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Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*

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Abstract The supply of larvae is a major determinant of population and community structure in coral reef fishes. However, spatial and temporal variation in condition (i.e. quality) of potential recruits, as well as their density (i.e. quantity), may influence survival and growth of juveniles. We conducted an experiment to test whether recent feeding history could affect growth, condition and post-recruitment survival in a Caribbean damselfish, *Stegastes partitus*. Fish were collected soon after settlement, and fed either low or high rations in aquaria for 7 days. Fish fed the high ration grew faster in aquaria and were in a better condition (higher total lipids and Fulton's condition factor) at the end of the feeding period. Subsequently, we released 50 fish in 25 pairs (one fish subjected to low rations, the other to high rations) on a Bahamian coral reef and monitored survival for 10 days. Survivorship of high-ration fish was double that of low-ration fish (80 vs 40% over 10 days). However, low-ration fish that survived 10 days were of similar condition and grew at similar rates to high-ration fish, suggesting that short-term ration differences may not persist in surviving fish. Laboratory experiments showed that low-ration fish were taken by piscivorous fishes before high-ration fish, indicating that differential predation may account for survival differences. This study highlights the potential of feeding history and condition to affect the relationship between patterns of larval arrival at reefs, and subsequent juvenile and adult population densities.

Key words Condition · Coral reef fish · Food ration · Post-settlement mortality · Predation

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Introduction

Processes regulating the densities of organisms are of fundamental interest to ecologists, but in many cases the relative roles of these processes are unknown. Survivorship, for instance, may depend on the physiological state, or condition, of the organism. Condition is known to vary seasonally (red deer: Loison and Langvatn 1998), with food quality and quantity (mosquito larvae: Yan and He 1991), with predator abundance (snowshoe hares: Boonstra et al. 1998), with density of conspecifics (caribou: Ouellet et al. 1997) and with social status (damselfish: Booth 1995). In turn, condition has been shown to affect reproductive output (red squirrels: Wauters and Dhondt 1995) and adult population dynamics (mosquitoes: Yan and He 1991).

In coral reef fishes, the supply of larvae to reef habitat is often thought to limit adult densities (e.g. Doherty 1981; Sponaugle and Cowen 1996). Both spatial and temporal fluctuations in the rate of larval influx may subsequently predict changes in population sizes (e.g. Victor 1986). Processes occurring after settlement are not, in this scenario, considered to be density dependent and will therefore not alter patterns of abundance established at settlement. In contrast, an alternate hypothesis is that processes affecting juveniles, such as differential growth and mortality, may alter patterns at settlement, and perhaps regulate local abundances (reviews by Jones 1991; Hixon 1991, 1998; Caley et al. 1996; Hixon and Webster, in press).

The idea that variation in larval influx (i.e. quantity) alone controls adult abundance implies that larval physiological state (i.e. quality) has no overall impact on spatial and temporal variation in probability of survival, and on subsequent population dynamics. However, it is well known that larvae vary greatly in physiological condition in temperate systems and that this variation is likely to be reflected in differential susceptibility to mortality (Theilacker 1986; Suthers et al. 1989; Suthers and Frank 1991). If condition varies temporally and spatially, and influences a recruit's ability to survive and grow, then

larval quality may ultimately play a role in regulating numbers of reef fish. Therefore, in this scenario, larval characteristics would interact with juvenile processes to affect adult densities.

Condition, or physiological state, of a fish may be measured in a variety of ways, such as lipid content, RNA/DNA, robustness, or by a variety of behavioural or developmental features (see McCormick and Molony 1993; review by Ferron and Leggett 1994; McCormick 1998; Suthers 1998). Surprisingly, these measures show only poor correlation among themselves when compared for the same set of individuals (Suthers and Frank 1991; McCormick and Molony 1993). Rarely, however, has the assumption been tested that any of the measures of condition influence components of fitness, such as survival.

The present study aimed to (1) examine the relationship between recent feeding history and growth/condition of new recruits, (2) investigate the link between recruit condition/feeding and early post-settlement survival, and (3) determine the relative susceptibility of high- and low-condition recruits to predation.

Materials and methods

Fish species and collection

Stegastes partitus, the bicolor damselfish (Pomacentridae), is ubiquitous on coral reefs in the western Atlantic and Caribbean (Allen 1990). Both new recruits and adults maintain small home ranges and forage on zooplankton and benthic algae. They spend from 27 to 31 days in the plankton prior to settlement (Wellington and Victor 1989), which occurs predominantly over the summer months (Booth and Beretta 1994; Sponaugle and Cowen 1996; M.A. Hixon, M. Carr, unpublished data).

