Fraser, Matthew Robert (2009) ***Egg predation at tropical reef fish spawning aggregation sites: trade-offs for fitness.*** **PhD Thesis, James Cook University.**

https://doi.org/10.25903/cqgm%2D6d63

Egg predation at tropical reef fish spawning aggregation sites: trade-offs for fitness

Thesis submitted by
Matthew Fraser (BSc Hons)
In October 2009

For the degree of Doctor of Philosophy in Marine Biology
In the School of Marine Biology and Aquaculture
James Cook University, Townsville, Queensland, Australia

Statement of access

I, the undersigned, the author of this work, understand that James Cook University will make it available for use within the University Library and, via the Australian Digital Theses Network, for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act and;

I do not wish to place any restrictions on access to this work.

______________________________ ____________________

Signature Date

Statement of sources

Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Signature Date

Electronic copy

I, the undersigned and author of this work, declare that the electronic copy of this thesis provided to the James Cook University Library is an accurate copy of the print thesis submitted, within the limits of the technology available.

Signature

Date

Statement on the contribution of others

Assoc. Prof. Mark McCormick originally conceived the topic for this doctoral thesis and provided primary guidance, and financial and technical support. Intellectual support was also provided by Prof. Geoffrey Jones as co-supervisor. While undertaking this thesis I was responsible for the project design, implementation, data collection and analysis, interpretation, synthesis and formatting for publication.

This project was financially supported by an Australian Research Council Grant to Assoc. Prof. Mark McCormick. Additional financial assistance was provided by Mahonia na Dari Research and Conservation Centre, and Walindi Plantation Resort. Personal financial assistance was provided by an Australian Post Graduate Award.

Acknowledgements

There are many people I would like to thank for their support and assistance throughout this project. I would firstly like to thank Mark McCormick for his initial insight for the project and his continual support and belief in my abilities. I am grateful to have had the opportunity to work on this project with Mark and have gained greatly from his guidance and expertise. Both Geoff Jones and Howard Choat have also been instrumental in teaching me some of their immense knowledge of marine ecology. To be able to learn from true experts in the field of marine science has been a great pleasure. My time spent in the field in PNG was made possible by the generosity and support of Max Benjamin at the Walindi Plantation Resort and Mahonia na Dari research and education centre. I am thankful for the logistical support (including the wonderful food) provided by Max and Mahoni na Dari. Their continued support to research students contributes greatly in advancing the knowledge of tropical marine ecology.

Many people assisted me with all the technical aspects of this project for which I am extremely grateful. Thank you to my assistants in the field including Mike Bird, Charlotte Johansen, Craig Syms, Juan Gabriel, Jo Mismen, Blazius Ponde, and many others from Kilu and Tamare villages. Thanks to Dave Feary and Marry Bonin for the supportive conversations during those many days when the fish just didn’t spawn. For the lab work and thesis write-up stage I thank Jenni Donelson for her wealth of advice on *Acanthachromis*, maternal provisioning, associated statistics and editing; Rocky de Nys for his general advice on how to do science; Craig Syms for help with statistics; Ashley Frisch and David Feary for editing earlier drafts of this thesis; and Tom Holmes for keeping me company in the office.

I received much personal support from many friends and family during my somewhat extended tertiary education. Thanks to Jenni, Dani, Dave and Ash for many lunch time gatherings and conversations during which we discussed almost everything over the years. I would like to thank my parents and their respective partners for their encouragement and support, especially mum and Rick for their emotional and financial support during the final stages of writing the thesis. Last, but definitely not least, I am forever grateful to my partner Laura for her love, support, encouragement and loyalty which enabled me to finish this project. Without your support I would probably still be going.

Finally, during the course of my PhD I lost two very close friends, Graham Clem and Brett McGough with whom I shared a similar passion for the marine environment. I miss you guys a lot. This work is in memory of you.

List of Figures

List of Tables

Abstract

Food resource availability has a fundamental role in shaping consumer populations. However, very few studies have investigated the role of natural fluctuations in food availability on tropical marine fish populations. Resource pulses are natural variations in food resource availability that result in a super abundant supply of a food resource and present a unique opportunity to examine the effects of natural variations in food availability on population processes. Tropical reef fish spawning aggregations provide a resource pulse for reef based planktonic egg predators, however the dynamics of egg predation at reef fish spawning aggregation sites (SASs) are largely unstudied. This thesis uses spawning aggregations as a model to study the effects of a natural variation in resource availability on reef fish population processes. The broad objectives of this study were to: (1) quantify egg predation among multiple reef fish SASs and to relate observed patterns to the reproductive behaviour of the pelagic spawners, and to (2) examine the numerical and energetic repercussions of egg predation for the egg predator community.

Reef fishes are hypothesised to spawn at SASs to minimise egg predation through: (1) using favourable locations to minimise egg predation by reef based egg predators and (2) rapidly increasing spawning intensity by synchronising spawning activity to swamp egg predators. In Chapter 2 I systematically quantified inter-specific and intra-specific differences in target egg predation among multiple SASs of resident fishes, and investigated the relationship between levels of target egg predation and spawning intensity. Levels of egg predation were significantly greater for the surgeonfish

Ctenochaetus striatus compared to other spawning species, and the levels of egg predation among species closely reflected differences in the mean volume of eggs released during a spawning aggregation event. For the spawner *C. striatus*, levels of egg predation were significantly greater at front reef SASs than at back reef SASs. In addition, front reef SASs had significantly higher densities of egg predators. At front reef SASs the damselfish *Abudefduf vaigiensis* attacked the greatest percentage of *C. striatus* spawning rushes. The relationship between spawning intensity and the rate with which rushes were attacked at front reef sites increased linearly, however there was no relationship between spawning intensity and target egg predation at back reef SASs. To test if egg predator swamping occurs at SASs it is imperative to measure rates of egg mortality rather than the number of rushes attacked. This study demonstrates that target egg predation varies greatly among spawning species, and among SASs, which result from differences in egg predator assemblages.

Theory predicts consumers will respond numerically to variations in food availability through changes in resident density and through an aggregation response. The extent to which eggs as a prey source influenced resident egg predator density and movement patterns were tested using *C. striatus* spawning aggregations. Firstly, the densities of egg predator species were compared among SASs and structurally similar non-SASs outside of spawning periods. Secondly, to determine if egg predators aggregate during spawning periods, the change in egg predator density between spawning and non-spawning periods at SASs and non-SASs were quantified. To determine the distance travelled to aggregate and feed on the pulsed resource, a movement study was conducted on tagged individuals of a key egg predator species. Densities of resident egg predators did not differ among SASs and non-SASs and only one egg predator species, *A. vaigiensis*, showed an increase in density at SASs during a *C. striatus* spawning aggregations. The movement study conducted with *A. vaigiensis* showed that tagged individuals travelled only ten meters to feed on *C. striatus* gametes, which is within their normal home range movements. These data suggest that insufficient eggs are consumed by egg predators to influence resident densities or to warrant greater aggregation movements by *A. vaigiensis*.

Populations are predicted to respond energetically to increases in prey abundance. This study examined the effects of the consumption of *C. striatus* eggs on the allocation of energy to condition, growth and reproduction in the damselfish, *A. vaigiensis*. Fish that fed on eggs at spawning aggregation sites (SASs) had significantly greater lipid storage in liver vacuoles compared to conspecifics from non-SAS. Growth histories of male *A. vaigiensis* were significantly different among SASs and non-SASs, however there were no differences in growth histories of females among SASs and non-SASs. Female *A. vaigiensis* from SASs had significantly greater gonadosomatic indices (GSI) than females from non-SASs, while there was no difference in the GSI of males among SASs and non-SASs. No differences were found in the life history traits of the reference species, *Pomacentrus moluccensis*, which does not consume eggs at the same locations. 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 reef fish SASs may also benefit trophically linked reef fishes.

The role of maternal nutrition is becoming increasingly recognised as an important energetic process that influences offspring phenotype and subsequent survival. In Chapter 5, I examine the role of egg consumption on the maternal effects on offspring morphology and survival in controlled laboratory conditions. Parents were fed either: (1) a control diet of plankton (*Acetes* spp.), (2) a plankton diet partially substituted with fish eggs and the same energy content as the control diet, or (3) a plankton diet supplemented with fish eggs but higher in energy content. Mothers fed diets containing fish eggs tended to produce larger offspring with greater yolk reserves, however these trends were not significantly different. Mothers fed diet 3 produced young that had significantly greater unfed survival. Collectively, these data suggest that mothers that consume eggs at reef fish SASs will produce young that have greater survival than the young produced by mothers that do not feed on eggs. Therefore, the consumption of eggs by reef based egg predators may enhance their reproductive success through both increased fecundity (Chapter 4), and enhanced offspring survival.

