

Gender-specific benefits of eating eggs at resident reef fish spawning aggregation sites

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ABSTRACT: Food resource availability has a fundamental role in shaping consumer populations through changes in energy intake. Tropical reef fish spawning aggregations provide a resource pulse for reef-based planktonic egg predators, and an opportunity to quantify the energetic repercussions of natural changes in food availability in tropical reef fishes. We examined the effects of the consumption of eggs from the broadcast spawning surgeonfish *Ctenochaetus striatus* on the allocation of energy to body condition, growth and reproduction in the planktivorous egg-predator damselfish *Abudefduf vaigiensis*. Fish that fed on eggs at resident fish spawning aggregation sites (FSASs) had significantly greater lipid storage in liver vacuoles compared to conspecifics from non-FSASs. Growth of male *A. vaigiensis* was faster at FSASs than non-FSASs. However, we found no differences in the growth of females among sites. Female *A. vaigiensis* from FSASs invested more into reproduction, having larger gonadosomatic indices (GSI) than females from non-FSASs, while there was no difference in the GSI of males among FSASs and non-FSASs. At the same locations, no differences were found in the life-history traits of the reference species, *Pomacentrus moluccensis*, which does not consume eggs. This study demonstrates the role of natural variations in food availability on energetic processes in reef fish. Furthermore, the sex-specific energy allocation strategy highlights the complexity of the interaction between natural variations in food availability and life-history strategies. This study demonstrates that the conservation of FSASs may also benefit trophically linked reef fishes.

KEY WORDS: Fish spawning · Spawning aggregation · Egg mortality · Egg predation · Prey switching · Maternal effects · Fecundity · Trophic ecology · Reef fish condition

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INTRODUCTION

Temporal variations in prey availability have a fundamental influence on predator population dynamics (Krebs 1994). Populations will respond energetically to temporal increases in prey availability by modifying their allocation of energy to life-history traits (May 1972). As such, individuals are expected to allocate energy to growth, condition and reproduction according to their life-history strategy that has evolved to maximise reproductive success over an individual's expected life span (Stearns 1992). To understand processes that govern population dynamics,

it is essential to understand the relationship between temporal pulses in natural food availability and trade-offs in energy allocation to life-history traits.

Evidence suggests that food is a limited resource for reef fishes in tropical marine waters (Forrester 1990, Jones & McCormick 2002). Manipulative experiments that artificially increased food availability to reef fishes showed that growth, both in juveniles (Jones 1986) and adults (Jones & McCormick 2002), and reproduction are tightly regulated by food availability (McCormick 2003). Because sexual maturity (Roff 1984) and mortality schedules (Gust et al. 2002) are related to size in fishes, energy allocated to

growth from increased food availability can also increase the size of a breeding population (Jones & McCormick 2002). However, in tropical reef fishes, little is known of the trade-offs in energy allocation to growth and reproduction in response to natural fluctuations in food availability (but see Clifton 1995). Jones (1986) highlighted the need to examine the response of demographic parameters in reef fishes to natural variations in preferred prey items. After almost 3 decades of subsequent research, few studies have addressed this paucity of knowledge, possibly due to the logistical difficulty of testing natural variations in food availability with appropriate controls. However, the study of natural pulses in food availability provides a unique opportunity to examine how reef fishes make trade-offs in energy allocation to growth and reproduction.

Many reef-associated fishes aggregate to spawn, and this provides a pulse of energy-rich eggs to planktivorous egg predators (Sancho et al. 2000, Nemeth 2012, Pears et al. 2012, Claydon et al. 2014). In the tropics, over 100 species from some 18 families have been found to spawn at highly localised fish spawning aggregation sites (FSASs; Domeier & Colin 1997, Claydon 2004, Claydon et al. 2014), most of which broadcast spawn their gametes above the reef. At these sites, breeding groups make rapid spawning rushes toward the water's surface to release their gametes into the prevailing current. At the apex of spawning rushes where visible gamete clouds are released, eggs are at much higher densities than alternative planktonic prey. Recently spawned eggs also have 20 to 25% greater energy content than other plankton (Kamler 1992). Planktonic eggs from a range of vertebrate and invertebrate marine taxa usually form a small portion of a tropical planktivorous fish's diet (Sano et al. 1984). However, egg predators aggregate to feed on spawners' gamete clouds at FSASs (e.g. Sancho et al. 2000). Therefore, it may be expected that eggs released at FSASs represent a valuable prey source with the potential to influence the life-history processes of egg predators. Analysis of how egg predators allocate energy in response to this natural pulse in egg abundance provides a unique opportunity to analyse energy partitioning in reef fish under natural conditions.

