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Filial cannibalism improves survival and development of beaugregory damselfish embryos

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Cannibalism of small numbers of offspring by a parent has been proposed as an adaptive parental strategy, by providing energy to support parental care. However, there are few empirical studies to support this hypothesis. We conducted field and laboratory experiments to investigate partial filial cannibalism in *Stegastes leucostictus*, a coral reef fish with paternal care. Partial cannibalism was shown to be common, and males were found to remove developing embryos from throughout a clutch in a random pattern, rather than in the more aggregated pattern seen during embryo predation. Males that received a diet supplement grew faster than control males, but did not engage in less cannibalism. Also, males did not concentrate cannibalism on early embryonic stages with the highest energetic value. Experimental reduction of embryo densities was found to significantly increase embryo development rate and survival from egg deposition to hatching, and experimental reduction of oxygen levels significantly increased rates of partial filial cannibalism by males. Artificial spawning sites with low oxygen levels were avoided by spawning females, and cannibalism rates by males were higher. We propose that partial filial cannibalism serves as an adaptive parental strategy to low oxygen levels in *S. leucostictus* by increasing the hatching success of embryos.

Keywords: oviposition choice; oxygen; parental care; paternal care; Pomacentridae

1. INTRODUCTION

Cannibalism is widespread and common among fishes and represents a special form of predation (Smith & Reay 1991; Fitzgerald & Whoriskey 1992). Filial cannibalism, the process of eating offspring, has been recorded in a range of fish species (reviewed by Smith & Reay 1991), and is commonly found in species giving parental care (Smith & Wootton 1995; Manica 2002). There are two ways in which filial cannibalism may be an adaptive parental strategy. Total or whole clutch cannibalism occurs when a parent eats its entire brood. Total cannibalism is usually of broods that are small or of low quality (Smith 1992). Parental care in fishes is a divisible resource, so per capita expenditure on offspring is higher for a small brood than for a large brood (Lazarus & Inglis 1986). The adaptive value of total filial cannibalism arises by allowing parental time and energy to be allocated to future, and potentially larger, broods, in accordance with the principle suggested by Williams (1966). Several studies have demonstrated that smaller broods are more commonly eaten by parents than larger clutches (Dominey & Blumer 1984; Ochi 1985; Schwank 1986; DeMartini 1987; Mrowka 1987; Sargent 1988; Petersen & Marchetti 1989; Lavery & Keenleyside 1990; Petersen 1990; Petersen & Hess 1991), and experimental reduction of clutches has demonstrated that parents have a threshold clutch size under which a brood is totally cannibalized (Mrowka 1987; Petersen & Marchetti 1989; Lavery & Keenleyside 1990).

Partial clutch cannibalism occurs when a parent, usually the male, eats a proportion of the offspring during the parental care period. Rohwer (1978) proposed a hypothesis for partial filial cannibalism in which he argued that parental males could consume some of their offspring to obtain energy to complete a parental cycle. Rohwer's hypothesis assumed that parental males are food limited and that offspring represent an adequate alternative energy source (Sargent 1992). These assumptions may be justified in some circumstances (but see Smith 1992). Thus, partial cannibalism is predicted to be both an investment in current and future reproductive success (Sargent 1992), and is adaptive because by eating some of their embryos, parental males can minimize any deterioration of their body condition caused by reduced foraging opportunities and the high energetic cost of care. Thus, partial filial cannibalism will enable a male to complete his current parental cycle, and remain in sufficiently good condition to engage in further breeding cycles (Rohwer 1978; Sargent 1992). However, empirical tests of Rohwer's hypothesis have proved equivocal. Only studies by Hoelzer (1992) and Kvarnemo *et al.* (1998) have shown any direct link between ration and partial cannibalism. Hoelzer (1992) demonstrated that male *Stegastes rectifraenum*, whose diets were supplemented with other males' embryos, decreased cannibalism of their own offspring, although cannibalism was never fully inhibited. Kvarnemo *et al.* (1998) also showed that supplementing the diets of male *Pomatoschistus minutus* could decrease cannibalism, although they found that embryos had no special nutritional characteristics compared with a normal diet. By contrast, studies by Lavery & Keenleyside (1990), Belles-Isles & Fitzgerald (1991), Kvarnemo (1997), Lindström & Sargent (1997) and Vinyoles *et al.* (1999) have all found no relationship between ration and cannibalism. Thus, it is questionable whether a nutritional benefit alone can account for the widespread occurrence of partial filial cannibalism in fishes.

Parental care has two functions; to maximize offspring survival and to promote their development (Smith & Wootton 1995). In fishes, the predominant form of care is guarding the offspring. In many species, parents also fan

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the embryos with their fins to oxygenate them. Besides predation, oxygen is the predominant factor affecting the successful development of embryos; reduced oxygen retards embryo development and causes mortalities (Kamler 1992).