The results from this thesis demonstrate that natural variations in food availability have an important role in shaping reef fish numerical and energetic population processes. Egg predation is highly variable and may be a significant source of mortality for some pelagic spawning species. Eggs released by pelagic spawners are potentially an important food source for some egg predator species and are capable of influencing their movement patterns and life history traits. Therefore the conservation of reef fish SASs will not only protect spawning species, but will also protect an important trophic link that benefits the egg predator community.

Chapter 1

General Introduction

A central goal of population ecology is to determine quantitatively the relative importance of ecological mechanisms in population regulation. Resource variability is a fundamental feature of natural systems and is one key factor that regulates consumer populations (Sinclair & Krebs 2002). Ecological processes that influence population dynamics can be categorised as numerical processes (those that directly influence the total number of individuals in the population) and energetic processes (those that influence the quality of individuals within a population) (Jones & McCormick 2002). In open populations, resource availability can alter numerical processes through sustaining greater numbers of consumers or influencing individual movement patterns (Jones & McCormick 2002). In addition, food availability can influence energetic processes, such as growth, condition and reproduction, which can ultimately influence individual reproductive output and the size of the breeding population (Krebs 1995). Since energy is often limited, understanding the relative significance of food availability in shaping numerical and energetic processes is of fundamental importance in formulating predictive models for the management of populations.

Resource pulses are becoming increasingly recognised as important sources of variation in food availability. Resource pulses are extreme variations in resource availability characterised by temporally succinct increases in resource availability (Holt 2008, Yang & Naeem 2008). Resource pulses are often caused by climatic episodes or reproductive events, and transitions in life phases of flora and fauna that often result in a ‘boom’ in resource availability (Anderson et al. 2008). These events can structure some cyclic ecosystems or can be anomalous (Nowlin et al. 2008). For example, the synchronised periodical emergence of cicadas in North American forests provides a pulse of prey for bird species (Yang & Naeem 2008). This large pulse in food availability influences bird populations both numerically and energetically through increased energy intake during periods of cicada emergence (Koenig and Liehbold 2005). Analysis of this resource provided direct evidence of the role that food availability has in shaping avian demographic parameters among years. For ecologists the key to understanding the effect of resource pulses is to determine the effects of a pulsed resource on consumer numerical and energetic processes, and to identify the trade-offs that will ultimately determine the level of resource exploitation.

Optimal foraging theory predicts that consumers will exploit a pulsed resource based on the trade-off between the energy gained and the costs or risks of exploiting the resource (Schoener 1971). Features that characterise resource pulses are also hypothesised to have an important role in the level of exploitation by consumers, including their variation through space and time (i.e. predictability), and their magnitude and duration (Holt 2008, Yang & Naeem 2008) (Fig 1.1). The predictability of a resource pulse is likely to determine if consumers actively target a resource or just exploit it opportunistically, therefore influencing how consumers allocate time to foraging and ultimately the level of exploitation. The magnitude and duration of the resource pulse will influence the amount of energy available to consumers. Features of the prey itself may also influence the benefits for consumers, and therefore foraging decisions, including the mobility/escape efficiency, and the energy content of the prey (Schoener 1971) (Fig 1.1).

The costs of accessing resource pulses will also influence foraging decisions and ultimately the benefits for consumer species (Schoener 1971) (Fig 1.1). These may include predator traits that influence their vulnerability to predation such as size, morphology and mobility. The proximity of prey in relation to predator habitat or normal home range movements may also influence vulnerability to predation, while migration distance to prey will also require energy expenditure and therefore influence net energetic gains (Fig 1.1). Collectively, these factors will interact to shape an optimal foraging strategy that represents allowable costs for energetic benefits. Since these factors vary greatly among natural environments, resource pulses and consumer species, the levels of exploitation and its effects on consumer populations are likely vary greatly. To date, few studies have investigated the dynamics that influence the trade-offs and benefits of pulse resource exploitation in the marine environment and how increased energy intake may affect consumer population dynamics. This thesis examines a resource pulse on coral reefs to determine how it influences numerical and energetic processes in coral reef fishes.

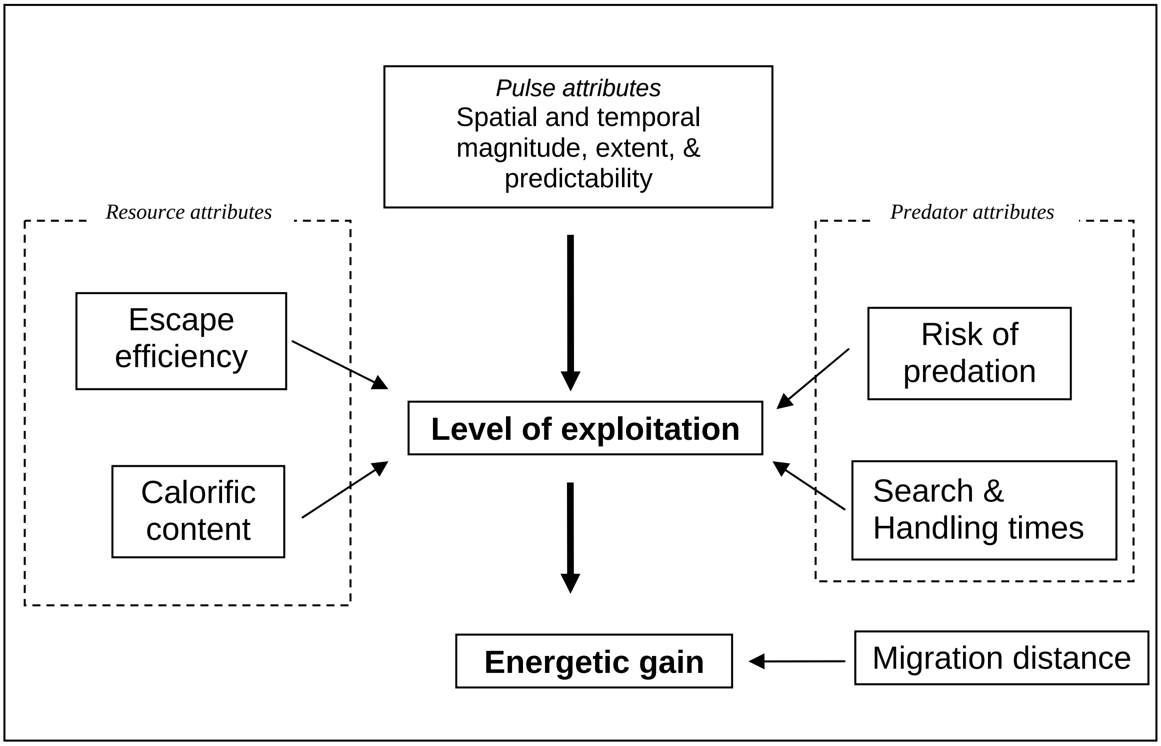

Figure 1.1 Diagram of factors predicted to influence the exploitation and energetic gain from a resource pulse by a resource exploiter (predator). Developed from Schoener (1971).

Life-history theory predicts that reef fishes will allocate dietary energy among life history traits (growth and reproduction) to maximise reproductive success (RS) during an individual's potential life span (Stearns 1992). Life-history strategies have been shown to vary with phylogeny, geographic distribution and sexual ontogeny which in turn drive a range of energy allocation strategies (Choat & Robertson 2002). In addition, reef fishes show a remarkable degree of plasticity in growth in response to food availability (Jones & McCormick 2002). Therefore, resource pulses may play an important role in structuring reef fish population dynamics. Life-history strategies may also determine the allocation of energy within individual female reproductive investment (maternal effects) (Bernado 1996) and the timing of reproduction (Wootton 1990). Theory predicts that in energy limited systems, females will make trade-offs between the quantity and quality of offspring to maximise their contribution to future generations (Marshall & Uller 2007). However, if resource pulses periodically provide conditions where food is not limited, females may be capable of maximising offspring quantity and quality, restricted only by their physiological limitations (i.e. body size) (Wootton 1990). Therefore, the predictability in both space and time of a resource pulse may play an important role in female reproduction. It may be expected that if females can predict the occurrence of a resource pulse, then the location and timing of reproduction may be altered to suit optimal periods of parental food availability (Robertson 1992). Alternatively, energy surpluses gained through exploiting unpredictable resource pulses may be stored and used during normal reproductive bouts (pulse-reserve paradigm) (Noy-Meir 1973), when environmental conditions suit larval survival (match/mismatch hypothesis) (Cushing 1990). Therefore, the predicted numerical and energetic responses of coral reef fish populations to pulses of food availability are likely to be complex and vary both inter- and intra-specifically.