The aim of this study was to determine whether feeding on eggs at reef FSASs influenced the life-history traits of a key egg predator, the damselfish *Abudefduf vaigiensis*. Specifically, we examined how this predator of nutrient-rich eggs allocated energy to growth, body condition and reproduction, and whether this was affected by gender.

MATERIALS AND METHODS

Study site and species

This study was conducted in Kimbe Bay, West New Britain Province, Papua New Guinea (5° 30' S, 150° 05' E), on 2 small inshore platform reefs (Hanging Gardens and Limuka). The reefs were steep-sided platform reefs, less than 1 km from shore, 800 m apart and separated by deep passages of water (>50 m deep), which made migration of small reef fishes between adjacent reefs unlikely (see Fig. 3 in Claydon et al. 2014). Sampling was conducted at 2 FSASs and 1 non-FSAS on Hanging Gardens Reef, and 1 FSAS and 1 non-FSAS on Limuka Reef. Non-FSASs were locations on the reef where reef fish spawning had never been observed but were of a similar size, aspect to the open ocean, coral cover and topographic complexity, and were over 100 m from FSASs.

At the studied FSASs, the shallow-dwelling surgeonfish *Ctenochaetus striatus* is known to form large spawning aggregations (up to 2000 individuals) a maximum of once per day per FSAS between 13:30 h and dusk (~18:00 h; Claydon et al. 2012). Spawning events by *C. striatus* are typified by 1 h of pre-spawning courting behaviour, followed by 10 to 15 min of intense synchronised spawning rushes that release visible gamete clouds near the water's surface (Randall 1961). Sampling of visible gamete clouds within 3 s of spawning using a 100 µm mesh plankton net found that on average, 1.24 l of eggs are released during a *C. striatus* spawning aggregation (Fraser 2010). FSASs used by *C. striatus* at this study location were identified initially in 2001 (Claydon 2005) and were still in use in March 2008, 7 yr later. In Papua New Guinea, as in many places around the tropical Pacific, *C. striatus* is a preferred prey species of spear-fishers, and its densities respond rapidly to the establishment of no-take marine protected areas (Jones et al. 2004).

Recently spawned gametes of *C. striatus* are known to suffer high levels of predation (Robertson 1983). The damselfish *Abudefduf vaigiensis* was the focal egg predator species for the study since it is the dominant predator of *C. striatus* eggs at this study location. *A. vaigiensis* attack 70% of the gamete clouds released by *C. striatus* (authors' pers. obs.). Furthermore, a movement study of *A. vaigiensis* showed that most tagged individuals at FSASs and non-FSASs did not move greater than 40 m, and the greatest movement observed was <80 m (Fraser 2010). To determine whether differences in *A. vai-*

giensis life-history traits resulted from the consumption of *C. striatus* eggs or another site-related effect, the lemon damselfish *Pomacentrus moluccensis* was used in comparison because this species is known not to consume *C. striatus* eggs (M.R. Fraser pers. obs.) and is relatively site attached (Beukers et al. 1995).

Egg predation and fish collection

Egg predation was quantified in October 2007 with behavioural observations at FSASs and non-FSASs during *C. striatus* spawning events. Scan observations of *A. vaigiensis* and *P. moluccensis* were performed by placing all individuals within an FSAS into 1 of several behavioural categories that represented their entire range of behaviours (Martin & Bateson 1993): (1) feeding on eggs, (2) feeding on plankton, (3) swimming, and (4) all other minor behaviours including benthic feeding, interacting and hiding. Feeding on eggs was clearly distinguished when fish actively attacked visible gamete clouds near the water's surface. For *A. vaigiensis* at FSASs, scan observations were performed for the duration of a *C. striatus* spawning event ($n = 30$ spawning events). At non-FSASs, scan observations were performed for the same duration when *C. striatus* spawning events were occurring at FSASs ($n = 13$ spawning events). In the same way, scan observations for *P. moluccensis* were performed at FSASs ($n = 8$) and non-FSASs ($n = 6$).