Our aim in this study was to investigate the role of both supplemental feeding and oxygen availability on partial filial cannibalism in a marine teleost fish with male parental care, the beaugregory damselfish *Stegastes leucostictus*. This fish has commonly been used in studies on breeding success (Itzkowitz & Makie 1986; Itzkowitz 1991; Itzkowitz & Haley 1998) and is known to perform partial filial cannibalism (Itzkowitz & Makie 1986), as are many congeners (*S. dorsopunicans* (Petersen 1990; Petersen & Hess 1991); *S. partitus* (Knapp & Kovach 1991; Knapp & Warner 1991); *S. rectifraenum* (Hoelzer 1988, 1992; Petersen & Marchetti 1989)). Males are territorial and use their territory for both feeding and reproduction (Ebersole 1977; Itzkowitz 1977, 1985, 1990; Itzkowitz & Makie 1986; Itzkowitz & Slocum 1995). Parental care consists solely of guarding, and males do not fan developing embryos (Breder & Rosen 1966; Thresher 1984; Itzkowitz & Makie 1986).

2. METHODS

(a) *Study site and artificial spawning habitat*

Field data were collected from two study sites within the back-reef area of Discovery Bay, Jamaica. The sites were *ca.* 75 m from the reef crest in a water depth of 1–2 m. Both sites consisted of areas of the sea grass *Thalassia testudinum*, sand and coral rubble with scattered coral heads of *Sidastrea siderea* (Woodley & Robinson 1977). *Stegastes leucostictus* occupies areas of coral rubble and often shares this habitat with other damselfish species (Itzkowitz 1977).

At study site A, 65 five-entry artificial spawning habitats, called 'condos' (Itzkowitz & Makie 1986; Itzkowitz 1991), were placed haphazardly throughout the coral rubble habitat. At site B, 30 single-entry and 35 five-entry condos were similarly placed. Not all condos were used in experiments simultaneously. The five-entry condos consisted of four PVC pipes measuring 100 mm (length) × 76 mm (diameter) bolted at right angles onto a Plexiglas base of 30 cm^2 (see Itzkowitz & Makie 1986). Males were able to enter each section of the pipe from either end and water was able to move freely through it. Single-entry condos had the top and three of the outer entrances blocked off with 8 cm^2 squares of Plexiglas, such that the males could only enter the condo through the single tunnel that was unblocked. Water movement through single-entry condos was more restricted than through five-entry condos. Male *S. leucostictus* guard condos and use them as a focus for territorial defence and as refuges, and females readily spawn on the inside of the PVC pipe tunnels (Itzkowitz & Makie 1986; Itzkowitz 1991). To enable us to make accurate counts of the egg masses in condos, acetate sheets measuring 90 mm × 280 mm, on which a grid of 4 mm^2 squares had been photocopied, were rolled into a cylinder and placed inside the pipe tunnels of every condo. All condos were occupied by male *S. leucostictus* within 72 hours of being placed on the reef. Males removed from condos in the course of experimental work were always replaced within 24 hours.

(b) *Evidence for partial filial cannibalism and patterns of embryo loss*

Over three consecutive mornings, 30 males, whose condos contained developing embryos, were caught with a hand net and immediately killed by cutting their spine at the base of the skull. They were placed on ice within 30 min and frozen within a further 20 min. Their gut contents were later examined under a low power microscope to assess the extent of cannibalism among males. All embryos found in the stomachs of males were counted and staged according to Brinley (1939). A record was made of the developmental stage of embryos in the condos from which each male was removed. Five non-parental males were also collected and their gut contents similarly examined. Only five non-parental males were examined for ethical reasons; to minimize the number of fishes that were sacrificed in the study. Previous behavioural studies had indicated that non-parental males rarely entered the nests of parental males to cannibalize embryos, and these fishes were dissected as a further assurance that non-parental males were not a significant source of embryo cannibalism. Before dissection, each male was weighed to the nearest 1 mg to provide a crude measure of body size, and his standard length (SL) measured (from the tip of the snout to the origin of the tail) to the nearest 0.1 mm.

In a further study with a different group of males, we investigated the pattern of removal of embryos by males during filial cannibalism. Acetate strips on which embryos had been laid were removed from nine condos and the clutches examined under a low power microscope. For each clutch a 20 mm × 40 mm square of embryos from the centre of the clutch (where egg density was highest) was selected, and the number of 4 mm^2 squares from which embryos were missing was recorded. Acetate strips with embryos on them were removed from a further nine condos and placed in the condos of males without embryos for *ca.* 5 min and allowed to be cannibalized. The acetate strips were then removed and the missing embryos were scored as described above. During this experiment, other fishes, principally *Thallasoma bifasciatum*, also sometimes participated in predation of embryos transferred between condos.

