POPULATION ECOLOGY

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Consumption of coral propagules after mass spawning enhances larval quality of damselfish through maternal effects

Abstract The synchronized spawning of corals in many parts of the Indo-Pacific represents a huge injection of biological material into the waters around reefs. Much of this material is consumed by fishes and filter-feeding invertebrates in the 5 or so days following spawning. The present study is the first to document the effect of the consumption of coral propagules on a population of facultatively planktivorous fish and the transference of physiological condition across generations. The study compares two populations of the damselfish *Pomacentrus amboinensis* that fed to differing degrees on coral propagules for 5 days after the annual mass spawning of corals at Lizard Island, Great Barrier Reef, Australia. Wind blew coral slicks over the outer lagoon to the inner lagoon some 1.5 km away. While coral propagules were abundant in the water column in the windward location, they were scarce by the time the water mass reached the inner lagoon. Behavioral observations 2–5 days after coral spawning showed that a significantly higher proportion of *P. amboinensis* was feeding on coral propagules in the windward location than in the inner lagoon location. Windward location females consumed coral propagules almost exclusively and had fuller guts than females from the inner lagoonal location. Five days after the mass coral spawning, windward location females had a higher condition factor and a larger liver mass relative to body mass compared to females within the inner lagoon or females from both locations 2 months later. Fish eggs laid by the windward location females soon after coral spawning yielded larvae that had 25% larger yolk sacs and 100% larger oil globules than did larvae produced from the females from the inner lagoon location, or larvae produced at either location prior to or well after coral spawning in 2 previous years. Larger yolk sacs and oil globules have been shown to have direct

survival benefits in the transition from endogenous to exogenous feeding. A feeding experiment conducted on patch reefs showed that diet supplementation of breeding females with a high lipid food for just 5 min per day was sufficient to significantly increase yolk-sac sizes of newly hatched larvae. Evidence suggests that females gain a fitness advantage from feeding on coral spawn and that this is passed on to their offspring.

Keywords Larval survival · Food availability · Body condition · Yolk sac · Oil globule

Introduction

Since the investigation of the first predator-prey relationships it has been shown that the reproductive output, offspring survival and population demography of predator populations are closely linked to cycles in the availability of prey (Gause 1934; Elton and Nicholson 1942; May 1972). Evidence suggests that predator populations are often food limited, with fitness being tied to the acquisition of prey (Krebs 1994). Predators may be expected to exploit an abundant prey resource if the energy gained from that resource is greater than the cost of attaining it and greater than obtaining another accessible resource (Stephens and Krebs 1986). Predators have therefore evolved to exploit prey species when they are predictably abundant and when there is a fitness advantage. This has led to predators switching between prey types based on availability and the benefits they will receive from its acquisition.

Food chains in the tropics are tightly regulated, and it is often suggested that the dynamics of populations are limited by the energy available to fuel them (Jones 1986; Jones and McCormick 2002). The synchronized spawning of scleractinian corals that occurs over much of their geographic range (Harrison et al. 1984; Willis et al. 1984; Babcock et al. 1986; Oliver et al. 1988) is an annual event that represents a large pulse of nutrient-rich food for those organisms that are able to exploit it. During this annual

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event, gametes rise to the surface and, in calm water conditions, float as slicks of dead coral spawn, unfertilized eggs and embryos (Oliver and Willis 1987). Estimates suggest that 10^6 eggs are released per square meter of live coral on the Great Barrier Reef (Hall and Hughes 1996). As they are composed of between 50% and 70% lipid (Richmond 1987; Arai et al. 1993), these coral propagules make a valuable food resource for organisms that consume them.

Obligate and facultative planktivorous fishes are known to switch their diets to opportunistically consume large quantities of coral propagules in the days following mass coral spawning (Westneat and Resing 1988; Pratchett et al. 2001). Coral slicks that cross shallow reefs are met by a "wall of mouths" that have been suggested to have a major impact on the survival of developing planulae (Pratchett et al. 2001). Hamner et al. (1988) estimated that a single cubic meter of water crossing the reef front of the Outer Barrier Reef is inspected and fed from by over 500 individual fish. To date, 40 species of fishes have been observed feeding on coral propagules immediately after the mass spawning (Westneat and Resing 1988; Alino and Coll 1989; Pratchett et al. 2001). The present study is the first to examine the ramifications of this large-scale event to the fitness of the individuals that consume these coral propagules.