Numerical and energetic responses to food availability in reef fishes

The current understanding of how food availability influences numerical and energetic processes in reef fish has been developed through artificial manipulations of food availability or from correlative studies. Artificial increases in food availability primarily influence a numerical response through increasing the number of juvenile recruits that survive to maturity (Forrester 1990). This suggests food availability limits the size of reef fish populations (Fig 1.2). Another study found that increased numbers of planktivores are found in higher current flow areas (and hence a greater supply of plankton) (Kingsford & MacDiarmid 1988). However, it was unclear if greater levels of food supported higher densities of resident planktivores or if planktivores had aggregated to temporarily to exploit the food resource. Food availability can also influence a numerical response through altering the movement patterns of consumer species (Fig 1.2). Whether this is a population level process will depend on the scale at which it acts, however movement patterns are still important determinants of local distribution and abundance (Jones & McCormick 2002). While the current evidence is not conclusive, evidence suggests that patchy food sources influences piscivore movement patterns (Zeller 2002) and distribution and abundance (Connell & Kingsford 1998).

Similar to numerical processes, evidence from manipulative and correlative studies suggests that food limits energetic processes such as growth, condition and reproduction in reef fishes. Studies that artificially increased food availability demonstrate increased growth in a density dependent manner (Jones 1986, Forrester 1990), while food availability has been found to correlate with growth in planktivorous reef fishes (Anderson & Sabado 1995). Since sexual maturity is determined by body size in many reef fishes, increased growth operating through enhanced food availability can directly influence the number of breeding individuals within a population (Jones & McCormick 2002). Increased energy intake also influences the energy available for storage and reproduction. Energy stored within the liver as lipids is particularly important for oocyte development in female fishes (Mommsen & Walsh 1988) and ultimately reproductive output. The energy that female fish consume may not only alter the number but also the quality of their offspring. Recent evidence shows that maternal provisioning greatly influences offspring morphologies and yolk provisioning (Gagliano &

McCormick 2007, Donelson et al. 2008, Donelson et al. 2009), which is thought to greatly influence offspring survivorship (Donelson et al. 2009). If energetic processes influence an individual's ability to compete or survive predation and/or influence the number of offspring that settle back to the reef (i.e. numerical processes), then determining the role that energy limitation plays in the life processes of individuals will greatly aid our understanding of population dynamics.

Unfortunately, previous studies investigating the role of food availability on numerical and energetic processes have several fundamental problems. Firstly, while supplemental feeding unequivocally demonstrates the importance of food availability to life processes, the response observed may not be realistic because the supplemental food source and the levels at which it is fed are often not natural. Secondly, correlative studies with natural food items do not demonstrate the cause of the patterns observed. An understanding of how food availability shapes numerical and energetic processes in reef fish will build on correlative studies by testing the effects of natural fluctuations in food availability with appropriate control treatments (for example see Clifton 1995) coupled with artificial food manipulations (for example see McCormick 2003) or measures of response variables in similar species that do not exploit the resource to detect site related effects.

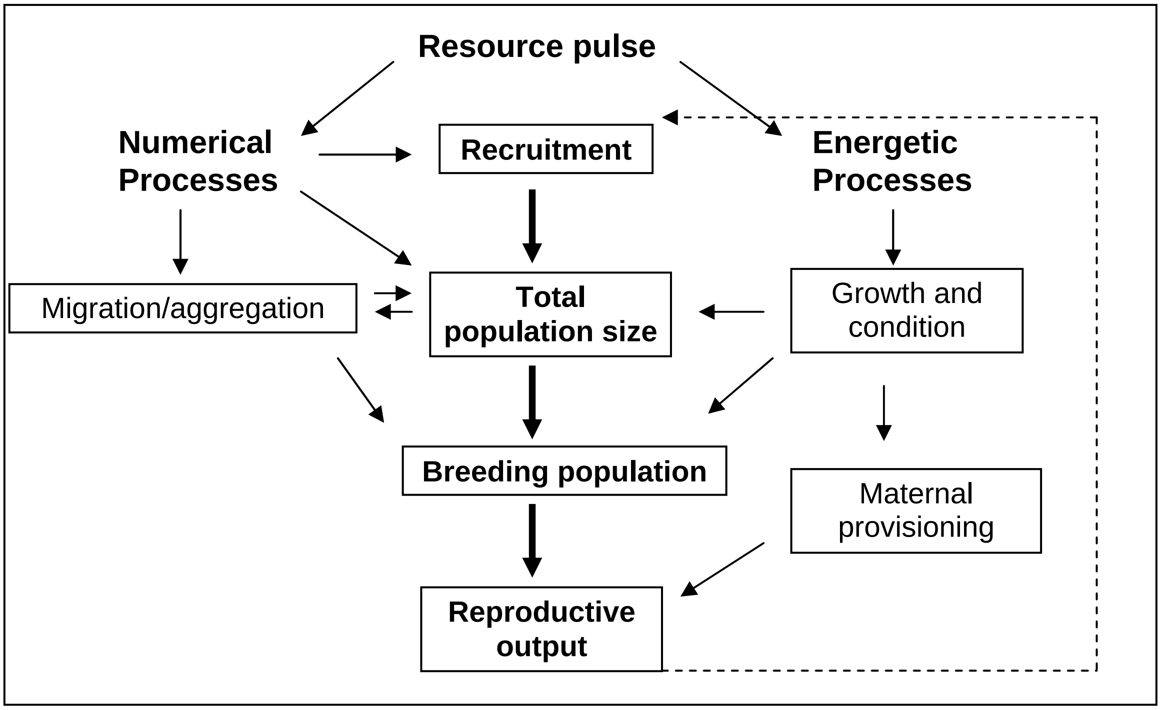

Figure 1.2 Proposed model of the effects of a resource pulse on reef fish population dynamics via numerical and energetic processes. Modified from Jones and McCormick (2002).

Reef fish spawning aggregations: a resource pulse for egg predators

A previously unstudied resource pulse on coral reefs is the periodic release of gametes at reef fish spawning aggregation sites that provides a pulse of energy rich eggs for planktivorous egg predators. Reef fish spawning aggregations are temporary aggregations of reef fishes and the majority of species spawn their gametes pelagically (Johannes 1978). The spawning rush is a ubiquitous feature of pelagic spawning and involves either a pair (one female and one male) or group (one female and several males) rushing towards the water's surface in unison to release visible gametes into the prevailing currents (Domeier & Colin 1997). For a brief period immediately after the spawning rush, eggs (and potentially sperm) are vulnerable to predation by obligate and facultative planktivorous reef fishes (Robertson 1983). Several features of spawning aggregations may make them vulnerable to egg predation and potentially a valuable food source for egg predators. Reef fish spawning aggregations are characterised by the use of predictable locations on the reef (spawning aggregation sites, SASs) which are traditionally used across multiple generations (Warner 1988) and are used on a range of species-specific temporal scales. The temporal periodicity of spawning aggregations falls broadly into one of two categories. Spawning aggregations can be categorised as 'transient', which involve long migrations with short reproductive periods usually determined by lunar phases. Conversely, 'resident' spawning aggregations involve shorter migratory distances over with spawning performed over longer periods and are often comprised of smaller bodied reef fish (Domeier & Colin 1997). Studies demonstrate that resident spawning aggregations can coincide with lunar phases (Robertson, 1983), tidal flow (Sancho 2000) or specific diel periods (Claydon, 2005). It may be expected that the spatial predictability and more frequent spawning aggregations by resident spawners provide a predictable pulse of food for the planktivorous egg predator community. In addition, fish eggs have energy contents that are 20 - 25% greater than alternative planktonic prey due to their high lipid content (Kamler 1992). Recently spawned eggs also have the exact nutrient profiles required for egg predator oogenesis in female egg predators. These characteristics suggest that eggs released at reef fish SASs may be an important food source for the egg predator community.

Meanwhile, spawners are expected to minimise egg predation, and therefore promote reproductive success, through behaviours that are characteristic of spawning aggregations. Theory predicts that SASs are selected to minimise egg predation through reduced numbers of egg predators and have off-reef currents that carry eggs away from reef based predators (Johannes 1978). In addition, the synchronisation of spawning rushes is proposed to swamp egg predators with available eggs and therefore promote offspring survival (Robertson 1983). However, no studies have demonstrated that SASs provide an advantage over other reef locations or that egg predator swamping is a function of synchronised spawning (Claydon 2004). The dynamic between the minimisation of egg predation by pelagic spawners and the trade-offs that determine levels of predation and ultimately influence the egg predator community is currently unknown.