(c) *Ration and partial filial cannibalism*

To investigate the effect of ration on filial cannibalism, 50 males, occupying five-entry condos at study site A, were randomly assigned to one of two treatments, diet-supplemented or unsupplemented. The males in the diet-supplemented treatment were fed every day with a *Nutrafin* freeze-dried tablet, which was pressed onto the Plexiglas base of the condo. The mean weight of the tablets was 468 mg (s.e. = 3.17 mg) and the mean calorific content was estimated as 432 J (s.e. = 2.93 J). Pilot studies had shown that males would feed readily on these tablets and would habituate to being fed. The males in the unsupplemented treatment received no extra food. On each day of the experiment the size of each new clutch acquired by the males and the size of clutches already present from previous spawnings were recorded by removing the acetate strip and counting the number of 4 mm^2 squares that the clutch covered. Each clutch within a condo was laid by a different female, although the same females may have spawned with the same male on different occasions over the course of the study. Occasionally, two clutches were laid adjacent to each other within a short period by different females. However, it was always clear from the pattern in which the eggs were deposited to which clutch eggs belonged and there was never ambiguity as to how many clutches had been laid. A record was kept of the appearance of every experimental male, noting distinguishing marks, to confirm whether the same male was resident on each day of the experiment. On the sixth day after the start of the experiment, 10 males belonging to both treatments were caught with a hand net and their SL measured. On the fourteenth day the same 20 males were re-measured. Males were measured to test whether supplemental feeding had any effect on growth during the experiment. Fish length, rather than weight, was used to estimate growth for practical and logistical reasons. After 14 days the supplemental feeding was stopped and 10 males from each treatment were monitored for a further 14 days. The experiment lasted a total of 28 days.

To quantify the calorific value of embryos at different developmental stages, a total of 15 acetate strips on which embryos were developing was removed from condos and transported in seawater to the laboratory. Embryos were removed with a scalpel blade to leave only a 20 mm × 40 mm patch of embryos. The total number of embryos remaining was then counted and staged according to Brinley (1939). These embryos were then blotted with tissue paper, removed from the acetate strip with a scalpel blade and placed on a piece of pre-weighed aluminium foil. The foil and embryos were weighed to the nearest 0.1 mg and dried in an oven at 60 °C. After 48 h the embryos were removed from the oven and re-weighed to obtain embryo dry weight. Estimates of the mean calorific content of the unhatched embryos were made using a mean calorific value of 23.48 J mg^{-1} dry weight (Kamler 1992).

(d) *Oxygen availability and partial filial cannibalism*

To investigate the effect of egg density on embryo developmental rate and survival rate, between egg deposition and hatching, 29 acetate strips on which embryos had been laid were collected from condos and transported to the laboratory in seawater. In each clutch two separate 100 mm^2 squares were selected that were surrounded on all sides by at least one other 100 mm^2 square completely covered with embryos. One of these squares was randomly assigned as a control and the other as the treatment. The density of embryos in the treatment square was reduced by a mean of 42% (s.e. = 2.37%), from an initial density of 108.6 embryos cm^{-2} (s.e. = 3.01 embryos cm^{-2}), by carefully removing embryos, in a haphazard manner, with a pair of fine forceps. The surrounding 4 mm^2 on each side of the treatment square was also reduced in density so that the treatment extended into the adjacent 100 mm^2 square. The numbers of embryos in the treatment and control squares were counted and every egg in the two squares was assigned to developmental stages using Brinley (1939). The density of embryos in the control squares was 107.5 embryos cm^{-2} (s.e. = 4.11 embryos cm^{-2}). The acetate strip was rolled up and placed inside a section of PVC tube of the same dimensions as that of a condo. The tube was placed inside a seawater tank measuring 51 cm (width) × 152 cm (length) × 10 cm (depth) with seawater flowing through it at a rate of *ca.* 5 l min^{-1}. After 24 hours the embryos were counted and staged in both the control and treatment squares. Exactly the same procedure was carried out for another batch of 26 clutches and the density of embryos in the treatment square was reduced by a mean of 41% (s.e. = 2.68%), from an initial density of 103.2 embryos cm^{-2} (s.e. = 3.12 embryos cm^{-2}). In this case they were left in the seawater tank for 48 hours. The density of embryos in the control squares was 104.1 embryos cm^{-2} (s.e. = 4.26 embryos cm^{-2}).