The nutritional pulse obtained by female fishes that feed on coral propagules may have benefits for the quality of the larvae they subsequently produce. Maternal history has a large influence on the size and provisioning of larvae through the nutritive products and on developmental and metabolic hormones that are sequestered into the egg during gametogenesis (Ojanguren et al. 1996; Kerrigan 1997; McCormick 1998, 1999). Larval size, volume of the yolk sac, and volume of the oil globule that lies within the yolk are three traits that are influenced by maternal quality and are of particular importance for larval survival (Chambers et al. 1989; Moodie et al. 1989; Leggett and Deblois 1994). Studies have found that small differences in traits early in the larval phase may have major ramifications for future growth and survival due to the high developmental and physiological rates that occur in tropical species (Houde 1989; Leis and McCormick 2002; McCormick and Nechaev 2002). Recent studies have shown that growth during early larval life, and in some instances, the characteristics at hatching, can predetermine survival throughout the larval and juvenile life phases (Searcy and Sponaugle 2001; Bergenius et al. 2002; Shima and Findlay 2002; Vigliola and Meekan 2002; Wilson and Meekan 2002).

The aim of the present study is to examine the prediction that the consumption by fish of a high-energy food resource, such as coral propagules, will enhance the quality of their larvae. I examine this prediction in two ways. First, I compare the morphology of larvae produced by females before and after the austral mass coral spawning at two locations, one with ad libitum access to coral propagules and the other with limited access.

Secondly, I compare results from this natural experiment to those of a manipulative field experiment in which I supplemented the diets of females and examined the flow-on effects to larval quality. The results suggest that the mass coral spawning represents a natural feeding experiment that elevates the body condition of fish who consume the spawn and leads them to produce higher quality larval offspring, which have a higher probability of surviving.

Materials and methods

The species

Pomacentrus amboinensis, like most damselfishes, is a protogynous hermaphrodite with males that guard demersal nests during a summer breeding season. On the northern Great Barrier Reef, where this study was conducted, the breeding season typically extends from the beginning of November through to the following February (McCormick, personal observation). Associated with each nesting male are between one and six females in various states of reproductive condition. Eggs are laid in a single layer of approximately 40 cm^2, containing ~3,000 eggs. Embryos hatch after 4.5 days (at 28 °C), about 15 min after sunset. Adults feed on benthic algae and plankton (Hall 1995) and are site attached, living their lives close to where they initially settled (McCormick and Makey 1997). Fish often inhabit the reef edge, where the coral rubble meets sand. Females can be distinguished from males by their smaller size, lack of nesting behavior, slight differences in body shape (males are proportionally longer between the pelvic fins and anus) and by the presence of a black margin on the caudal fin of males (during the breeding season).

Sampling locations

Data were collected from two locations in the lagoons of Lizard Island, on the northern Great Barrier Reef, Australia (14°41′S, 145°27′E). Vicki's Reef, on the edge of the Research Lagoon, faced the prevailing northwesterly water current during the 2001 mass coral spawning (7 and 8 December) and for 5 days afterwards. The other location was in Blue Lagoon, 1.5 km down current from Vicki's Reef. Both study locations consisted of approximately 300-m-long sections of shallow reef edge.

Coral propagule consumption

To quantify the extent to which fish were feeding on coral propagules, behavioral observations were conducted during the 3 days following coral spawning and over a 3-day period 2 months after the mass coral spawning. Scan observations (Martin and Bateson 1993) of *P. amboinensis* were made in both locations between 0800 and 1200 hours. During these observations, fish above 45 mm standard length (the size of maturity, McCormick unpublished data) were placed into one of four behavioral categories the instant they were observed, which encompassed their whole behavioral repertoire: (1) feeding in the water column on coral propagules; (2) feeding in the water column on other planktonic prey items; (3) feeding from the benthos; and (4) other behaviors (interactions, traveling, sheltering, nesting). Coral propagules were clearly visible in the water column, and it was possible to determine whether or not fish were targeting these. The percentage of females undertaking the various behaviors was calculated for each census (n=3 censuses) from the number of females in each behavioral category of the total number of females seen (~103 females). Scan sampling of this type has been shown to be an efficient way of obtaining information on the behavioral

budgets of a censused population (Martin and Bateson 1993). This methodology gives no information about the rate at which individuals undertake a particular behavior (e.g., feeding) but rather gives the proportion of individuals undertaking a behavior over the sampling period.

Two collections of 10 females from each location were made using a fence net for the examination of their gut content and body condition. One sample was collected 5 days after coral spawning (12 December 2001), while the second sample was collected 2 months after coral spawning (6 February 2002). After weighing and measuring (total and standard length) each fish, the alimentary tract was removed and stored in 10% calcium buffered formalin (FAAC). The liver was removed from the preserved alimentary tract and weighed. The occurrence of prey items in the gut was quantified by placing the stomach contents into a petri dish and identifying the items under 50 random points along transects through the contents. Coral spawn was recognized using the criteria of Westneat and Resing (1988). An index of gut fullness was calculated as the weight of the alimentary tract (without the liver) standardized by gutted body weight.