During November 2007, fish were collected from each FSAS immediately after a *C. striatus* spawning event, when possible. However, for logistical reasons associated with spawning occurring at dusk, collections were also made the morning after a spawning event. Collections of *A. vaigiensis* ($n = 59$ from FSASs and $n = 47$ from non-FSASs) and *P. moluccensis* ($n = 40$ from FSASs and $n = 39$ from non-FSASs) were made using a fence net and a dilute solution of clove oil, or a spear gun. All fishes were euthanized with an overdose of clove oil before the stomach was injected with exactly 0.1 ml of buffered formalin and placed immediately on ice for no longer than 4 h prior to processing. Fishes were weighed (0.01 g) and measured (0.1 mm; *A. vaigiensis*, fork length; *P. moluccensis*, standard length), and the head of each fish was removed and stored in 100% ethanol prior to removal of the otoliths for dry storage (for ageing purposes). The contents of the peritoneal cavity were removed and preserved in 10% buffered formalin. Analysis of stomach contents of *A. vaigiensis* from FSASs collected immediately after a *C. striatus*

spawning event ($n = 4$) revealed that fish eggs comprised 52 to 80% of the of the total stomach contents. However, too few *A. vaigiensis* were collected to provide meaningful statistical analysis.

Growth, body condition and reproduction

Ages of *A. vaigiensis* and *P. moluccensis* were determined by counting visible growth bands from transverse sections of sagittal otoliths. Otoliths were prepared following methods given by Wilson & McCormick (1997). Growth bands have been validated as annual for a number of tropical pomacentrid species (Meekan et al. 1999). Therefore, growth bands in *A. vaigiensis* and *P. moluccensis* were assumed to be annual growth increments. Growth histories were determined with length versus age plots, and slopes were compared among FSASs and non-FSASs using analysis of covariance (ANCOVA). Length data were natural log transformed to meet assumptions of linearity, homogeneity of slopes and normality (Quinn & Keough 2002).

The effects of egg predation on body condition were determined using 3 condition indices for both *A. vaigiensis* and *P. moluccensis*. An indication of the relative weight of a fish at the time of capture was determined using length versus eviscerated body weight plots. Slopes were compared between fish from FSASs and non-FSASs using ANCOVA. Length data were natural log transformed to meet assumptions of ANCOVA. The relative weight of the liver, (hepatosomatic index, HSI) and liver vacuolation were also determined to yield measures of physiological condition. Preserved livers were weighed to the nearest 0.01 g, and HSI was determined using the formula $HSI = WL \times 100/WB$, where WL is preserved liver weight and WB is gutted body weight (McCormick 2003). Liver vacuolation in fishes is indicative of lipid and glycogen storage within the liver (Green & McCormick 1999, Pratchett et al. 2004, Hoey et al. 2007). To quantify liver vacuolation, livers were prepared histologically following the methodology of Hoey et al. (2007). Two 5 μm sections were taken from each of the anterior, middle and posterior portions of each liver. The proportion of hepatocyte vacuolation from each section was determined with a Weibel eyepiece by recording the proportion of points that intersected (out of 121) with vacuoles at 40 \times magnification. Raw data analysed were the mean values of the 6 estimates of liver vacuolation from each fish. For each species, HSI data were compared among FSASs and non-FSASs using 1-factor

ANOVA. Data were examined for homogeneity of variance using residual analysis (Quinn & Keough 2002).

Reproductive state of female *A. vaigiensis* and *P. moluccensis* at capture were determined using the relative weight of the gonad (gonadosomatic index, GSI). The state of maturation of preserved ovaries was visually assessed and ovaries were weighed. Ovary weight was divided by eviscerated body weight to give GSI. The equality of mean GSI values from FSASs and non-FSASs were examined for both species using 1-factor ANOVA.

RESULTS

Egg predation

Only *Abudefduf vaigiensis* at FSASs fed actively on eggs during *Ctenochaetus striatus* spawning events (Fig. 1). A total of 88% *A. vaigiensis* (of 834 individuals) fed on eggs within visible gamete clouds, while no *A. vaigiensis* (of 125 individuals) observed at non-FSASs fed on eggs during the same period. As a consequence of this difference in foraging behaviour, a smaller proportion of the time budget of *A. vaigiensis* behaviour was spent swimming (6.6%) and feeding on plankton (5.1%) at FSASs during *C. striatus* spawning aggregations. *A. vaigiensis* at FSASs spent 61.9% more time feeding on eggs and plankton compared to fish at non-FSASs. In contrast, *Pomacentrus moluccensis* were never observed feeding on eggs at FSASs (92 fish) or non-FSASs (61 fish; Fig. 1).

