscle fibre frequency distributions from all fish within the experimental treatments were skewed; maximum fibre diameter in FF and PF fish (100 µm and 130 µm, respectively) was greater than in ST individuals (85 µm). ST and PF fish exhibited bimodal frequency distributions, ST fish had peaks in muscle fibre size at 10 to 20 µm and 35 to 45 µm, PF fish peaked at 20 to 30 µm and 40 to 50 µm. In PF fish, 11.7% of the fibres were greater than 60 µm in diameter, similar to FF fish (9.9%), but contrasting with only 3.3% in ST fish. This pattern suggests that muscle fibre growth is

somewhat restricted in field and ST fish relative to FF and PF juveniles.

DISCUSSION

This study demonstrated the inter-relationships between food availability, body chemistry, and resulting somatic growth in a recently settled, juvenile tropical reef fish. Four principal findings emerged. (1) Feeding history strongly influenced the growth of post-settle-

ment juvenile *Pomacentrus amboinensis*. (2) In contrast, the response of muscle fibre recruitment and growth to variable feeding regimes was conservative. (3) Size hierarchies developed within each tank. The coefficient of variation for standard length varied between treatments, and was the highest in groups of fish with an abundant food supply. (4) Complex changes occurred in the body chemistry that were partly explained by feeding regime.

The somatic growth rate and deposition of total lipid reserves in recently settled *Pomacentrus amboinensis* reflected their variable feeding histories. Partially fed and fully fed juveniles attained a larger size, weighed more, and exhibited higher concentrations of total lipid in their tissues than starved and field fish. A larger size and higher levels of energy reserves (total lipids) for a given post-settlement age confers a number of advantages over smaller conspecifics. The risk of predation, the outcome of competitive or aggressive interactions with conspecifics, and subsequent growth are widely reported as being size dependent (Rice et al. 1987, Miller et al. 1988, Pepin 1988/1989, Tsukamoto et al. 1989). Jones (1984, 1986, 1987a, b) provided a mechanism by which these post-settlement events potentially modify recruitment patterns, by determining time to reproductive maturity and therefore recruitment into the adult reef fish population. This mechanism is particularly relevant in size-structured populations, where size primarily determines position in the social hierarchy and subsequent growth rate. Extensive evidence exists for a range of species that food supplementation enhances juvenile growth, reducing the time to reproductive maturity (for bass, Gutreuter & Anderson 1985; trout, Abbott & Dill 1989; and pomacentrids, Jones 1986, Forrester 1990). The growth rates of well-fed juveniles in this experiment suggest that, in the absence of adults and with an abundant food supply, recruits have the ability to reach reproductive maturity in their first year. Reproductive maturity of *P. amboinensis* has been recorded at 50 mm SL in the southern GBR (Jones 1986) and 45 mm SL in the northern GBR (author's unpubl. data).

The growth rate of newly settled reef fish is particularly important in size-structured populations. Size hierarchies, once established, play a prominent role in determining the potential growth of individuals (Werner & Gilliam 1984). Evidence exists for the social control of feeding regime of subordinate individuals through dominants controlling the feeding rate and quality of food eaten (pomacentrids, Coates 1980, Jones 1987a; salmonids, Metcalfe 1986, McCarthy et al. 1992). This study showed that, in the presence of an abundant food supply (the fully fed treatment), marked size hierarchies were established. Once size hierarchies are established they remain stable (Bachman

1984, Forrester 1990). Furthermore, subordinates in a social group experience physiological stress which reduces their growth efficiency (Wirtz & Davenport 1976, Abbott & Dill 1989, Boisclair & Leggett 1989, Pickering 1993). Therefore, post-settlement factors which influence the quality and quantity of food consumed by an individual act individually or synergistically to influence growth efficiency. In the absence of dominance hierarchies that regulate growth, compensatory growth in juvenile stages of pelagic and benthic fish species occurs. McCormick & Molony (1992) showed that pre-settlement mullids that were initially starved and then re-fed grew and attained a size and condition status similar to fish that had been constantly fed. This compensatory growth is possible because intraspecific interactions play a very minor role in the growth dynamics of these species. The plasticity in growth is principally governed by food availability, which in the pelagic environment is primarily driven by hydrological features (Kingsford et al. 1991), and the individual's ability to obtain that food. Hence, their growth regime is opportunistic in contrast to reef fish recruiting into size-structured populations.