Body condition

To determine the potential influence of feeding on coral propagules on the body composition of female *P. amboinensis*, three measures of body condition were determined. Two condition indices were calculated: the Fulton's condition factor and the hepatosomatic index (HSI). Fulton's condition factor (K) was defined as:

$$K = \mathrm{WB} * 100/L^3$$

where WB is gutted body weight (g) and L is standard length (mm).

HSI was calculated as:

$$\mathrm{HSI} = \mathrm{WL} * 100/\mathrm{WB}$$

where WL represents the liver weight (g).

To quantify the physiological condition of female *P. amboinensis*, hepatocyte vacuolation was measured (i.e., the proportion of liver tissues occupied by intracellular vacuoles). This yields a measure of liver lipid and glycogen storage, with fish that consume more or higher-quality food having a higher density of vacuoles (Theilacker 1978). After fixing, hepatic tissues were dehydrated in a graded ethanol series and embedded in paraffin wax. Tissues were sectioned at 5 μm and sections were stained using Mayer's hematoxylin and eosin. The proportion of vacuoles in hepatic tissues was then quantified using a Weibel eyepiece, recording the proportion of points (out of 42) that intersected hepatocyte vacuoles viewed at 400× magnification. Estimates of hepatocyte vacuolation were obtained from five sections from the anterior, mid, and posterior parts of each liver, giving a total of 15 estimates for each fish. The mean values of the three condition measures were compared using two-way ANOVA. Hepatocyte vacuolation data required log$_{10}$ transformation to meet the assumption of homogeneity of variance.

Larval collections

To quantify the transference of physiological condition across generations, the morphological characteristics of the larvae produced by *P. amboinensis* in the two locations were quantified. At each location 20 natural nests guarded by male *P. amboinensis* were replaced with artificial nesting surfaces consisting of either half of an 18-cm diameter PVC water pipe (30 cm long), split lengthwise or terracotta half pipes of a similar dimension. These pipes presented a uniform concave nesting surface of dimension and defensibility similar to that of natural nests (up-turned clam shells). Nests were monitored daily for egg clutches. Larvae from four clutches of eggs were collected in the first fish spawning that occurred after coral spawning at both locations. This was accomplished by collecting monitored nests containing eggs that were

within a few hours of hatching and transferring them to well-aerated aquaria in the laboratory. Larvae hatched ~15 min after sunset. Larvae were collected with a fine plankton mesh net, preserved in 2.5% glutaraldehyde in seawater for 2 h at room temperature, rinsed in seawater, then transferred to fresh seawater and refrigerated for morphometric analyses. Standard length (SL), head depth (through the eye), eye diameter (maximum), yolk-sac area, and oil droplet area (within the yolk) of 15–50 larvae from each nest were measured. Yolk-sac area provided a measure of yolk reserves available for subsequent development. Images of larvae were recorded against a scale bar with a digital camera attached to a binocular microscope. Larvae on these images were then measured using image analysis software (Scion Image).

The morphology of larvae from these samples was compared to *P. amboinensis* larvae collected in the same way from the same locations from two previous collections: one during November 1993 (1 month prior to corals spawning on 6 December); the other during December 2000 (5 weeks after the mass spawning of corals on 17 and 18 November). These samples serve two purposes. First, they aid in assessing the variability in larval traits during a time when the condition of females is not likely to be affected by the consumption of coral propagules. Secondly, the temporal series of samples serve to determine whether there is usually a difference in the morphology of larvae produced by females from the two localities (i.e., whether the result simply represents a location-specific effect).

Influence of experimental feeding on maternal condition and larval traits

To determine whether differences in female condition and larval morphology found in this natural experiment could be attributed to differences in feeding history, results were compared to the findings of a field experiment. A field experiment was conducted using *P. amboinensis* at a location on the leeward side of Lizard Island. Breeding pairs of *P. amboinensis* were placed on 10 isolated patch reefs (1×2m size of live and dead *Pocillopora damicornis*), 40 m off the reef edge and at least 40 m apart in 8–12 m water depth. Half of the breeding pairs were supplementarily fed a high-lipid diet of ground pilchards and prawns for 5 min a day (i.e., five pairs per treatment). Both pilchards and prawns are known for their high lipid contents (up to 20% in pilchards, Bandarra et al. 1997; García and Giménez 2002; 8–16% in prawns, Keys 2003). Moreover, the lipid in pilchards is dominated by triacylglycerols, which have a very high energy content (Bandarra et al. 1997). In contrast, coral propagules have been shown to contain 50–70% lipids (Richmond 1987; Arai et al. 1993). Although the supplementary diet in the present experiment does not mimic coral spawn, the experiment does enable the examination of the influence of additional maternal dietary energy on offspring characteristics.