We conducted a further experiment to measure the response of males, in terms of rates of partial filial cannibalism, to low oxygen conditions. The experiment was conducted in four seawater tanks measuring 110 cm (width) × 160 cm (length) × 31 cm (depth) that were supplied with recirculating seawater and containing a five-entrance condo. Two treatments, of high and low oxygen, were used. In the high oxygen treatment the water in the tanks was aerated strongly and water flow through the tank was high (at a rate of *ca.* 10 l min^{-1}). In the low oxygen treatment the water was not aerated and water circulation was minimal. Parental male *S. leucostictus* at study sites A and B were caught with a hand net and transported, along with the acetate strips with their embryos, to the laboratory in seawater. The number of embryos in eight randomly selected squares of 100 mm^2 of each male's clutch were quickly counted in a tray of seawater and the embryos staged. Once the counting and staging was complete, the acetate strips with embryos on them were placed inside the condo in the tank and the male was released into the tank. Males were randomly assigned to either the high or low oxygen treatment. After 24 hours and 48 hours the clutch was removed and the number of embryos in the same eight squares were again counted and staged. Oxygen levels in the experimental tanks were monitored inside each condo by taking water samples twice a day at 0600 and 1500. A tube attached to a 60 ml syringe was inserted into the centre of a condo and a water sample drawn slowly into the syringe. The water sample was immediately placed into the bottom of a 50 ml glass volumetric flask, such that the water entering the flask replaced the air in the flask but did not mix with it. The oxygen content of the water samples was determined using the Winkler method (Parsons *et al.* 1984).

(e) *Spawning site choice and partial filial cannibalism*

Acetate strips on which embryos had been laid were collected from 35 single- and 37 five-entry condos and transported to the laboratory in seawater. The number of embryos on between five and ten 1 cm^2 squares were counted and staged. The density of embryos at each developmental stage in each condo type was compared to investigate whether egg density differed between condo types.

For single-entry condos alone, we also monitored, over a period of two weeks, the number of clutches that each male received and where inside the condo each clutch was spawned, with a distinction drawn between eggs laid in the single open-ended tube and the three blind-ended sections. On each day of the experiment, the size of each new clutch and the size of clutches already present were recorded. To investigate the oxygen conditions in single- and five-entry condos, water samples were taken from inside the tunnels of seven of each condo type, using a 60 ml syringe with a tube attached. Once water had been drawn into the syringe, it was transferred to a glass 50 ml volumetric flask on an accompanying boat. Reagents were added to enable a Winkler titration for oxygen analysis to be carried out. Water samples were placed in a lightproof box and transported to the laboratory for titration. Water samples for oxygen determination were also collected from the water column above condos using a 300 ml glass bottle with a modified stopper. The stopper had two tubes, one allowing water into the bottom and another shorter one allowing air to escape at the top, preventing mixing of the sampled water and air in the bottle. Water samples were collected between 0530 and 0630, at a time when oxygen levels were at their lowest level on the reef.

(f) *Data analysis*

All data were tested for normality using a Kolmogorov–Smirnov test and for equality of variance using a Bartlett's test. For comparing the stage of embryos in males' stomachs and their nests, a χ^2-test was used and the weights of the cannibalistic and non-cannibalistic males were compared using an unpaired t-test. An index of dispersion was used to quantify patterns of egg loss in clutches (Krebs 1989), and an unpaired t-test was used to compare the patterns of egg loss by unrelated males (or predation) and filial cannibalism.

For the ration and filial cannibalism experiment, the lengths of males in the 'supplemented diet' and 'unsupplemented diet' treatments were compared using a paired one-tailed t-test. We used a one-tailed test because we predicted *a priori* that supplementing the diets of males would have the effect of increasing their growth rate, and we used a paired design to control for variability in growth rates among locations on the reef. A Mann–Whitney U-test was used to compare the instantaneous mortality rates of embryos due to partial cannibalism and unpaired t-tests to compare the number and size of clutches received by males in each treatment. In the case of the comparison of partial cannibalism at different time stages, the Scheirer–Ray–Hare test was used as a non-parametric equivalent of the two-way ANOVA (Dytham 1999). An ANCOVA, with the number of clutches received as the covariate, was used to compare 10 males from the two treatments during and after imposing each treatment. The calorific content of embryo developmental stages was compared using a one-way ANOVA, with Fisher's least significance difference (LSD) method as a *post hoc* comparison. A Wilcoxon signed ranks test was used to compare the treatment and control squares in the manipulation of egg density experiment, and a paired t-test was employed to compare the numbers of embryos hatching after 48 hours. Oxygen concentrations in experimental tanks in the afternoon and morning between treatments were compared in the oxygen and partial cannibalism experiment using a two-way ANOVA. Unpaired t-tests were used to compare instantaneous mortality rates between high and low treatments after 24 hours and 48 hours. A two-way ANOVA was used to compare the density of embryos in five- and single-entry condos at different developmental stages. A paired t-test was used to compare the number of clutches received in the different sections of single-entry condos, and a one-way ANOVA to compare the oxygen concentrations of five- and single-entry condos, with Fisher's LSD method used to identify where significant differences lay.