To date, 243 species from 29 families have been reported to spawn pelagically (Claydon 2005) and of these a significant number spawn in large aggregations with massed synchronisation of grouped spawning rushes (Robertson 1983). The synchronisation of spawning rushes releases visible gamete clouds simultaneously resulting in large volumes of eggs being vulnerable to predation by reef based planktivorous fishes. Planktonic eggs usually comprise about 2% of the volume of a planktivorous reef fish's diet (Sano et al. 1984), however at least 32 species are reported to attack gamete clouds at SASs, potentially making eggs a larger component of the diets of these fishes (Robertson 1983, Moyer 1987, Colin & Clavijo 1988, Colin & Bell 1991, Sancho et al. 2000). While the higher densities, energetic value and spatial predictability of recently spawned eggs at SASs may provide energetic benefits, several costs may also be associated with exploiting this food resource. It is likely that egg predators are exposed to similarly increased levels of piscivory as spawning species at SASs (Moyer 1987, Sancho et al. 2000). It is currently unknown if egg predators aggregate to exploit recently spawned eggs, however energy expenditure and the risk of predation while migrating are predicted to influence patterns of egg predation. It is currently unknown how these trade-offs shape the levels of egg predation at reef fish SASs and how the net energetic gains are partitioned among life history traits to ultimately influence numerical and energetic processes that affect egg predator populations.

The study system

Most of the field work for this thesis was conducted using resident reef fish SASs on the inshore reefs adjacent to Kilu and Tamare villages of Kimbe Bay, West New Britain Provence, Papua New Guinea (Fig 1.3 and 1.4). The reefs used in this study are small inshore reefs that contain multiple SASs (Fig 1.3 and 1.4). The reefs are in close relative proximity but separated by deep passages of water (~80 m deep). The SASs used in this study (Fig 1.5 and 1.6) were originally identified by (Claydon 2005) (Fig 1.5 and 1.6) and this study builds upon his original observation of egg predation at these sites. As such, the SAS nomenclature used in this study is adopted from (Claydon 2005). This previous body of work reported spawning aggregations by 37 species of reef fish with little seasonality in spawning activity. Physical attributes of these SASs have been studied in detail and show that SASs have a greater seaward projection than other reef locations, however topographic rugosity and reef slope do not differ from other reef locations (Claydon 2005). Furthermore, this study location is characterised by small tidal movements that do not influence current flows typical of tidal driven systems (i.e. change in tide does not influence current flow or direction) and current speeds are small (range between 6 cm/sec and 20 cm/sec) compared with studies that examined spawning aggregations at other geographic localities (Claydon 2005). Claydon (2005) comprehensively examined patterns of SAS physical features (i.e. tides, currents and topography) at this study location. Therefore this study does not deal specifically with these processes, but rather aims to quantify egg predation among spawning species and SASs and examine the effects of this food source on the egg predator community.

Chapter 2 of this thesis identifies the surgeonfish *Ctenochaetus striatus* as the most prolific spawner and the species that suffers the highest levels of egg predation of all the observed spawning species. Therefore, chapters 3 and 4 use *C. striatus* as the focal spawning species. Targeting the spawning aggregations of this species improved the likelihood of collecting sufficient quantities of data of an otherwise rare behavioural event. At this study location *C. striatus* spawn in large aggregations (up to 2000 fish) with synchronised spawning rushes that release large volumes of visible gamete clouds into the water column (Claydon 2005). *Ctenochaetus striatus* form aggregations with a highly predictable diel spawning period (Claydon 2005), that typically involve pre-spawning courting behaviour for a period of 30 – 45 minutes followed by 5 – 10 minutes of intense spawning. The spawning acts involve one female and one to five males performing a rapid spawning rush. The synchronisation of spawning rushes produces large visible clouds that are often heavily exploited by egg predators before the remaining eggs and sperm are carried away from the reef.

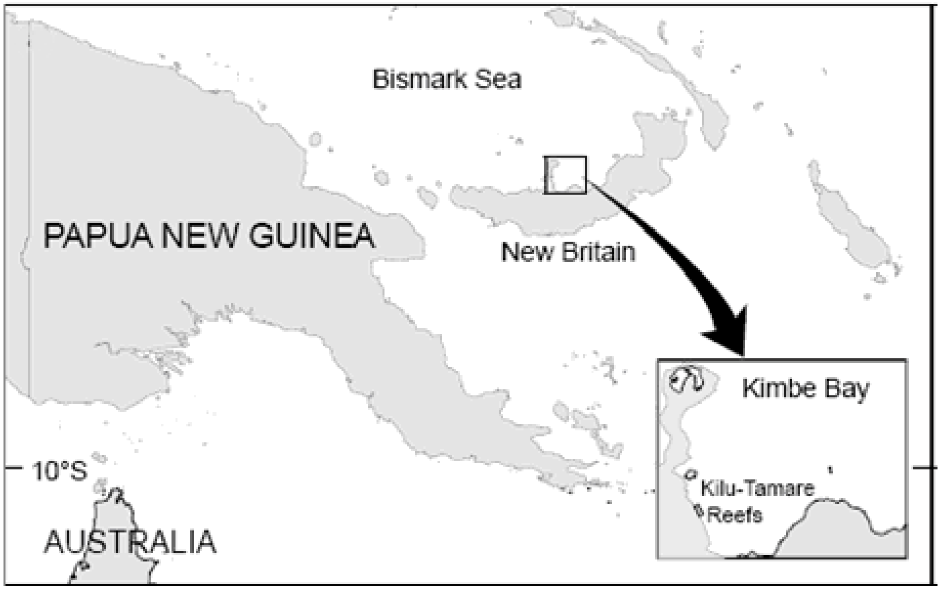

Figure 1.3 Map of the study location, with permission from Srinivasan (2007).

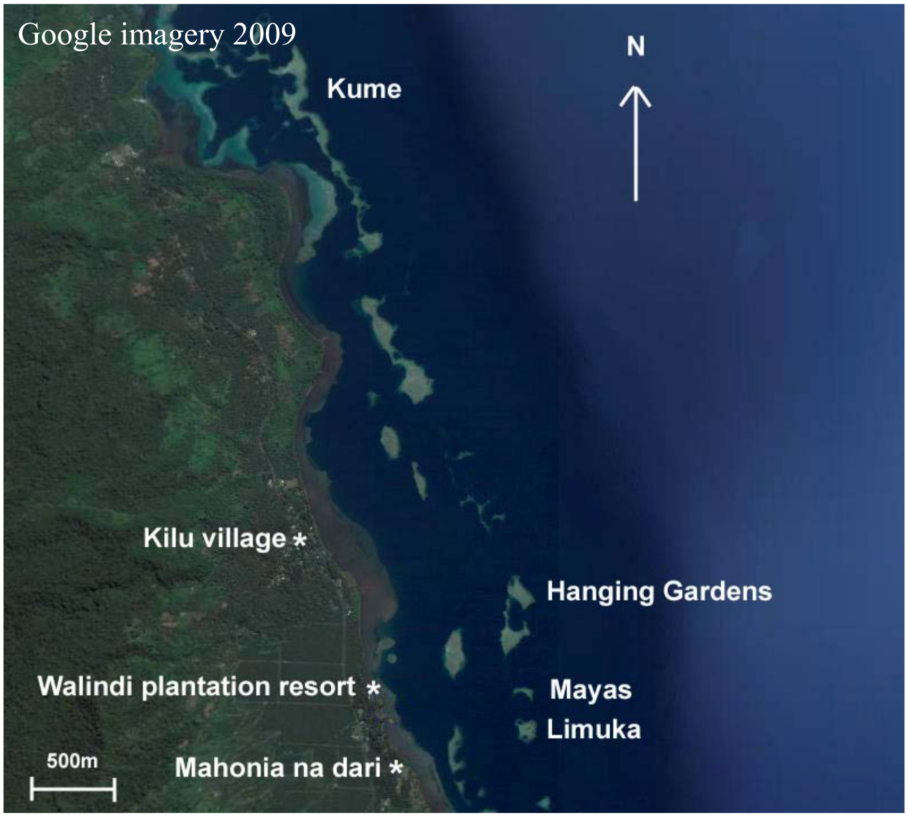

Figure 1.4 Inshore study reefs adjacent to Kilu village, Walindi Plantation Resort and Mahonia na Dari Research and Education Centre.