Treatments were initially randomly assigned to pairs of fishes. Spawning was monitored daily for 6 weeks and larvae were collected, preserved, and measured as previously described. To test for the equality of means between treatments, analyses of variance were undertaken on the larval traits (SL, yolk-sac area, head depth, eye diameter) using clutch means as replicates (rather than using larvae as replicates, due to the problems of non-independence among larvae). Females were collected at the end of the experiment and Fulton's K and hepatosomatic index were both calculated using total body weight, rather than gutted body weight as above. Since supplementarily fed fish were not fed on the day of collection, it is assumed that the relative differences in stomach fullness would be small and would not affect the calculated ratios in a systematic way. Data are a subset of a larger experiment that examined the effect of food and social interactions on larval traits (see Kerrigan 1997).
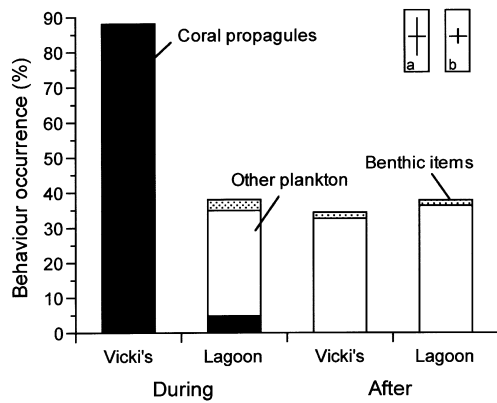
Fig. 1a, b Comparison of the mean occurrence of feeding on three different prey categories out of the total behavioral repertoire of female *Pomacentrus amboinensis* at two locations immediately after the coral spawning and 2 months later (*n*=3 censuses). Prey categories are: coral propagules floating in the water column; other plankton; benthic prey items. Tukey's 95% confidence limits are inset for comparisons of other plankton (**a**) and benthic items (**b**) among post-spawning locations and the pre-spawning lagoonal location (Sokal and Rolf 1995)

Results

Coral propagule consumption

Observations during the first 4 days after coral spawning indicated that coral propagules, which were in high densities in the first 2–3 m of the water column at the Vicki's Reef location, were not in high densities at the lagoon location. Of the 105 (±2.1 SE) females observed at the Vicki's location, an average of 88% were found to be in the water column feeding on coral propagules over the first 3 days after coral spawning (Fig. 1). In contrast, at the lagoon location only 38% of females were feeding (out of a total 101±3.3 SE individuals) and of those, only less than 5% were feeding on coral propagules. An additional 30% of females in the lagoon location were feeding on other plankton in the water column, and a further 3% directed bites to the benthic substratum. Two months after coral spawning, females at both locations showed similar patterns of foraging, with about 34% feeding on plankton, while 2% fed from benthic substrata.

Consumption patterns suggested that females at the Vicki's Reef location consume more coral propagules than those in the lagoonal location (Figs. 2, 3). Guts (without livers) were heavier relative to body weight for Vicki's Reef specimens compared to lagoonal fish immediately after coral spawning (ANOVA on relative gut weight, $F_{3, 36}$=44.97, P=0.001; Tukey's HSD on Fig. 2). The high relative gut weight at the lagoonal location immediately after coral spawning when compared to the relative gut size of both locations 2 months after coral spawning (Fig. 2) and the low quantities of coral propagules in their guts (Fig. 3) suggest that females may simply eat more during the early part of the summer.

Patterns of consumption showed that fish at the Vicki's Reef location had been feeding exclusively on coral
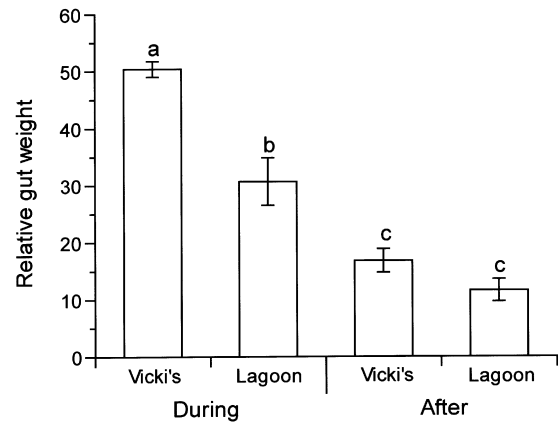

Fig. 2 Comparison of the gut weight (minus the liver) expressed as a percentage of gutted body weight at two locations immediately after the coral spawning and 2 months later. Letters above bars represent groupings from a posteriori Tukey's HSD means comparisons
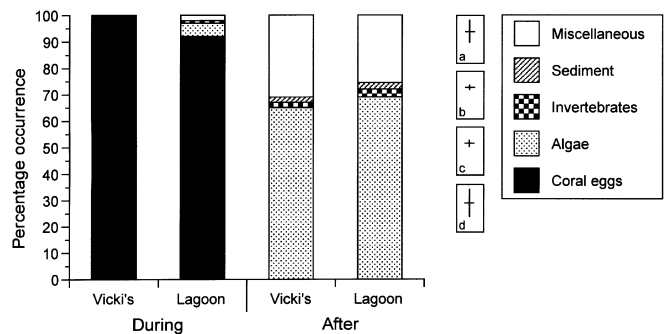