New recruits were collected from Barb's Bay, on Norman's Pond Cay, adjacent to Lee Stocking Island, near Exuma, Bahamas, on 19 and 20 June 1998. Fish were captured using hand nets and the anaesthetic quinaldine (Sigma) and transferred live to buckets for transport to the Caribbean Marine Science Center on Lee Stocking Island.

Aquarium housing

Fish were measured [total length (TL), mm] and weighed (wet weight, g) before being allocated to 15-l aquaria (two fish in each). Half the water in aquaria was replaced daily, and aquaria were shaded to maintain a constant water temperature of 27°C, similar to ambient water conditions.

Feeding and food analysis

The ration consisted of pre-weighed pellets of Marine Start AL1 dry food (Le Guessant, France), each from 300 to 500 µm in diameter. Food composition was: fish, krill, fish oil and minerals, composed of proteins (64%), fats (12%), raw cellulose fibre (3%), ash (10%), vitamin A (20,000 UI/kg), vitamin D3 (2,400 UI/kg), vitamin E (180 mg/kg) and vitamin C (800 mg/kg). The weight of food found in stomachs of similar recruit damselfish in the field ranges from 0 to 8% body weight with the daily ration estimated at between 0 and 5% body weight (D.J. Booth, unpublished data). Therefore, fish were fed either 10% body weight per day (high-ration treatment) or 3 1/3% per day (low ration) for 7 days.

Growth and condition

Length and weight measurements were taken after 7 days in the laboratory and subsequently after 10 more days in the field. These measurements were compared with those taken at the time of capture to yield mean growth estimates for each fish. These estimates were also used to calculate Fulton's condition index $\{10^5 \times [(\text{weight, g}) / (\text{length, mm})^3]\}$ for each fish. Additionally, a subsample of fish was taken at capture (day 0, $n=10$), at day 7 ($n=7$ high ration, $n=6$ low ration) and at day 17 ($n=20$ high ration, $n=10$ low ration) for lipid analysis. Each fish was stored for analysis in 100% methanol in a tightly capped vial upon capture. After fish had been freeze-dried, total lipids were determined using chloroform-methanol extraction (Bligh and Dyer 1959; Mann and Gallagher 1985), with the storage methanol included in the first rinse. Extracted lipids were dried and weighed, and expressed as a percentage of dry body weight.

Field survival

After the 7-day feeding treatments, 25 fish in each treatment were randomly chosen to test the effects of differential ration on survivorship in situ. All fish were tagged using a visible elastomer implant (Northwest Marine Technology). Each fish in the low-ration treatment was paired with a high-ration fish, by closely matching their initial total lengths. Both members of each pair were transferred to small (approx. 30–50 cm diameter) coral patch reefs, isolated by at least 5 m of seagrass bed, in Barb's Bay on 26 June 1998. The 25 patch reefs were then censused every day for 10 days. Thorough searches of nearby reefs confirmed that absent fish had died (rather than emigrated).

Predation risk

To test the hypothesis that low-ration fish were more susceptible to predation, we conducted six trials where we placed a piscivorous fish (*Epinephelus fulvus*, Serranidae) of approximately 15 cm length into an 80-l aquarium (1.3×0.4×0.4 m), including a concrete-block at one end to serve as a shelter. A tagged pair of *S. partitus* (one low and one high ration, of similar length) was introduced behind a wooden partition near the opposite end of the tank and left for 5 min. The partition was then removed, and subsequent behaviour of predator and prey noted, using direct observation and digital video, until at least one fish was consumed, or for up to 10 min.

Results

Influence of ration on growth and condition of recruits

On initial allocation to feeding treatments, low-ration fish were slightly yet non-significantly longer and heavier than high-ration fish (Fig. 1A,B). However, the growth rate of low-ration fish was significantly lower than that of high-ration fish during the 7-day laboratory feeding period (t -test: increase in weight, $t=6.8$, $P<0.05$; increase in length, $t=3.7$, $P<0.05$; Fig. 1A,B). The weight of low-ration fish dropped on average 20% during feeding, and the mean length and weight of fish from both treatments were similar at the end of the feeding period. In contrast to the laboratory feeding period, growth in length and weight was not significantly different for both feeding treatments over the 10-day field period (t -tests: $P_s>0.05$).