3. RESULTS

(a) *Evidence for partial filial cannibalism and patterns of embryo loss*

Of the 30 males caught whose nests contained embryos, 13 had embryos in their stomachs. There was no difference between the stages of embryos in the stomachs of males and those the males were guarding ($\chi^2 = 0.71$, d.f. = 2, $p = 0.703$). There was no difference in the body weights of males with embryos in their stomachs and those without ($\log_{10}$ transformation, unpaired t-test: $t = 1.08$, d.f. = 24, $p = 0.283$), indicating that males who had recently cannibalized embryos were not significantly smaller or in a worse condition than males that had not recently cannibalized embryos. Embryos in the stomachs of males were not dead or fungus-infected; in some cases they appeared to have been eaten within minutes and appeared normal healthy embryos. Of the five males whose stomach contents were examined that were not guarding embryos, none had embryos in their stomachs.

The index of dispersion for the pattern of egg losses on acetate sheets by filial cannibalism indicated a random pattern of egg loss (mean = 0.7, s.e. = 0.08), whereas clutches that had undergone cannibalism by unrelated males and predation were aggregated (mean = 2.0, s.e. = 0.35). This difference was highly significant ($\log_{10}$ transformation, unpaired t-test: $t = 4.79$, d.f. = 16, $p < 0.001$), indicating that non-kin cannibalism and predation were characterized by the removal of embryos in large patches, whereas filial cannibalism typically involved the removal of a few embryos from many areas throughout a clutch.

(b) *Ration and partial filial cannibalism*

The sub-sample of males in the supplemented diet treatment, whose growth rates were measured between days 6 and 14, showed a significantly greater increase in body length compared with control males over the study period (one-tailed paired t-test: $t = 2.05$, d.f. = 18, $p = 0.028$). The mean specific growth rate of fed males was 0.98% (s.e. = 0.102%), and for unfed males 0.68% (s.e. = 0.107%). However, there was no difference in the instantaneous mortality rates of embryos guarded by males that received supplemental feeding and those that did not (Mann–Whitney U-test: $U = 278.5$, $n = 50$, $p = 0.509$). There was also no difference in the number of clutches received by males in the two treatments (unpaired t-test: $t = 0.35$, d.f. = 48, $p = 0.725$), or of the size of clutches that males received (unpaired t-test: $t = 0.83$, d.f. = 48, $p = 0.408$). The mean number of clutches received by fed males over the 14 day study was 6.88 (s.e. = 0.609) and for unfed males 6.56 (s.e. = 0.669). The mean size of clutches was 28.6 cm^{-2} (s.e. = 1.80 cm^{-2}) for fed males and 26.5 cm^{-2} (s.e. = 1.62 cm^{-2}) for unfed males. There was no significant difference in the rate of mortality of embryos at different developmental stages (Scheirer–Ray–Hare: $\chi^2 = 0.54$, d.f. = 3, $p = 0.459$), despite more embryos being eaten between days 4 and 5, when they were close to hatching (figure 1). There was no difference in the rate of embryo mortality of clutches guarded by males during and after the imposition of treatments ($\log_{10}$ transformation, ANCOVA: $F_{1,28} = 0.382$, $p = 0.541$).

The energetic values of embryo stages 1–2, 3–5 and 6–8 were significantly different (ANOVA: $F_{2,18} = 7.99$, $p = 0.003$). Stages 1–2 had the highest calorific content and stages 6–8 the lowest. There was no difference between stages 3–5 and stages 6–8 (Fisher's LSD: $p = 0.155$), whereas stages 1–2 differed significantly from both (Fisher's LSD: $p = 0.001$ and $p = 0.016$, respectively) (figure 2).

(c) *Oxygen availability and partial filial cannibalism*

After 24 hours, embryos in the treatment squares had developed significantly faster than embryos in control squares (Wilcoxon signed ranks test: $W = 190$, d.f. = 27, $p < 0.001$). The median stage of 19 treatment squares was at least one full development step more advanced than paired controls. The same was true after 48 hours

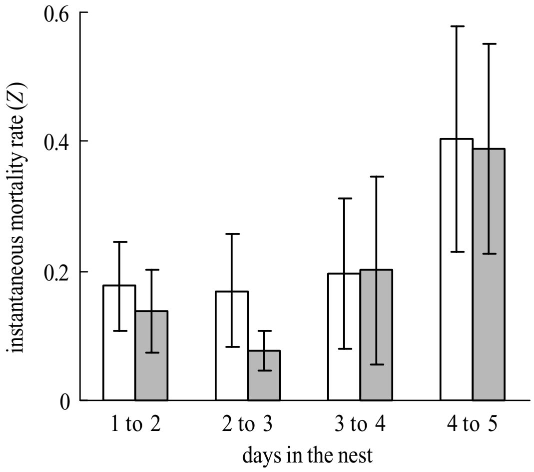

Figure 1. Mean (± 1 s.e.) instantaneous mortality rates of *Stegastes leucostictus* embryos guarded by males with a supplemented diet treatment (white bars) and unsupplemented diet treatment (stippled bars) at four periods following spawning.