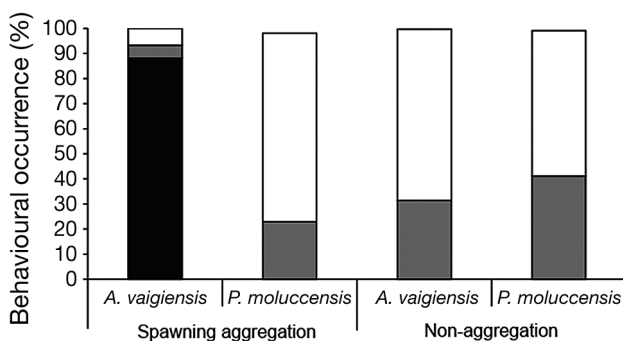


Fig. 1. Mean occurrence of behaviours of *Abudefduf vaigiensis* and *Pomacentrus moluccensis* at fish spawning aggregation sites and similar non-aggregation sites during periods of *Ctenochaetus striatus* spawning. Behavioural categories: black, feeding on gamete clouds; grey, feeding on plankton; white, swimming

Body condition

Length versus weight relationships did not differ for female (ANCOVA, $F_{1,44} = 2.748$, $p = 0.104$) or male (ANCOVA, $F_{1,24} = 3.145$, $p = 0.088$) *A. vaigiensis* between FSASs and non-FSASs. Similarly, there was no significant difference in the relative body condition of female (ANCOVA, $F_{1,24} = 0.345$; $p = 0.557$) and male (ANCOVA, $F_{1,12} = 0.088$; $p = 0.771$) *P. moluccensis* between FSAS and non-FSASs.

Hepatocyte vacuolation of the livers from *A. vaigiensis* differed between FSASs and non-FSASs for females ($F_{1,26} = 13.787$, $p < 0.001$) and males ($F_{1,19} = 6.5718$, $p = 0.019$; Fig. 2), with fish from FSASs having more than double the levels of vacuolation compared to those from non-aggregation sites. In contrast, there was no difference in the hepatocyte vacuolation for *P. moluccensis* females ($F_{1,33} = 0.322$, $p = 0.527$) or males ($F_{1,12} = 1.181$, $p = 0.298$) between FSASs and non-FSASs.

Despite the difference in vacuolation, there was no difference in HSI between FSASs and non-FSAS for female ($F_{1,18} = 4.091$, $p = 0.058$) or male ($F_{1,21} = 2.582$, $p = 0.123$) *A. vaigiensis*. Likewise, female and male *P. moluccensis* also did not differ in HSI between FSAS and non-FSASs (females: $F_{1,20} = 1.726$, $p = 0.203$; males: $F_{1,12} = 0.275$, $p = 0.609$).

Growth

The *A. vaigiensis* collected at the present study location were remarkably short-lived, with ages ranging from 2 to 4 yr (see Figs. 3 & 4). Despite managing to collect only relatively small sample sizes of males from FSASs and non-FSASs (15 and 11, respectively), male *A. vaigiensis* at FSASs had significantly faster growth compared to males from non-

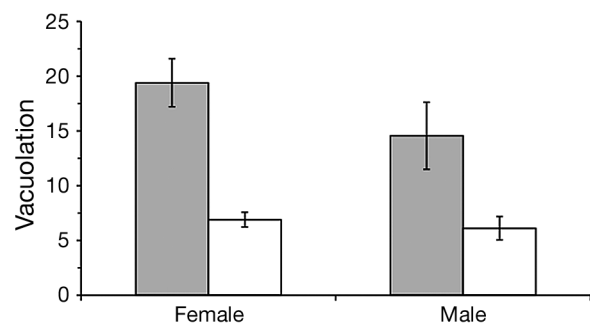


Fig. 2. Liver hepatocyte vacuolation (mean % ± SE) of female and male *Abudefduf vaigiensis* from spawning aggregation sites (grey) and similar non-aggregation sites (white)

FSASs (ANCOVA, $F_{1,24} = 6.156$, $p = 0.021$; Fig. 3). The difference in growth was predominantly due to higher growth early in life (Year 2), with the older (Years 3 and 4) age-classes being of a similar length. No significant difference was found in the growth histories of female *A. vaigiensis* among FSASs and non-FSASs (ANCOVA, $F_{1,50} = 3.311$, $p = 0.075$). The growth histories of male (ANCOVA, $F_{1,24} = 0.747$, $p = 0.396$) and female (ANCOVA, $F_{1,12} = 0.391$, $p = 0.544$) *P. moluccensis* did not differ significantly between FSASs and non-FSASs.