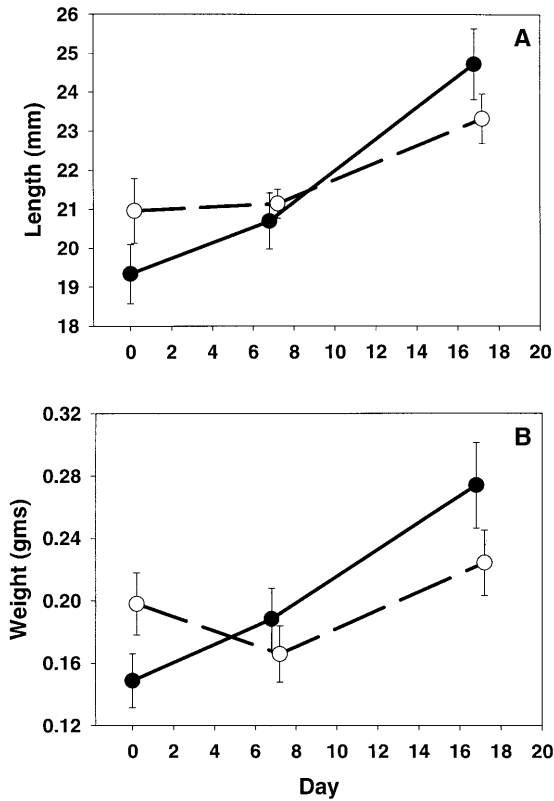


Fig. 1 Change in total length (A) and wet weight (B) of recruit *Stegastes partitus* assigned to two ration treatments: high ration (solid line and symbols), and low ration (broken line, open symbols). Mean \pm SE shown, $n=20$ high ration, 10 low ration. Data plotted at start of feeding (day 0), at end of feeding (day 7) and after 10 days in the field (day 17)

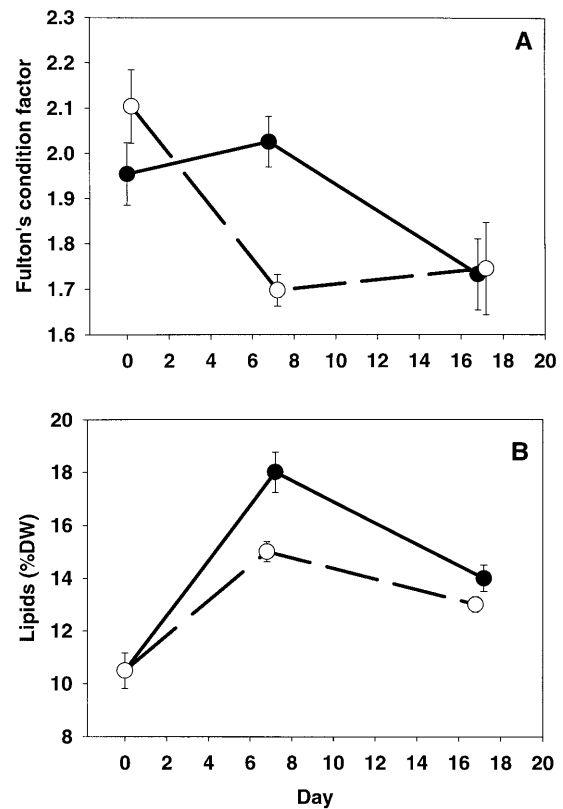


Fig. 2 Change in Fulton's condition factor ($10^5 \times \text{weight}/\text{length}^3$) (A) and lipid content (% dry weight) (B) of recruit *S. partitus* assigned to two ration treatments: high ration (solid line and symbols), and low ration (broken line, open symbols). Mean \pm SE shown. Data plotted at start of feeding (day 0), at end of feeding (day 7) and after 10 days in the field (day 17). **A** $n=20$ high ration, 10 low ration. **B** $n=10$ (day 0), 10 (day 7 low ration), 10 (day 7, high ration), 10 (day 17, low ration), 20 (day 17, high ration)

Condition, measured as Fulton's condition factor (K), deteriorated rapidly during laboratory feeding for the low-ration fish, and was relatively constant for the high-ration fish (Fig. 2a). However, after assignment to coral heads in the field, K of high-ration fish fell, and was similar to that for low-ration fish at the end of the 10-day field trial. Lipid levels of fish at the start of the laboratory feeding period were around 10.5% dry weight, increasing to 18% after 7 days in the high-ration fish, and to 15% in the low-ration fish (t -test for high- vs low-ration fish after 7 days, $P < 0.05$; Fig. 2B). For the fish remaining at the end of the 10-day field trial, lipid levels dropped in both treatments, with high-ration fish having only slightly but significantly greater lipid levels than low-ration fish (t -test, $P < 0.05$; Fig. 2B).