Fig. 3a–d Gut contents of female *Pomacentrus amboinensis* at two locations 5 days after the coral spawning, while coral propagules were still available in the water column, and 2 months later. Tukey's 95% confidence limits are inset to give variance estimates for **a** miscellaneous material, **b** sediment, **c** invertebrates, and **d** algae (Sokal and Rolf 1995)

propagules 5 days after coral spawning. Females collected from the lagoon contained largely coral propagules but also contained filamentous algae, a small number of invertebrates (amphipods), and miscellaneous organic material (Fig. 3). Two months later, fish from both locations had very similar diets that comprised 65–70% algal material (mostly filamentous), a small quantity of invertebrates and sediment, and over 25% miscellaneous organic material (Fig. 3). This latter material is believed to be partly planktonic in origin, containing some gelatinous components.

Body condition

The gutted body weight of the females collected from the two locations immediately after and 2 months after coral spawning did not differ from one another ($F_{3,36}$=1.94, P=0.141). A comparison of the body condition of females
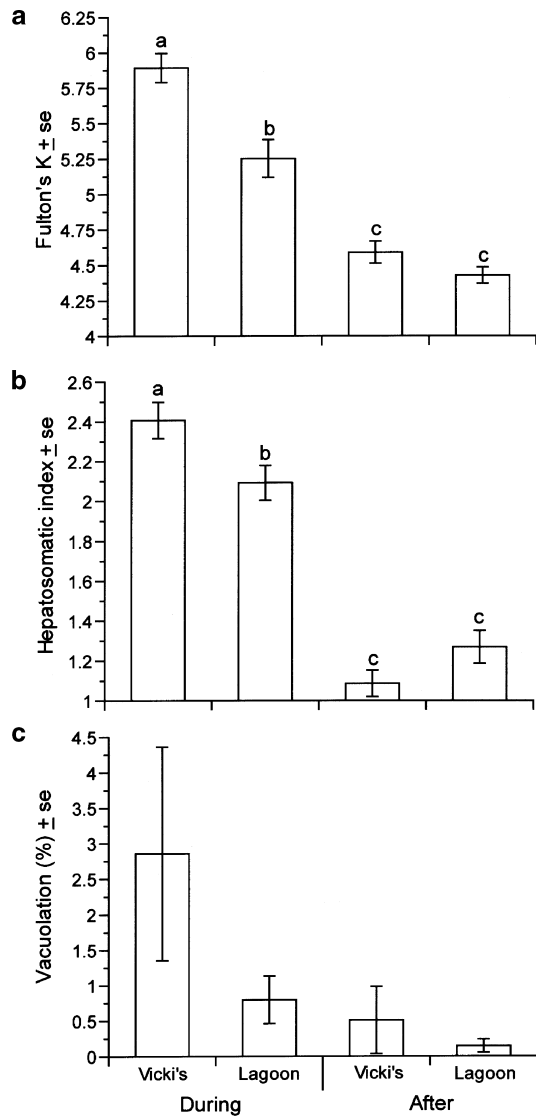
Fig. 4a–c Comparison of three measures of the body condition of female *Pomacentrus amboinensis* at two locations immediately after the coral spawning and 2 months later. **a** Fulton's condition factor (K×10^3). **b** Hepatosomatic index. **c** Proportional occurrence of hepatocyte vacuoles in lipid tissue. Means with standard error are displayed. Letters above bars represent groupings from a posteriori Tukey's HSD means comparisons

Fig. 5 Comparison of the morphology of *Pomacentrus amboinensis* larvae at hatching between the Vicki's Reef and Lagoon locations, over three times (once prior to coral spawning in November 1993, once 5 weeks after spawning in December 2000, and once immediately after spawning in December 2001). Larval traits examined are: total length, yolk-sac area, and oil-globule area. Letters above bars represent groupings from a posteriori Tukey's HSD means comparisons

5 days after and 2 months after coral spawning suggests that females had higher body condition at the Vicki's location, where fish had fed extensively on coral propagules (Fig. 4). Females at the Vicki's Reef location had significantly higher condition factor values (Fulton's K, ANOVA interaction, $F_{1,37}$=6.50, P=0.015) and higher hepatosomatic index values (ANOVA interaction, $F_{1,37}$=9.05, P=0.005) (Fig. 4a, b). Females from these locations did not differ from one another in either of these condition measures 2 months after coral spawning (Fig. 4a, b).