Muscle growth in juvenile *Pomacentrus amboinensis* showed a conservative response to fluctuations in food availability. Despite the marked differences in final standard length and weight of fish between treatments, only small differences in muscle growth occurred. However, fully and partially fed fish had a greater proportion of larger diameter muscle fibres (> 60 μm) than field fish. This result suggests that muscle growth via an increase in muscle fibre size was restricted in fish under sub-optimal feeding regimes. Alternatively, muscle development has been modified by the physical conditions experienced by fish in the field (e.g. sustained swimming in currents). Conservancy in muscle growth has also been recorded in experimental manipulations of trout and bluntnose minnow, where temperature and feeding regimes had a marked influence on somatic growth, but only a slight or negligible influence on muscle fibre diameter frequencies (Weatherly & Gill 1985). In juvenile teleosts, muscle growth also occurs through the recruitment of new fibres developing from myosatellites (Weatherly et al. 1988, Kundu & Mansuri 1990). The relative importance of the 2 modes of muscle growth, increase in fibre diameter and the recruitment of new fibres, is species and size specific. In this study, all juvenile *P. amboinensis*, irrespective of feeding regime, had high proportions of recruiting muscle fibres, denoted by the 5 and 10 μm size classes. Similar results were found in juvenile rainbow trout, where fibre recruitment occurs independently of somatic growth rate (Weatherly et al. 1980). In contrast, McCormick & Molony (1992) showed that feeding regime during the

pre-settlement phase in mullids determines both somatic growth and muscle development by altering the recruitment rate of new fibres and the growth rate of existing fibres. Enhanced muscle development would confer advantages in terms of swimming ability, predator avoidance and maintenance of position in high currents during feeding. Based on this premise, all juvenile fish from the experiment, irrespective of feeding history, appear to have fairly similar swimming abilities.

The response of individual fish to stress (aggressive interactions, food shortages) is, in part, a function of their nutritional condition or body chemistry. Lipids are a principal energy reserve in teleosts, and are often the first components to be mobilised during periods of stress (Driedzic & Hochachka 1978). In this study, juvenile *Pomacentrus amboinensis* with an abundant food supply laid down 3.5 times more lipid in their tissues than fish growing in the field. Within the well-fed treatment the dominant individuals had higher lipid levels, presumably conferring energetic and physiological advantages. Juvenile reef fish with elevated lipid levels can mobilise such reserves and thereby sustain optimal growth during periods of stress. Therefore, the effect of ambient food levels on the growth dynamics of a fish will depend, in part, on the individuals nutritional condition or body chemistry. This has important ramifications for reef fish where the outcome of post-settlement processes such as intraspecific interactions, risk of predation, and time to reproductive maturity are all size dependent (Jones 1991).

Patterns in protein and carbohydrate levels cannot be interpreted so clearly. Within the experimental treatments, starved fish had a significantly lower concentration of carbohydrate than fed and partially fed fish. The relatively low levels of carbohydrate reserves in starved fish suggests that carbohydrates are being mobilised to provide a rapid supply of energy. However, field fish, although approximately $\frac{3}{4}$ the size of the fully and partially fed fish, contained similar concentrations of carbohydrate. The patterns in the levels of carbohydrate in the aquarium and field fish must be viewed cautiously, as carbohydrate can be synthesised from either lipid or protein during periods of starvation (Love 1980).

Alternatively, Black & Love (1988) reported that carbohydrate levels in cods were influenced by stress of capture, which resulted in a rapid decrease in muscle glycogen. Stress results in changes, for example in glucose and glycogen in fish tissues (Wieser et al. 1986, Schwalm & Mackay 1991), but does not alter the overall concentration of total carbohydrate which was measured in this study. All *Pomacentrus amboinensis* from the aquaria and the patch reefs in the field were captured and killed as quickly as possible to minimise

stress. Therefore, the carbohydrate levels measured are assumed to be the true levels present in fish tissue.

In contrast to lipids, proteins are generally conserved, being the last energy reserve to be mobilised during periods of stress (Love 1980, Molony 1993). Feeding history had no significant effect on the absolute quantity of protein per individual fish. However, there is a trend towards an inverse relationship between protein and lipid. Starved and field fish had relatively higher protein levels and less lipid than fully and partially fed fish. Weatherly & Gill (1983) have documented a similar relationship in juvenile rainbow trout, raised under variable food and temperature regimes. This trend towards more protein in field fish compared to fish reared in aquaria may also relate to fundamental differences in the activity levels. Alternatively, Wood et al. (1957) proposed that the higher fat content and the lower protein levels in juvenile salmonids raised in a hatchery compared to wild caught fish were due to differences in diet. The similarity in lipid and protein levels between starved and field fish suggests that both activity levels and diet (quantity and quality) are influencing body chemistry.

This experiment has shown that feeding regime influences the growth dynamics and total lipid levels of juvenile *Pomacentrus amboinensis* in a predictable way. Fish growing under conditions of an abundant food supply were able to maintain higher relative growth rates, in addition to laying down greater fat reserves, than those with a limited food supply. Information on the biochemical composition (especially lipid and water content) of reef fish at different stages of their life history will give ecologists insight into the potential effects of post-settlement processes on the growth and survival potential of individuals. It has been shown for a wide range of commercially important species (reef, pelagic and freshwater taxa) that somatic growth and sensory development rates, and subsequent survival of larval and juvenile fish is, in part, a function of their body chemistry (lipid content, fatty acid profile, triacylglycerol levels) (Love 1980, Chambers et al. 1989, Sieg 1992). Therefore, nutritional condition may play a vital role in modifying the effects of demographic events during the immediate post-settlement phase. Assessing the biochemical composition of reef fish in experiments that test the effect(s) of post-settlement processes, in addition to collecting growth and mortality estimates, will play a central role in enhancing ecologists understanding of reef fish population dynamics.

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