Reproduction

Female *A. vaigiensis* from FSASs had larger ovaries relative to body weight (GSI) than females from non-FSASs ($F_{1,49} = 4.861$, $p = 0.032$; Fig. 4), despite ovaries having a range of reproductive states from both locations, ranging from stage 1 to stage 3. In comparison, GSI in male *A. vaigiensis* did not differ between FSASs and non-FSASs ($F_{1,25} = 0.665$, $p = 0.422$; Fig. 4). The mean GSI of female ($F_{1,21} = 0.489$, $p = 0.492$) and male ($F_{1,10} = 1.207$, $p = 0.298$) *P. moluccensis* also did not differ among FSAS and non-FSASs.

DISCUSSION

Identifying sources of variation in food availability on coral reefs and how reef fishes make trade-offs in energy allocation between growth and reproduction

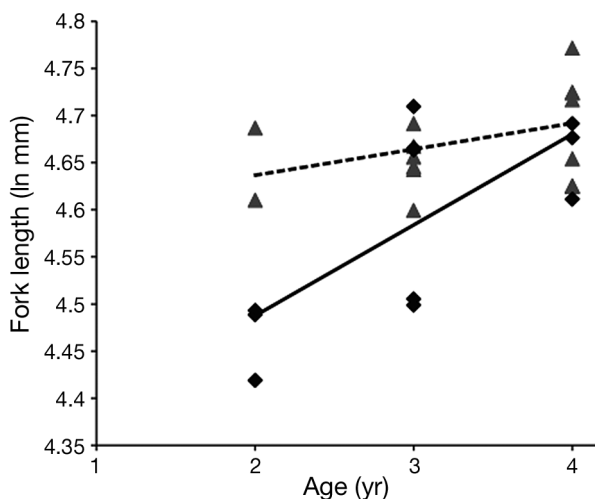


Fig. 3. Growth relationships of male *Abudedefduf vaigiensis* collected from fish spawning aggregations sites (triangles and dashed line, $n = 15$) and similar non-aggregation sites (diamonds and solid line, $n = 11$). Fork length is displayed as a natural logarithm

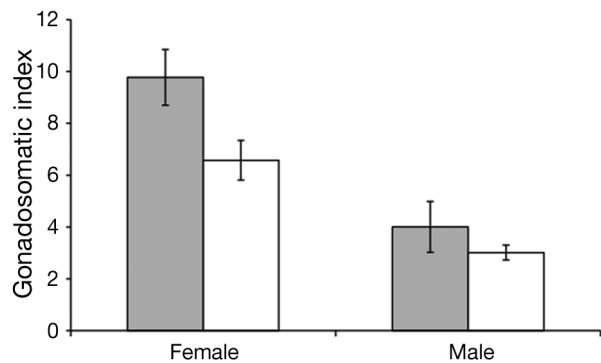


Fig. 4. Gonadosomatic index of female and male *Abudedefduf vaigiensis* from fish spawning aggregation sites (grey) and similar non-aggregation sites (white). Error bars are \pm SE

is fundamental to understanding population dynamics. Observations of egg predation at FSASs has prompted the suggestion that egg predators benefit energetically from consuming eggs at FSASs (Heyman et al. 2001), but our study is the first to quantitatively examine the energetic effects of this trophic link. Feeding on this rich source of energy benefited the egg predator, but how these benefits were realised was gender-specific. While egg predation did not influence overall body condition or bulk of *Abudedefduf vaigiensis*, both males and females stored more energy products in their liver vacuoles. From there, males allocated excess energy to growth, while females allocated greater energy to current reproduction. This study underscores the importance of eggs as a food source for the egg-predator community and highlights the potential benefits that capitalising on this predictable, pulsed resource to local reproductive output and life-history strategies of the egg predator community.