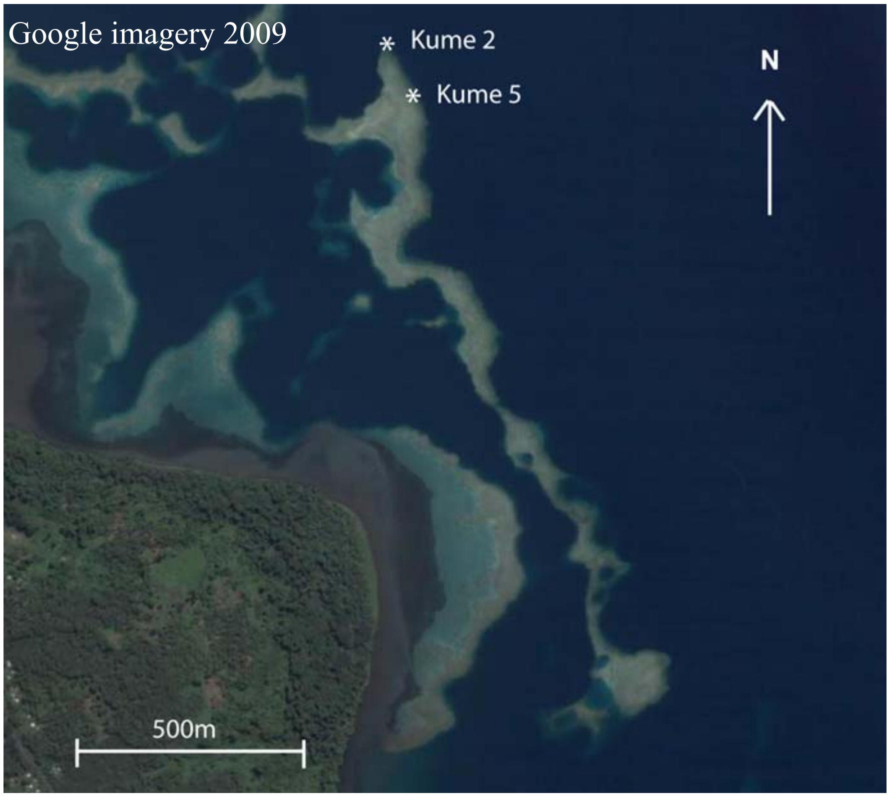

Figure 1.5 Spawning aggregation site (Kume 2 and Kume 5) on Kume Reef.

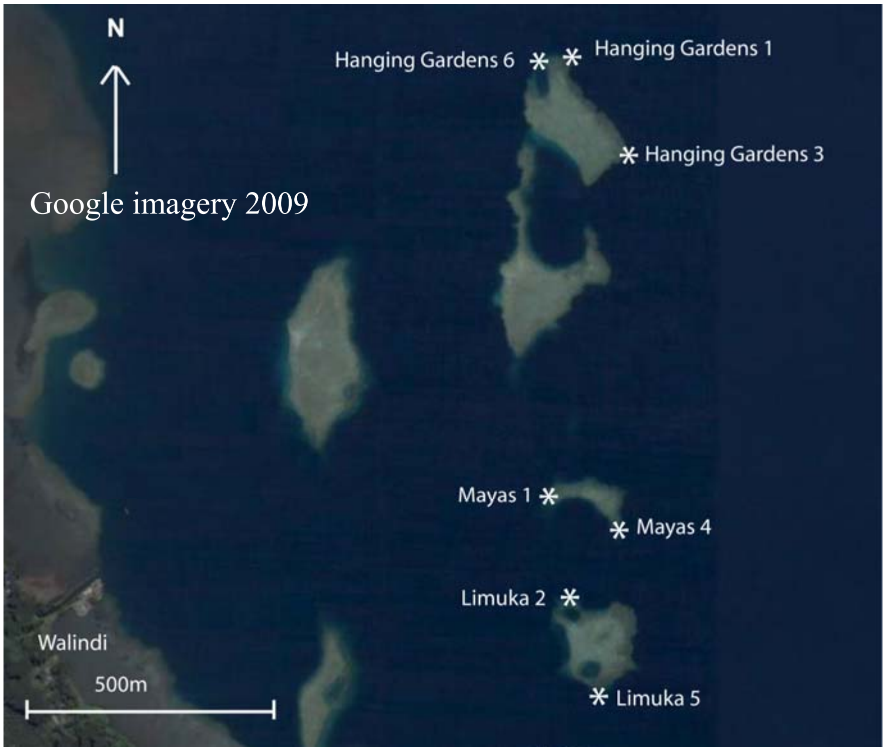

Figure 1.6 Spawning aggregation sites (HG 1, HG 3, HG 6, M 1, M 4, L 2 and L 5) at Hanging Gardens, Mayas and Limuka Reefs.

Aims and thesis outline

This thesis uses field studies and a laboratory manipulation to quantify egg predation at SASs and examine how eggs as a pulsed food resource influence numerical and energetic processes in the egg-predator community. This study has four primary objectives: (1) explore patterns of spawning activity and the associated levels of egg predation among SASs and spawning species, (2) examine the distribution and abundance of all known egg predators and movement patterns of a key egg predator species in relation to SAS and *C. striatus* spawning activity, (3) determine the effects of egg predation on energy allocation among life history traits in a key egg predator, (4) determine how the consumption of eggs influences maternal provisioning in the offspring of a known egg predator species.

Each chapter of this thesis is written to address separate stand-alone aims for the purpose of future publication, however each chapter is connected conceptually. **Chapter 2** quantifies patterns of spawning activity and the associated levels of egg predation among SASs and among spawning species. This is the first study to systematically quantify egg predation at more than one SAS. The findings of this study are discussed in relation to possible causal factors of the observed patterns including egg predator abundance among SASs, the volumes of eggs released (i.e. food availability) among species and spawning behaviour. This study also serves to identify the candidate spawning and egg predator species for subsequent chapters. **Chapter 3** tests the hypothesis that eggs as a food pulse will influence the abundance and/or movement patterns of egg predators. I predicted that SASs will have higher densities of resident egg predators and/or egg predators will actively aggregate to exploit eggs at *C. striatus* spawning aggregations. However, there are likely to be species specific responses by egg predators. I test this hypothesis by comparing the abundance of egg predators among SASs and non-SASs during both spawning and non-spawning periods. After identifying an increase in the abundance of *Abudefduf vaigiensis* at SASs during spawning periods, a movement study was conducted by tagging *A. vaigiensis* to further resolve their movement patterns in relation to spawning activity at SASs. **Chapter 4** tests the hypothesis that feeding on the recently spawned eggs of *C. striatus* will influence the life history traits of the resident egg predator, *A. vaigiensis*. I predict that *A. vagiensis* that feed on *C. striatus* eggs will have increased growth, condition and reproduction. Here the growth histories, body condition and reproductive output of *A. vaigiensis* are compared among SASs and non-SASs. To detect any site related effects I use *Pomacentrus moluccensis* (which does not feed on eggs at SASs) as a reference species. Finally, **Chapter 5** tests the hypothesis that the consumption of eggs will influence maternal effects on offspring life history traits either through increased energy intake and/or through their nutrient profile. For logistical reasons this study was conducted under controlled laboratory conditions. I predict that maternal provisioning will be influenced by increased food quality and/or increased energy intake. The known egg predator species, *Acanthachromis polyacanthus*, were fed a control diet or a control diet partially substituted (isocalorific) or supplemented with eggs (greater caloric content) of a pelagic spawner.

Chapter 2

Patterns of target egg predation at resident reef fish spawning aggregation sites

---

Introduction

The immediate predation of eggs is hypothesised to be a key influence on the reproductive behaviours that characterise reef fish spawning aggregations (Randall and Randall 1963, Robertson & Hoffman 1977, Johannes 1978, Lobel 1978, Warner 1988). Characteristic behaviours of many resident reef fish spawning aggregations are massed aggregations with synchronised spawning rushes that rapidly release gametes into the water column (Robertson 1983), and the shared use of predictable spawning aggregation sites (SASs) among spawning species (Johannes 1978). Theory suggests these behaviours minimise egg predation through: (1) synchronising the release of gametes in order to swamp egg predators with available eggs (egg predator saturation hypothesis), and (2) the selection of favourable locations to minimise egg predation by reef based predators (egg predation hypothesis) (Johannes 1978, Lobel 1978, Robertson 1983). Since recently spawned eggs may be vulnerable to predation, spawning adults are expected to adopt behaviours that maximise reproductive success (Robertson 1983). However, few studies have accurately quantified egg predation (except see Robertson 1983, Moyer 1987, Sancho et al. 2000) and little is known of the underlying causes that shape this process (Robertson 1983, Shapiro et al. 1988). The present study addresses this paucity of information regarding resident reef fish spawning aggregations.

The predator saturation hypothesis predicts that egg predation will asymptote with increasing egg density due to restrictions in egg predator handling time (Type II functional response) (Claydon 2004, 2005). Consequently, prey density continues to increase and the probability of any one egg being preyed upon decreases (Johannes 1978). This strategy has been proposed to explain the phenomenon of large aggregations of resident spawners (e.g. acanthurids, labrids and scarids) that synchronise the release of their spawning rushes (Robertson 1983). Synchronising the release of spawning rushes is suggested to rapidly increase spawning intensity to swamp egg predators. However, no studies have quantitatively documented this strategy by measuring levels of egg predation in relation to spawning intensity.