The high mean proportion of hepatocyte vacuoles in the liver at the Vicki's location 5 days after spawning suggests that at 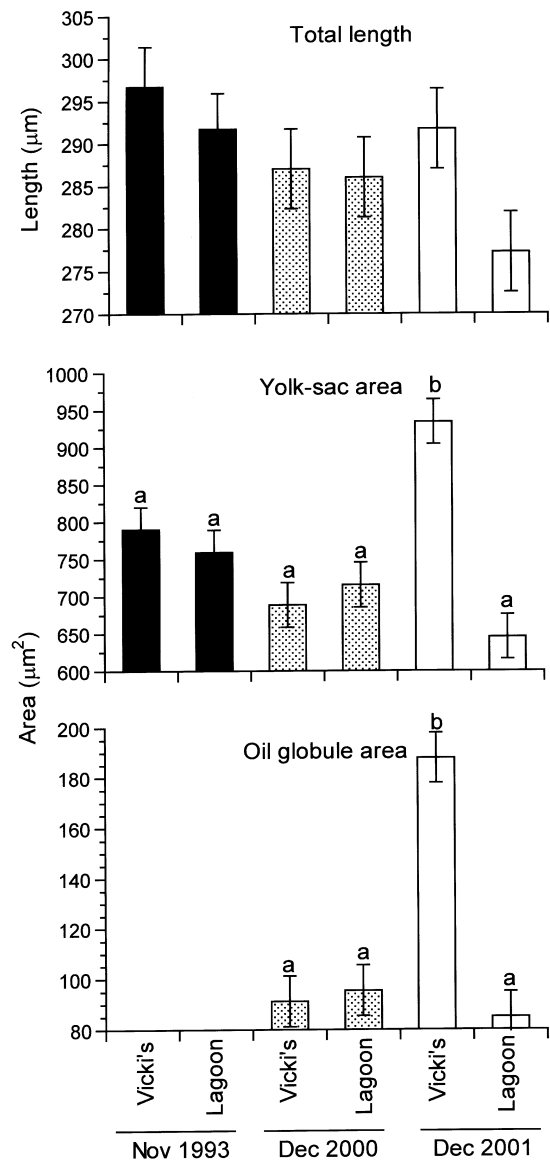least some of the difference in relative liver size (i.e., HSI) was due to increased storage of lipids and glycogen within the vacuoles. Hepatocyte vacuoles were highly variable in occurrence among females within a sample. This high variability meant that there was no significant difference in vacuole occurrence among samples (Fig. 4c, ANOVA interaction, $F_{1,37}$=0.78, P=0.384). Some fish had no vacuoles, while others had up to 15.2% of their liver composed of vacuoles. When vacuoles did occur they were not concentrated in any specific part of the liver but rather occurred throughout the liver.
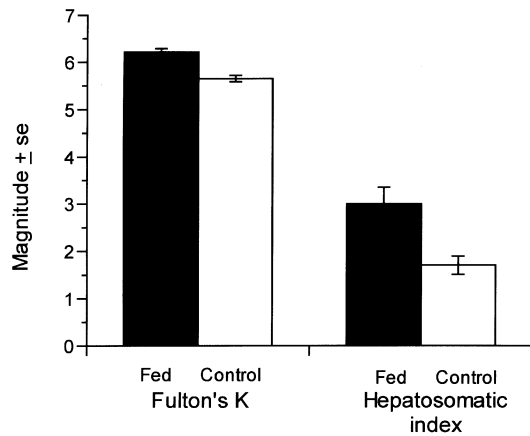
Fig. 6 Comparison of Fulton's condition factor ($\times 10^3$) and hepato-somatic index for female *Pomacentrus amboinensis* that have either been supplementarily fed for 5 min per day (*Fed*) or not supplementarily fed (*Control*)
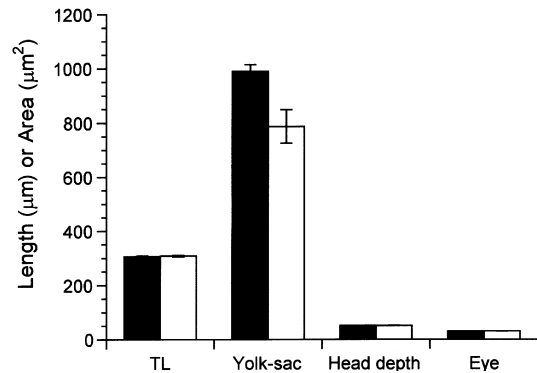

Fig. 7 Comparison of morphologies of larvae at hatching from *Pomacentrus amboinensis* females that have or have not been supplementarily fed for 5 min per day

Larval morphology

There was no significant difference in the total larval lengths at hatching among any of the samples collected from the two locations over the three summer periods ($F_{5,19}$=2.058, P=0.116, $\log_{10}(x)$ transformed; Fig. 5a). Although there was no statistical difference, it is interesting to note that the largest difference between the estimated means of the locations was for those larvae collected immediately after coral spawning.