Theory predicts that trade-offs in energy allocation between growth and reproduction evolved to maximise reproductive success over an individual's expected lifetime (Stearns 1992). Our findings show that males that fed on eggs allocated more energy to growth, while their investment in gametes (quantified here as GSI) remained similar to fishes that did not feed on eggs. Body size is a key determinant of superiority in many aspects of performance and ecology for many organisms (Okie et al. 2013). Size is often a strong predictor of dominance and with that, preferential access to resources, mating opportunities and hence fitness. Females can give mating preference to larger males (Cote & Hunte 1989, Cole & Sadovy 1995), and larger nest-guarding males often have higher clutch survivorship (Cote & Hunte 1989). Our data suggest that male *A. vaigiensis* may trade

immediate investments in reproductive products for size-dependent, socially-mediated future reproductive success. In addition, size is closely linked with age of reproduction in reef fishes (Jones & McCormick 2002). Therefore, male *A. vaigiensis* that have access to eggs as a food resource may also reach sexual maturity at a younger age, potentially giving them more breeding opportunities during their short lifespans. Collectively, our data suggest that male *A. vaigiensis* from FSASs may effectively contribute more to the breeding population than conspecifics elsewhere.

In contrast to males, females allocated greater energy to current reproduction relative to females that did not consume eggs. Our results suggest that female *A. vaigiensis* trade an immediate increase in egg production against accelerated growth in body size, and therefore an immediate increase in egg production rather than a greater fecundity associated with larger female size (Maddams & McCormick 2012). Because increases in body size may also mitigate the risk of predation (Sogard 1997), females may also trade potentially lower rates of mortality for immediate reproductive investment. The reason for this strategy may be explained by the extended breeding season and short reproductive life span of *A. vaigiensis* at this study site. A previous study at the same low latitudinal study reefs showed that damselfishes have extended breeding seasons spanning 6 mo that coincide with the dry season (Srinivasan & Jones 2006). In addition, our study shows that *A. vaigiensis* have a relatively short life span of 4 yr compared to over 20 yr for similar Pomacentrid species from cooler latitudes (Fowler & Doherty 1992, Meekan et al. 2001). Our study highlights how sex-specific life-history strategies can influence the utilisation of energy obtained from natural fluctuations in food availability and ultimately alter demographic parameters.

Energy that is allocated to reproduction can be used to produce more gametes of a similar quality, place more energy into each gamete, or a combination of both (Marshall & Uller 2007). Unfortunately, the offspring of egg predators could not be obtained in the present study, so which option was adopted at the studied FSASs is unknown. McCormick (2003) found that ambon damselfish *Pomacentrus amboinensis* that switched to feeding on coral spawn during the annual mass spawning produced the same number of embryos, but these hatched with 25% larger yolk sacs and 100% larger oil globules. The eggs consumed by damselfish at FSASs have the exact nutrient profile necessary for their own repro-

duction and are rich in essential fatty acids and amino acids capable of influencing fecundity and maternal provisioning (Sargent et al. 1999). Increased essential nutrients enhance reproduction and maternal provisioning in the natural diets of the zebra finch *Taeniopygia guttata* (Royle et al. 2003), and the limitation of essential nutrients has been proposed to describe patterns in reproduction in wrasses *Thalassoma bifasciatum* (Schultz & Warner 1991). The finding of improved offspring provisioning with increased pre-spawning maternal conditioning is common among a wide range of organisms (Bernardo 1996, Green 2008). Regardless of whether *A. vaigiensis* in the present study produces higher-quality or more offspring as a result of feeding on eggs released at spawning sites, it is likely that this nutritious and predictable food source leads to a valuable reproductive benefit to those fish that are willing to exploit it.

In summary, this study shows that natural variations in food supply influence demographic parameters in reef fish. Given the regular nature of this high-energy food resource (Claydon et al. 2014), eggs released at spawning sites appear to represent an important energy source that has beneficial repercussions for the individuals that exploit it. This study suggests that males grow faster and females put more energy into reproduction. Given the demonstrated beneficial effects of advantages in early development to subsequent developmental trajectories, growth, performance, fitness and survival (e.g. Gagliano et al. 2007, Walker et al. 2007, McCormick et al. 2010), it is likely that egg predators feeding at FSASs will make a greater contribution to the next generation for their species at the cost of the species aggregating to spawn. If this is the case, then the periodicity in spawning intensity at spawning sites (and hence egg predation) may influence the periodicity of recruitment of egg predator juveniles through enhanced larval survival. Over the last 2 decades, the protection of FSASs from harvest has been promoted as a broadly applicable management strategy to avoid the overexploitation of many commercially important species, particularly serranids (Claydon 2004, Sadovy & Domeier 2005, Russell et al. 2012). The current findings highlight that protecting spawning aggregations will also benefit trophically linked reef fishes, with important consequences for the resilience of associated reef species.

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