Influence of ration/condition on early survival of recruits

Of 25 pairs of tagged recruits assigned to coral heads during the 10-day field trial, both the high- and low-ration fish survived in 10 pairs, both fish disappeared in 5 pairs, and the low-ration fish alone disappeared in 10

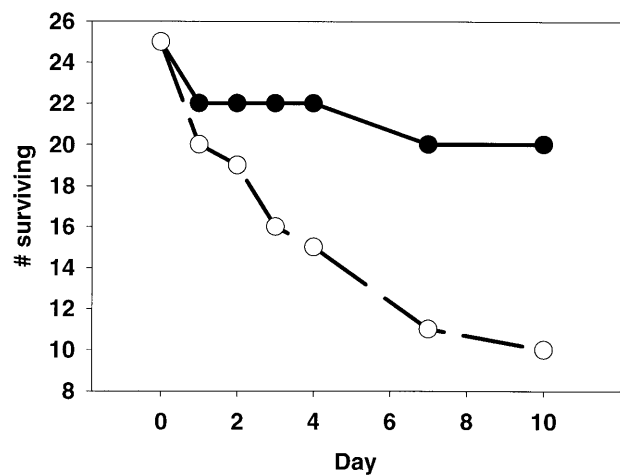


Fig. 3 Survivorship curves in situ for *S. partitus* recruits assigned to two ration treatments: high ration (solid line and symbols), and low ration (broken line, open symbols). Twenty-five fish in each treatment, paired and assigned randomly to coral heads at day 0

pairs. After 10 days in the field, a significantly higher proportion of the low-ration fish had disappeared (15/25 low ration vs 5/25 high ration, χ^2 -test with Yates correction=4.05, $P < 0.05$; Fig. 3).

Influence of ration/condition on risk of predation

Of six pairs of *S. partitus* recruits (one high and one low ration), the piscivorous fish attacked and consumed the low-ration fish first in all cases (binomial test, $P=0.016$).

Discussion

Both growth and condition of recruits in this study responded rapidly to changes in ration, and subsequently exhibited ration-related differences in early survival. However, differences in condition, measured in two ways, were all but gone after 10 days in situ. This result suggests that the influence of early condition on survival occurs only during the first days post-settlement. The recruits of lowest condition in both treatments possibly did not persist, and since more fish disappeared in the low-ration treatment, the average condition of the remaining fish increased relative to survivors in the other treatment. Other studies have shown that mortality is highest over the first week post-settlement, and may be up to 80% in some species before levelling off (e.g. Doherty and Sale 1986; Victor 1986; Booth 1991; Carr and Hixon 1995). Our results suggest that these high rates of early mortality are partly related to the body condition of new recruits. There is some indication in this study (see Fig. 3) that survivorship curves started to level off after 1 week. It should be noted that, although the experimental fish were new settlers at the commencement of the laboratory feeding regimes, they were young, but not new, recruits when transplanted onto the reef.

Laboratory and field evidence from temperate freshwater systems suggests that the condition of prey fish can affect interactions with predators (e.g. Miller et al. 1988; Rice et al. 1993). The mechanism underlying this effect probably involves degraded physiological functions in starved fish, such as muscular coordination (e.g. McCormick and Molony 1992). In this study, we observed low-ration recruits swimming in an erratic manner prior to predator attack, and this behaviour may have indicated decreased muscular coordination for burst swimming. Other characteristics of new recruits and pre-settlement larvae, such as body size, may also influence early mortality in coral reef fishes (e.g. Groll 1984; Booth 1995). In contrast, M.I. McCormick and B.A. Kerrigan (personal communication) found that lizardfish (*Synodus* sp.) preyed non-size-selectively on new-recruit goatfish (*Upeneus tragula*). Recruits in this study from both treatments were paired, and pairs were matched for length and weight, reducing the possible confounding effects of body size. Pairing had the additional advantage of reducing stochastic spatial differences in risk of mortality between treatments. On the other hand, pairing may have led to establishment of dominance of the high- over the low-ration fish, complicating the link between predation risk and condition. However, we did not observe such dominance within pairs for the 25 pairs transplanted to the field (personal observation). In any case, predation is clearly the major source of early post-

settlement mortality in many reef fishes (Hixon 1991; Hixon and Carr 1997), including *S. partitus* (M. Carr and M.A. Hixon, unpublished data).

Larval condition has the potential to alter spatial and temporal patterns set at the time of settlement if two criteria are met. First, condition has to bear on components of the fitness of individuals, through effects on survival and/or growth. This study has demonstrated such an effect for a small species of damselfish. The second criterion is that condition must vary significantly among sites and/or times. It is well known that condition varies cross-shelf in a systematic manner for fish larvae in temperate marine waters (Theilacker 1986; Suthers et al. 1989), and there is growing evidence in support of such differences in coral reef fishes. Kerrigan (1996) showed that the condition of two damselfish species showed a spatial coefficient of variation of over 30%, while McCormick and Molony (1993) measured variation in lipids of pre-settlement goatfish (*U. tragula*) at over 50% between samples. D.J. Booth (unpublished data) found significant variation in lipid levels of pre-settlement and new recruit *Pomacentrus moluccensis* among six sites separated by 1–2 km, over a 3-month period. These studies indicate the importance of larval condition in individual-based models of population regulation of coral reef fishes.

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