Reef based obligate and facultative planktivores are the primary predators of eggs at reef fish SASs (Moyer 1987, Colin & Clavijo 1988, Colin & Bell 1991, Sancho et al. 2000). The distribution and abundance of such predators varies greatly with habitat and food availability (Thresher 1983, Williams 1991, Jones & McCormick 2002). Therefore it is unlikely that predation pressure on recently spawned eggs will be uniform among SASs. However, previous studies that have quantified egg predation at SASs have little or no replication among sites (Robertson 1983, Moyer 1987, Colin & Bell 1991, Sancho et al. 2000) and there is no information about the variability in the spatial distribution of egg predator assemblages. Comparisons among previous studies have been made to assess differences in egg predation among locations, however each study focused on different species (Leis & McCormick 2002). Therefore, the role of egg predation may have been incorrectly inferred, since levels of egg predation also differ among spawning species (Sancho et al. 2000). A detailed understanding of inter-specific and intra-specific differences in egg predation among SASs forms the foundation for understanding the significance of egg predation in resident SAS selection.

Egg predation can occur as target or non-target egg predation and is differentiated by egg predator behaviour (Colin & Bell 1991, Claydon 2004). Target egg predators are obligate and facultative planktivores that actively seek gamete clouds and prey directly on the visible gamete cloud. Target egg predators may also continue to feed on the gamete clouds by drifting in the projected direction of the gamete cloud after it is no longer visible. Non-target egg predators are strictly planktivorous fishes that do not actively pursue gamete clouds. Direct predation of gametes by these egg predators is not visible and the only change in behaviour is rapid and haphazard feeding behaviour down current of spawning rushes. Accurate identification and quantification of non-target egg predation is often difficult, and the present study deals only with target egg predation.

This study quantified patterns of target egg predation among seven tropical spawning aggregation sites for the resident spawning surgeon fish, *Ctenochaetus striatus*, the parrot fish *Chlorurus bleekeri*, and the wrasse, *Thalassoma hardwicke*. *C. striatus* is known to spawn in large aggregations with synchronised spawning rushes. Synchronisation is thought to swamp egg predators with available eggs with a Type II functional response by rapidly increasing spawning intensity (Robertson 1983). Therefore, the present study investigated whether levels of egg predation vary in relation to *C. striatus* spawning intensity. The purpose of this study was to: (1) explore the role of synchronised spawning as an egg predator swamping strategy, and (2) determine if egg predation varies with egg predator assemblages among SASs.

Materials and Methods

Study site and spawning aggregation sites

This study was conducted in Kimbe Bay, West New Britain Province, Papua New Guinea (5° 30'S, 150° 05'E) (Fig 1.3) on three small inshore platform reefs (Hanging Gardens, Mayas and Limuka) (Fig 1.4). The reefs are located approximately 500 – 800 m from shore, separated by deep passages of water (≈ 80 m) and are exposed to small tides (< 1 m range; one ebb and one flood movement/day). The platform reefs are characterised by front and back reef zones. The windward or front reef zone has high coral cover, steep topographic relief/vertical wall, and is exposed to south-east winds. The leeward or back reef zone is characterised by coral rubble and sand and isolated patches of coral, a gentle topographic relief, and is protected from south-east winds. Seven spawning aggregation sites, identified and named by (Claydon 2005), at depths ranging from 2 - 4 m, were monitored for spawning activity. Each spawning aggregation site was in either a front reef zone (Hanging Gardens site 1, HG 1; Hanging Gardens site 3, HG 3; Mayas site 4, M 4; Limuka site 5, L 5) or a back reef zone (Hanging Gardens 6, HG6; Mayas 1, M 1; Limuka 2, L 2) (Fig 1.6).

Spawning activity and egg predation

Spawning activity and egg predation were monitored by a single snorkeller performing spot surveys across all spawning aggregation sites daily between 1400 hrs and dusk (≈ 1800 hrs) 20th August to 11th October 2005. Surveys were performed during this diel period since the majority of fish species known to spawn at this study site do so during this time (Claydon 2005). When a spawning aggregation was encountered the entire event was monitored until all spawning rushes and courtship-related behaviours ceased. Spawning aggregations that had commenced prior to being encountered were not incorporated in data analysis. All spawning activity was recorded including the species and number of fish that aggregated to spawn, the number of spawning rushes performed during an aggregation, and the spawning duration. Target egg predation was quantified by recording the number of spawning rushes attacked. These data and the number of spawning rushes performed during a spawning aggregation were used to calculate the proportion of spawning rushes preyed upon. During a target egg predation event, the species and number of egg predators actively feeding on the gametes cloud were also recorded.

Egg predator surveys

Egg predator surveys were conducted at each spawning aggregation site that was monitored previously for spawning activity. Quadrats of a known area (ranging from 31.6 to 156.5 m^2) were constructed by laying fine cord around the area in which spawning was observed. During a single spawning event, a single observer recorded all egg predators present within the quadrat to calculate egg predator density.

Egg collection, quantification and volume measurements

The eggs from spawning rushes of *C. striatus* (n = 17), *C. bleekeri* (n = 24) and *T. hardwicke* (n = 25) were caught with a plankton net (100 μm plankton mesh, diameter 330 mm, length 1000 mm) towed by a snorkeller. Only visible gamete clouds were collected less than three seconds after release by passing the net through the cloud for a three second period. Eggs from each rush where filtered using 100 μm plankton mesh and stored in a 2% seawater buffered formaldehyde solution. Preserved samples were decanted into seawater to 100 ml, mixed thoroughly and three 1 ml sub-samples taken. All eggs were counted from each sub-sample and the arithmetic mean used to calculate eggs released per spawning rush. Egg volumes for each species were determined by photographing eggs from each species (n = 30). The measurements required to calculate the volume of each egg were determined using Image Tool (UTHSCSA, San Antonio, USA). The mean volume of eggs released per rush multiplied by the mean number of rushes observed during a spawning event gave an estimate of the mean volume of eggs released during a spawning aggregation for each species.

Statistical analysis

Proportions of spawning rushes of *C. striatus* and *C. bleekeri* attacked by target egg predators among spawning aggregation sites were compared using two-way ANOVA ($\alpha = 0.05$). Data for *T. hardwicke* were not included in analyses due to the occurrence of many zeroes, however those data are presented in Fig 1. Data were square root transformed to meet the assumptions of normality and homogeneity of variances. Post-hoc comparisons were performed with Student-Newman-Keuls (SNK) stepwise means comparison test. Mean proportion of rushes attacked by target egg predators and mean abundances of all target egg predators were analysed with a non-parametric MANOVA (using Bray-Curtis dissimilarity matrices) (Anderson 2001). Rates of egg predation versus spawning intensity plots were fitted to a simple linear regression. Differences in the proportion of rushes attacked, individual egg volume and total egg volume per spawning event among spawning species were individually compared with one-way ANOVA ($\alpha = 0.05$). Data were square root transformed to meet assumptions of homogeneity of variance and normality. Post-hoc comparisons were performed using Tukeys HSD.

Results

Spawning activity

A total of 25 reef fish species from five families were observed spawning during the study period (Table 2.1). Only *Ctenochaetus striatus*, *Chlorurus bleekeri* and *Thalassoma hardwicke* were observed spawning at all the spawning aggregation sites monitored. Pair spawning was the dominant spawning mode among all species. However, group spawning was observed in *C. striatus, T. hardwicke, T. amblycephalum, Stethojulis strigiventer* and the greatest number of spawning rushes observed resulted from group spawning. On several occasions after a spawning rush by *C. bleekeri*, *T. hardwicke* and *Epibulus insidiator* the male from a spawning rush was observed chasing an egg predator, however this only occurred after pair spawning rushes (Table 2.1).

Table 2.1 Fish species that were observed to spawn during the study period (at seven spawning aggregation sites) and the numbers of spawning rushes observed versus those attacked by target egg predators. n = the number of spawning aggregations observed; Sites = number of sites spawning was observed from the seven sites monitored; G = group spawning, P = pair spawning and S = streaker.