The yolk-sac area of larvae from Vicki's Reef was 45% larger than those from lagoonal larvae hatched after the coral spawning of December 2001 ($F_{5,19}$=11.395, P<0.001, a posteriori Tukey's HSD tests; Fig. 5b). The Vicki's Reef larvae from December 2001 also had significantly larger yolks than larvae from either sampling location in the 1993 and 2000 samples (Fig. 5b). Oil-globule area mirrored the trends in yolk-sac area, being 2.2 times larger in Vicki's Reef larvae than those oil reserves found in the larvae collected from the lagoonal location at the same time ($F_{3,12}$=56.616, P<0.001; Fig. 5c).

Influence of experimental feeding on maternal condition and larval traits

Supplementary feeding with a high lipid diet for 5 min per day resulted in females that had a higher condition factor than those who were not fed additional food ($F_{1,7}$=33.327, P=0.001; Fig. 6). Fed females also had a higher relative liver weight than did their non-fed counterparts ($F_{1,7}$=11.688, P=0.011, Fig. 6). There were no significant differences in total length, head depth, or eye diameter at hatching between larvae from the supplementarily fed and not-fed treatments (Fig. 7). However, yolk-sac area was significantly larger in larvae from the supplementarily fed females than were those from females that had not been fed ($F_{1,5}$=7.042, P=0.04; Fig. 7).

Discussion

Evidence suggests that the damselfish *Pomacentrus amboinensis* is an opportunistic forager that switches from foraging on benthic items and a range of planktivorous prey to a diet dominated by coral propagules when available. This supports research that has shown that other planktivores exhibit prey switching to capitalize on an energy-rich diet of coral spawn (Westneat and Resing 1988; Pratchett et al. 2001). Evidence from the present study showed that the consumption of coral propagules in the days following the mass coral spawning increased the condition of *P. amboinensis* and that this increased body condition led to a potential survival advantage for the larvae they subsequently produced. The current findings reinforce the importance of non-genetic maternal contributions to offspring success for organisms with complex life cycles. Similar positive relationships between maternal nutrition and maternal investment per offspring have been found in such diverse animals as copepods, bivalves, and sea urchins (Bayne et al. 1978; Thompson 1982; Guisande and Harris 1995), but few data exist for marine fishes (e.g., Chambers and Leggett 1996; Heath and Blouw 1998).

The agreement between results from the natural and patch-reef experiment suggests that the consumption of coral propagules directly resulted in enhanced female body condition. Field and laboratory studies have shown that damselfish that receive elevated levels of food display similar increases in body condition (Coates 1980; Jones 1986; Forrester 1990; Kerrigan 1994). Similar results were found by a recent study of the effects on body condition of the consumption of coral propagules by two other damselfish species. Pratchett et al. (2001) found that *Pomacentrus moluccensis* and *Abudefduf whitleyi* that had consumed large quantities of coral propagules exhibited increased lipid storage within their liver. This contrasted with another planktivore, *Caesio cunning*, collected at the same place and time and that had not eaten coral propagules, which showed no elevation in storage vacuoles in the liver.

Studies that have found impacts of feeding levels or diet on egg or progeny quality have manipulated food for weeks to months (e.g., Hislop et al. 1978; Coward and Bromage 1999). The present study suggests that a pulse of high-energy food lasting only 5 days can have detectable and advantageous effects on larval quality. This rapid mobilization of nutritional products into the eggs is a facet of a reproductive mode that enables the species to serially spawn ~3,000 eggs every 2 days for the duration of an approximately 4-month reproductive season (Kerrigan 1995; McCormick unpublished data). Other damselfishes have been found to have similar reproductive modes (Moyer 1975; Doherty 1983; Danilowicz 1995; Richardson et al. 1997), suggesting that the enhanced larval quality that resulted from females consuming coral propagules may be a general result for the broad array of fishes that feed on the gametes released during the annual mass spawning of corals.

The present study suggests that females that fed on a high-lipid diet produced larvae that had large yolk sacs at hatching. This was true for both females that had fed extensively on coral propagules for 5 days and those that had been supplementarily fed for just 5 min per day. There is a large body of research on temperate fishes to suggest that a larger yolk sac enhances the probability of surviving the crucial period when larvae have just hatched and are learning to feed effectively (Blaxter and Hempel 1966; Johns and Howell 1980; Blaxter 1988). These yolk reserves can be mobilized to sustain maintenance and growth during periods of physiological stress or limited food availability, thereby increasing the time to irreversible starvation (Bagarinao 1986; Heming and Buddington 1988). In a detailed study of the early life-history traits that influenced survival in capelin larvae, Chambers et al. (1989) found a moderately strong positive relationship ($r=0.54$) between yolk volume at hatching and post-hatching lifespan. The author knows of no study of a tropical species to support this link between yolk-sac size and survival. However, a recent study of a tropical surgeonfish, *Acanthurus chirugus*, found a strong relationship between growth around the time of first feeding and cohort strength, suggesting that a large yolk sac could be advantageous (Bergenius et al. 2002).