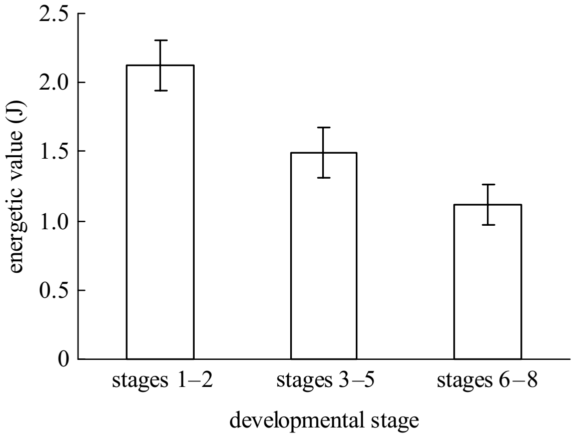

Figure 2. Mean (± 1 s.e.) energetic value (J) of embryos at three developmental stages.

(Wilcoxon signed ranks test: $W = 105$, d.f. = 24, $p = 0.001$), with two cases in which the median stage of embryos in treatment squares was two full development steps more advanced than the control. A significantly greater proportion of embryos hatched from treatment squares compared with control squares after 48 hours (paired *t*-test: $t = 3.28$, d.f. = 19, $p = 0.004$).

As anticipated, the dissolved oxygen level of seawater in the experiment to measure the response of parental males to oxygen conditions was significantly lower in the low oxygen treatment than in the high oxygen treatment (ANOVA: $F_{1,52} = 15.09$, $p < 0.001$). Oxygen levels varied between morning (0600) and afternoon (1500), with mean morning oxygen concentration in the high oxygen treatment 4.09 mg l^{-1} (s.e. = 0.042 mg l^{-1}) and in the low oxygen treatment 3.74 mg l^{-1} (s.e. = 0.098 mg l^{-1}). The mean afternoon oxygen concentrations were 4.31 mg l^{-1} (s.e. = 0.100 mg l^{-1}) and 3.95 mg l^{-1} (s.e. = 0.100 mg l^{-1}), respectively. There was a significant difference between morning and afternoon oxygen levels (ANOVA: $F_{1,52} = 5.83$, $p = 0.019$) as a consequence of algal respiration and photosynthesis, although no interaction between treatments and the time oxygen levels were measured (ANOVA: $F_{1,52} = 0.013$, $p = 0.910$).

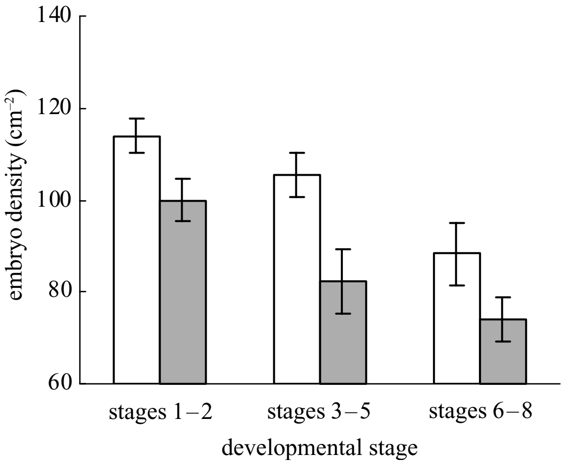

Figure 3. Mean (± 1 s.e.) embryo density for five-entry (white bars) and single-entry condos (stippled bars) at three developmental stages.

The mean instantaneous mortality rate of embryos due to partial filial cannibalism after 24 hours was significantly higher for the low oxygen treatment than for the high oxygen treatment ($\log_{10}$ transformation, unpaired *t*-test: $t = 2.35$, d.f. = 20, $p = 0.029$). The mean instantaneous mortality rate for the low treatment was 0.33 (s.e. = 0.105) and for the high treatment 0.24 (s.e. = 0.184). After 48 hours the mean mortality rate for the low oxygen treatment was 0.34 (s.e. = 0.126) and for the high treatment it was 0.05 (s.e. = 0.007) and this difference was highly significant ($\log_{10}$ transformation, unpaired *t*-test: $t = 5.08$, d.f. = 16, $p < 0.001$).

(d) *Spawning site choice and partial filial cannibalism*

The mean density of embryos in five-entry condos was 103 cm^{-2} (s.e. = 3.41 cm^{-2}) and in single-entry condos 86 cm^{-2} (s.e. = 3.65 cm^{-2}) (figure 3). This difference was significant (ANOVA: $F_{1,66} = 15.12$, $p = 0.002$). There was also a significant difference in the density of embryos at different stages of development (ANOVA: $F_{2,66} = 11.09$, $p < 0.001$). The mean density at stages 1–2 was 107 cm^{-2} (s.e. = 3.23 cm^{-2}), at stages 3–5 it was 94 cm^{-2} (s.e. = 4.72 cm^{-2}) and at stages 6–8 it was 81 cm^{-2} (s.e. = 4.46 cm^{-2}) (figure 3). However, there was no significant interaction between developmental stage and condo type (ANOVA: $F_{2,66} = 0.46$, $p = 0.633$).