Family Species	n	Rushes observed	Rushes attacked	Chased egg predator	Sites	Spawning mode
Acanthuridae						
Ctenochaetus striatus	61	1882	678	No	7	G, P
Zebrasoma scopas	5	7	0	No	5	P
Zebrosoma veliferum	2	2	0	No	1	P
Labridae						
Chelinus trilobatus	8	10	1	No	5	P
Epibulus insidiator	16	30	0	Yes	6	P
Gomphosus varius	2	2	0	No	1	P

	Halichoeres hortulanus	11	15	4	No	5	P
	Halichoeres margaritaceus	2	2	0	No	3	P
	Halichoeres marginatus	2	2	1	No	2	P
	Halichoeres melanurus	2	2	0	No	3	P
	Halichoeres purpurescens	1	1	1	No	1	P
	Hemigymnus melapterus	2	2	0	No	1	P
	Labrichthys uniliteatus	7	7	1	No	4	P
	Novaculichthys taeniorus	4	6	0	No	4	P
	Stethojulis strigiventer	14	29	9	No	6	G
	Thalassoma amblycephalum	20	37	2	No	2	G, P
	Thalassoma hardwicke	31	140	13	Yes	7	G, P
	Thalassoma jansenii	2	2	0	No	2	P
	Thalassoma lunare	17	32	5	No	3	P
Mullidae							
	Parupeneus bifasciatus	1	1	0	No	1	P
	Parupeneus multifasciatus	6	8	0	No	4	P
Ostraciidae							
	Ostracion meleagris	5	5	0	No	1	P
Scaridae							
	Chlorurus bleekeri	80	213	16	Yes	7	P, S
	Scarus dimidiatus	7	10	0	No	3	P
	Scarus microrhinos	3	4	0	No	1	P

Patterns of egg predation were examined among SASs for *C. striatus* and *C. bleekeri*. There was a significant interaction in levels of egg predation among spawning species and among SASs ($F_{12,114} = 42.73$; $p < 0.001$) (Fig 2.1). *C. striatus* suffered significantly greater levels of egg predation on spawning rushes released at front reef sites (HG 1, HG 3 and M 4) than at back reef sites (HG 6, M 1 and L 2) ($p < 0.05$).

Significantly fewer spawning rushes of *C. bleekeri* were attacked ($p < 0.05$) and there was no significant difference among SASs ($p > 0.05$). Spawning rushes of *T. hardwicke* were only preyed upon at one site (HG6). Hanging Gardens 6 was the only site where spawning rushes of all three species were preyed upon (Fig. 2.1).

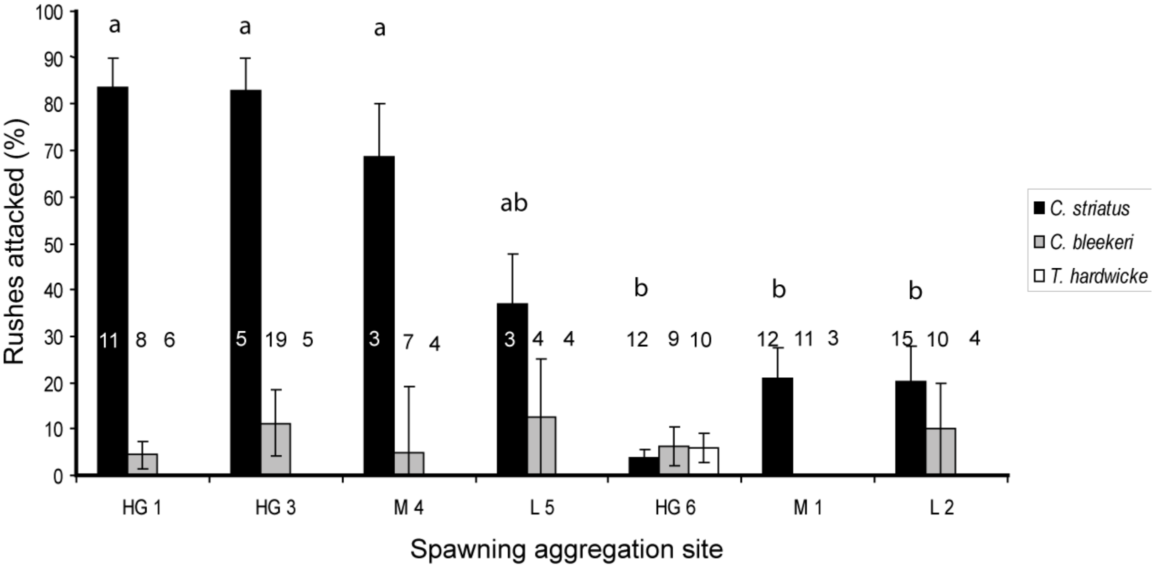

Figure 2.1 Proportion of spawning rushes (%± SE) of *Ctenochaetus striatus*, *Chlorurus bleekeri* and *Thalassoma hardwicke* preyed upon by target egg predators. Spawning aggregation sites HG 1, HG 3, M 4 and L 5 are located at the reef front. Spawning aggregation sites HG 6, M 1 and L 2 are located at the back reef (see Fig. 1 for locations). Replicate spawning events are given in or above each bar. Superscripts (letters a or b) denote groupings of means determined by SNK post-hoc means comparison for *Ctenochaetus striatus* only.

Egg predation for C. striatus and egg predator density among reef zones

Rates of egg predation on *C. striatus* spawning rushes by each target egg predator species were examined among front and back reef zones. The rates of target egg predation at front reef sites differed significantly from rates of predation at back reef sites ($F_{1,40} = 21.59$; $p = 0.001$) (Fig 2.2). The greatest proportions of rushes were attacked by *Abudefduf vaigiensis* at front reef sites. The proportions of rushes attacked by all other egg predator species were similar among front and back reef locations (Fig 2.2).

Similarly, the densities of target egg predators were examined among reef zones. The density of target egg predators at front reef sites differed significantly from densities of target egg predators at back reef sites and reflected patterns in egg predation by each egg predator species among front and back reef zones ($F_{1,6} = 11.60$; $p = 0.02$) (Fig 2.3). *A. vaigiensis* were the most abundant egg predator at front reef sites and were absent from back reef zones (Fig 2.3).

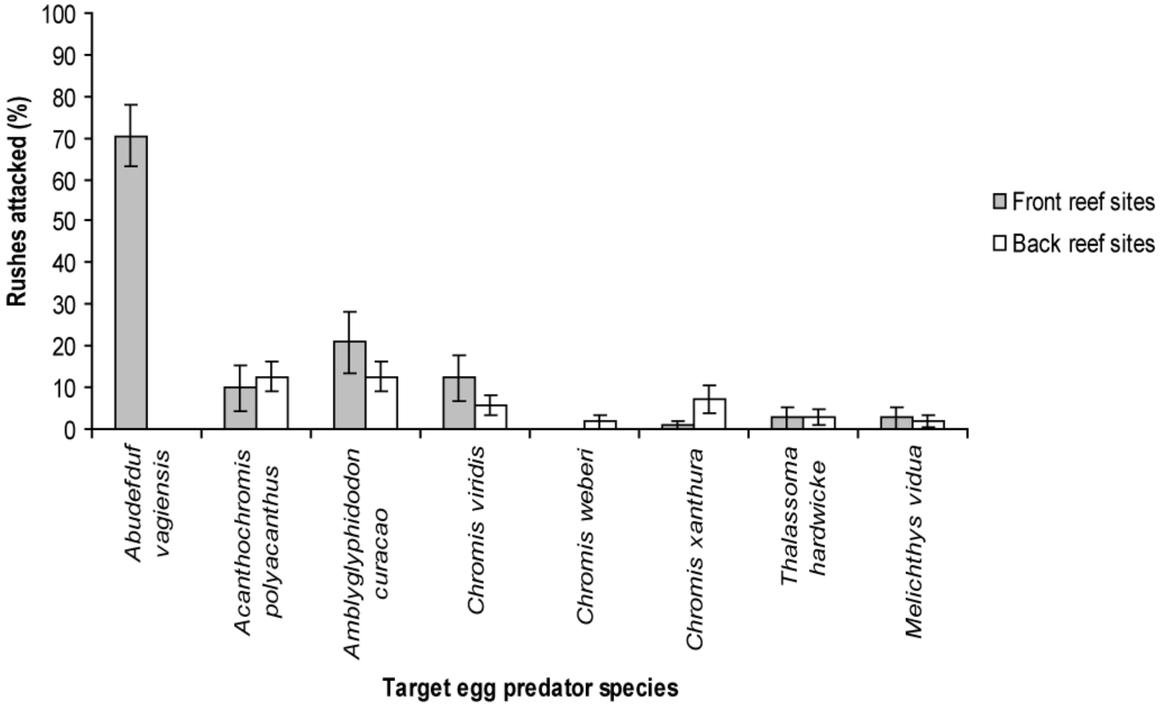

Figure 2.2 Mean proportion of *Ctenochaetus striatus* spawning rushes attacked by each target egg predator at front reef (n = 4) and back reef spawning aggregation sites (n = 3).