Females with higher body condition produced not only larvae with larger yolks but also larvae with oil globules that were double that of less well-fed females. Studies on fish larvae with oil globules in the yolk suggest that the size of the oil globule after hatching may be important for post-hatching survival (e.g., Blaxter 1969; Avila and Juario 1987; Chambers et al. 1989; Rønnestad et al. 1998). Evidence suggests that the energy is stored in different forms in fishes that have oil droplets in their yolk compared to those that must depend exclusively on yolk matter (Rønnestad et al. 1998). Eggs containing an oil globule have high lipid content, and a substantial amount of the energy required to sustain early development and growth comes from the utilization of lipids from the oil globule (Rønnestad et al. 1994; Fyhn and Govoni 1995; Finn et al. 1995; Rønnestad et al. 1998).

Utilization of this lipid store changes with the development of the embryo and larvae (e.g., Kuo et al. 1973; Ehrlich and Muszynski 1982; Avila and Juario 1987; Rønnestad et al. 1998). Studies that have examined utilization of yolk components in marine fishes that possess discrete oil globules in their yolk indicate that prior to hatching, lipid classes are used unselectively. However, once hatched, there is a selective catabolism of triglycerides from within the oil globule, while phospholipids in the rest of the yolk are incorporated into structural components (e.g., membranes) of the developing fish (Heming and Buddington 1988; Rønnestad et al. 1994; Wiegand 1996). Although the yolks of teleost fishes are composed of more protein than lipid (35–89% versus 3–54%, respectively, depending on species; Kamler 1992), lipids are the most important energy reserve in developing fish due to their higher calorific value. It is estimated that there is 1.7 times as much energy in the lipids within the oil globule than is contained within the proteins and phospholipids that comprise the yolk platelets (Heming and Buddington 1988). Moodie et al. (1989) suggested that oil globule use may be related to larval well-being. Their results showed that walleye salmon (*Stizostedion vitreum*) that grew well delayed utilization of the oil globule, while slower-growing larvae used oil more rapidly. They suggested that the ratio of oil volume to length could be used as an indicator of larval vigor. They also found that those larvae that hatched from eggs with larger yolk and oil globule volumes suffered lower mortality. Likewise, Chambers et al. (1989) found that larvae of the capelin (*Mallotus villosus*) that had larger oil reserves survived longer when starved. Thus, this high-energy source within the oil globule is important for fueling the transition to exogenous feeding and therefore for the survival of larvae (Bagarinao 1986).

The size of the oil globule is also important because the oil globule is the last part of the maternally derived nutrition that is utilized during larval development (Avila and Juario 1987; Rønnestad et al. 1998). The relative size of the oil globule may be a better indicator of larval condition at hatching than the size of the yolk alone due to its importance as a source of energy in the days immediately after hatching. This is supported by Chambers et al. (1989), who found that the size of the oil globule was a better predictor of post-hatching longevity for capelin larvae than was yolk-sac size ($r=0.68$ and 0.54, respectively).

Any factor that enhances the condition of breeding females is likely to result in the production of progeny of higher quality that have a better chance of survival. By the time the annual mass spawning of corals occurs, 3–4 days after the full moon in spring, many tropical fishes are well into their own annual reproduction cycle. The present study demonstrates that the consumption of coral gametes not only helps fuel some of the high energy demands associated with gametogenesis but also results in the production of higher-quality larvae. Experiments that assess the survival and performance of larvae of variable yolk and oil reserves are required before predictions can

be made regarding the importance of the levels of variability found in the present study.

It is also unknown whether the enhancement of larval quality that stems from the maternal consumption of coral spawn leads to increased cohort success. Recent studies suggest that growth advantages obtained early in larval life not only predispose individuals to surviving the rigors of the larval phase but also enhance survival after settlement (Bergenius et al. 2002; Vigliola and Meekan 2002). This suggests that larvae released from spawnings by females who have consumed coral propagules may result in a pulse of superior larvae and settlers. Although spawning intensity accounts for much of the variability in the temporal patterns of recruitment in some benthic spawning coral reef fishes (Meekan et al. 1993), the huge differences in abundance among pulses of recruits are presently unexplained. Differences in the quality of individual larvae derived from maternal sources may account for some of this variability in larval survival.

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