The open tube of single-entry condos received a mean of 4.6 clutches male^{-1} (s.e. = 0.31 clutches male^{-1}), whereas the three closed tubes received a mean of 0.44 clutches male^{-1} (s.e. = 0.07 clutches male^{-1}), a highly significant difference (paired *t*-test: $t = 13.25$, d.f. = 71, $p < 0.001$). The mean oxygen concentration in five-entry condos was 2.87 mg l^{-1} (s.e. = 0.08 mg l^{-1}), and for single-entry condos 2.65 mg l^{-1} (s.e. = 0.05 mg l^{-1}). The oxygen concentration in the water column above the condos was 2.84 mg l^{-1} (s.e. = 0.04 mg l^{-1}) (figure 4). There was a significant difference between the three sample sets (ANOVA: $F_{2,18} = 3.90$, $p = 0.039$), with the five-entry and single-entry condos showing a significant difference (Fisher's LSD: $p = 0.018$). However, only the

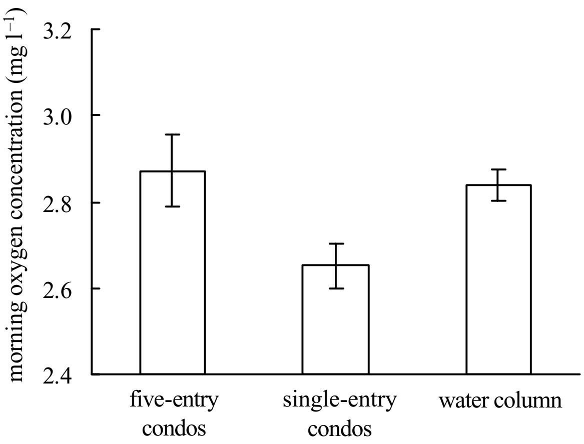

Figure 4. Mean (± 1 s.e.) morning oxygen concentrations of water samples taken from five-entry condos, single-entry condos and the water column above condos.

single-entry condos differed from the water column (Fisher's LSD: $p = 0.042$).

4. DISCUSSION

We detected clear evidence from stomach content analysis for partial filial cannibalism in *S. leucostictus* at the study site, and the same has been demonstrated in other fish species (e.g. Hoelzer 1988; Belles-Isles & Fitzgerald 1991; DeWoody *et al.* 2001). Predation did not appear to be the primary cause of embryo losses within a clutch. The pattern of embryo loss from clutches cannibalized by parental males was distinctly different from those eaten by other male *S. leucostictus* and other fish species. Clutches from which parental males removed embryos had a small number of embryos removed from many areas throughout the entire clutch, whereas conspecifics or other fishes removed embryos in larger patches in a more aggregated pattern, indicating that filial cannibalism and predation are distinct.

Males that were provided with a supplemented diet grew more than those that did not receive a diet supplement. Thus, parental care may limit the foraging of males, as has been shown for other species (Sargent 1985; Itzkowitz & Makie 1986; DeMartini 1987; Hoelzer 1992; Smith & Wootton 1995). However, there was no difference in the mortality rates of embryos guarded by males with supplemented and unsupplemented diets. Thus, filial cannibalism appeared to be unrelated to energetic status. All parental males examined in this study had food in their stomachs, and while they benefited from a diet supplement, they also appeared to have access to food within their territory and appeared able to maintain themselves in good enough condition to complete a breeding cycle. The lack of a clear relationship between filial cannibalism and nutritional status has been found in other fishes (Lavery & Keenleyside 1990; Belles-Isles & Fitzgerald 1991; Kvarnemo 1997; Lindström & Sargent 1997; Vinyoles *et al.* 1999). Males in our study that were monitored for a further 14 days after supplemental feeding stopped also showed no difference in rates of filial cannibalism, further indicating that cannibalism was not strongly related to diet. Also, Rohwer (1978) and Sargent (1992) predicted that eggs and embryos should be eaten at an early developmental stage, when they contain most energy. However, in the present study, despite developmental stages 1–2 having a higher energetic value, embryos were not eaten to a greater extent at this stage.

Besides predation, oxygen is the predominant factor affecting embryo development and survival (Davis 1975; Kamler 1992). Reducing the density of embryos at all stages had the effect of increasing developmental rate, reducing mortalities and increasing hatching success, and these factors are likely to be mediated through oxygen availability. Thus, if a male were to decrease the density of the embryos for which he was caring by cannibalizing some of them, survival and developmental rate might be improved by increasing the oxygen available to the remaining embryos, and thereby the male's overall fitness may be maximized. We found that males exposed to low oxygen levels consumed more embryos than those exposed to higher oxygen levels. Thus, our findings implicate oxygen availability and embryo development and survival as the principal factors that determine filial cannibalism in beaugregory damselfish, in contrast to the traditional energy-based explanations derived from Rohwer's hypothesis. We propose that partial filial cannibalism in *S. leucostictus* is performed by parental males as an adaptive behaviour to maximize the survival and developmental rate of their offspring.

Behavioural adaptations for facilitating oxygenation of embryos in fishes with external fertilization are diverse. Many fishes fan developing embryos with their fins or bodies to provide a current of oxygenated water to the eggs, behaviour that can be energetically expensive (Smith & Wootton 1995). Fishes often deposit eggs in monolayers, beaugregory damselfish included (Brinley 1939), which may function to prevent embryos suffocating each other. In the European bitterling (*Rhodeus sericeus*), a species of fish that spawns on the gills of freshwater mussels, females use oxygen as a cue to locate mussels in which their eggs will suffer lowest mortalities from suffocation (Smith *et al.* 2000). By sampling the oxygen emerging from the exhalent siphon, the females may detect the suitability of mussels as spawning hosts (Smith *et al.* 2001). Several studies have demonstrated that females prefer to spawn with males that already have egg clutches present in their nest (e.g. DeMartini 1987; Sargent 1988; Gronell 1989; Sikkel 1989; Knapp *et al.* 1995). However, this preference is reversed under low oxygen conditions (Reynolds & Jones 1999), females preferring to spawn with males that occupy a nest that has high oxygen levels even if they do not have eggs. This response of females has been interpreted as females avoiding males that are forced to increase their fanning rate and consequently being unable to care for the clutch. However, this may also be due to the females' selection of sites for oviposition with respect to prevailing oxygen conditions. Other species of fish, including the beaugregory damselfish, will not lay their eggs close to clutches that are near hatching (Sikkel 1994; Knapp *et al.* 1995), and embryos close to hatching have a high oxygen demand (Davis 1975; Kamler 1992). Filial cannibalism appears to be another adaptive behavioural mechanism by which a parent can enhance survival and development of offspring under low oxygen conditions.

Our hypothesis that filial cannibalism may function in oxygenating embryos has broad implications for understanding filial cannibalism in fishes, and may allow reinterpretation of results from previous studies that have produced equivocal results (Smith 1992; Manica 2002). In the present study, this hypothesis provides an adaptive explanation for the finding that density of embryos was lower in single-entry condos, which had low oxygen levels, than in five-entry condos in which oxygen levels were significantly higher. The two possible explanations for this difference are that either females lay eggs at a lower density in single-entry than five-entry condos, or males may cannibalize clutches to a greater extent in single-entry condos. There is clear evidence that female fishes are choosy about where they spawn (Itzkowitz & Makie 1986; Gronell 1989; Sikkel 1989, 1994; Itzkowitz 1991; Knapp *et al.* 1995; Smith *et al.* 2001), and females of some species appear able to distribute a single clutch among several males (e.g. Trexler *et al.* 1997; Jones *et al.* 2001), indicating some control over clutch size. Thus, it would appear that females may avoid spawning sites with low oxygen conditions, and may exert some control over clutch size in relation to the oxygen conditions in a nest site, while males may reduce the numbers of embryos in condos to match prevailing oxygen levels. Itzkowitz & Makie (1986) also observed that single-entry condos contained fewer embryos, which they attributed to a female's preference for laying its eggs in sites with good ventilation to ensure hatching larvae could join the plankton.

However, these results raise the question of why females lay more eggs than can survive, as overproduction of eggs will tend to result in increased cannibalism. Mock & Parker (1997) provide three possible pay-offs for the overproduction of offspring. These are that a parent may: (i) better capitalize on unpredictably favourable environmental conditions; (ii) provide backup offspring to replace those that are flawed (and/or dead or infertile); and (iii) produce surplus offspring that may be capable of assisting siblings. The first explanation corresponds with the 'resource-tracking' hypothesis (Temme & Charnov 1987), and in the case of the beaugregory damselfish, females might benefit from producing a large clutch if oxygen conditions in a spawning site improve or at least do not worsen. In a situation where oxygen conditions do deteriorate, for example if water temperature increases or further clutches are deposited in the nest, the male is able to respond to the change in conditions and correct the clutch size downwards.

The 'replacement offspring' (or 'progeny-choice') hypothesis assumes that a proportion of offspring is expendable, but provides insurance against a female depositing an undersized brood. This hypothesis also accommodates the possibility that offspring quality may vary within a clutch and that the parent can selectively cannibalize lower quality offspring. The 'offspring facilitation' hypothesis supposes that offspring have some capacity for helping siblings. In the context of beaugregory damselfish filial cannibalism, this explanation appears unlikely as the developing embryos have no obvious means by which they can provide a service to one another, except through a dilution effect if the clutch is attacked by a predator.

Further research is required to explore how widespread filial cannibalism in response to oxygen availability is in fishes and the response of females to filial cannibalism in terms of oviposition choice and clutch size.

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