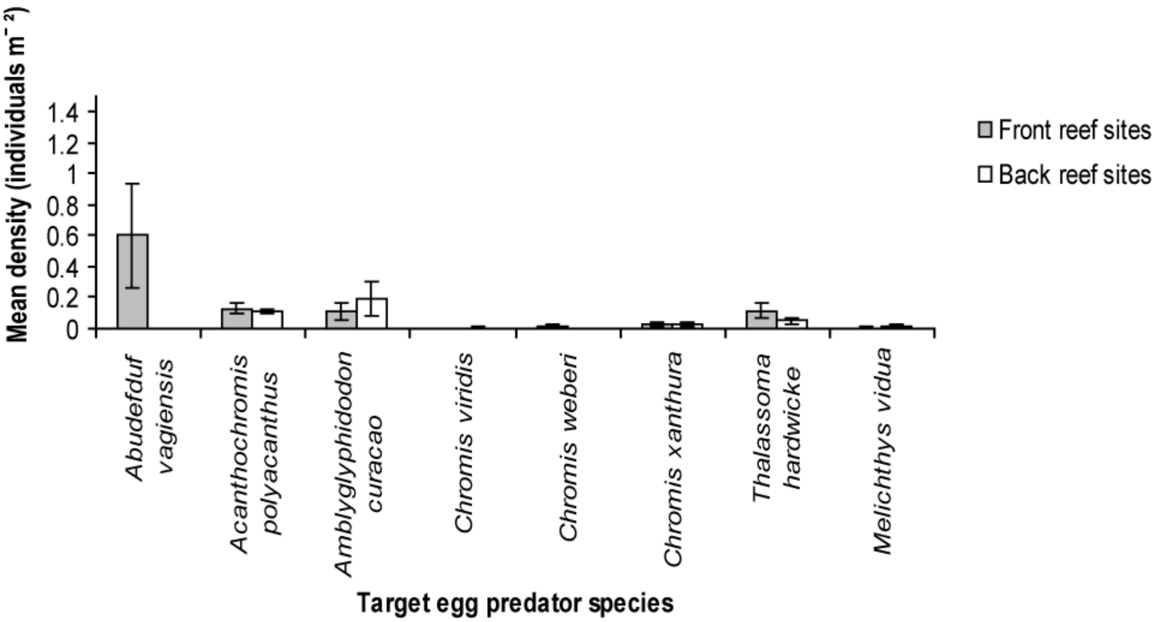

Figure 2.3 Mean abundances of all target egg predators at front reef (n = 4) and back reef spawning aggregation sites (n = 3).

Egg predator functional response to Ctenochaetus striatus spawning intensity

To examine the functional response of egg predators to the availability of *C. striatus* eggs, I examined the relationship between the rushes attacked per minute and spawning intensity as the number of spawning rushes per minute (as a measure of egg availability). Levels of egg predation increased linearly with spawning intensity of *C. striatus* at front reef sites ($r^2 = 0.929$) (Fig 2.4). At back reef sites, no relationship was observed between the proportion of rushes attacked and spawning intensity ($r^2 = 0.093$) (Fig 2.5).

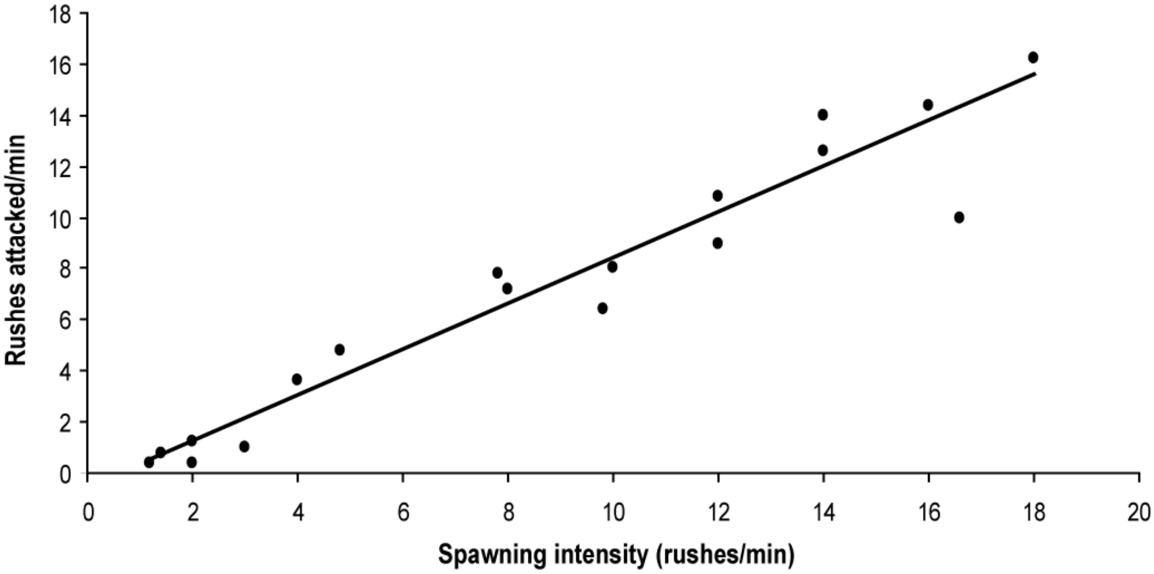

Figure 2.4 Relationship between the rate of rushes attacked per minute and spawning intensity (rushes/minute) for *Ctenochaetus striatus* at front reef spawning aggregation sites ($r^2 = 0.929$). Each point represents a single spawning aggregation event.

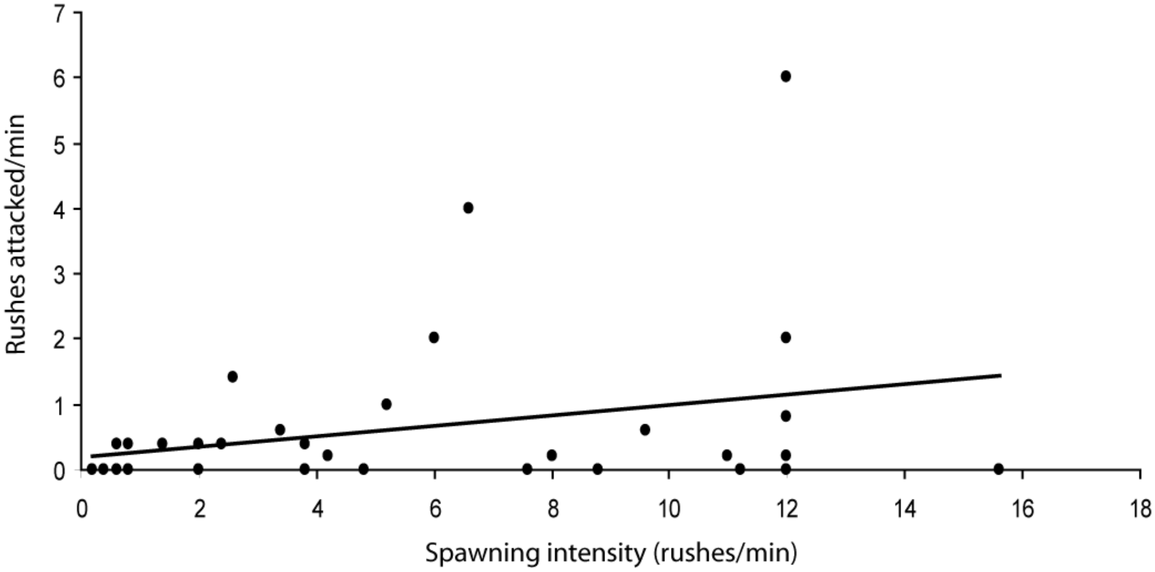

Figure 2.5 Relationship between the rate of rushes attacked per minute and spawning intensity (rushes/minute) of *Ctenochaetus striatus* at back reef spawning aggregation sites ($r^2 = 0.093$). Each data point represents a single spawning aggregation event.

Patterns of egg predation among spawning species and egg characteristics

Mean egg volume and mean volume of all eggs released during a spawning aggregation by *C. striatus*, *C. bleekeri* and *T. hardwicke* were examined in order to determine if differences in volumes were reflected in rates of egg predation among spawning species. The proportion of rushes attacked differed significantly among spawning species ($F_{2,160} = 31.47$; $p < 0.001$). *Ctenochaetus striatus* suffered the greatest proportion of spawning rush attacks (mean = 36.3 ± 4.8 SD; $p < 0.001$), and levels of egg predation did not differ significantly between *C. bleekeri* and *T. hardwicke* (mean ± SD: 7.7 ± 2.8, 2.0 ± 1.1 respectively; $p = 0.611$). Similarly, mean egg sizes differed significantly among species ($F_{2,87} = 39.72$; $p < 0.001$). *Ctenochaetus striatus* had significantly larger eggs (mean ± SD: $4.16*10^6 \pm 8.81*10^4$ μm^3; $p < 0.001$), and the egg size of *C. bleekeri* and *T. hardwicke* did not differ significantly (mean ± SD: $3.55*10^6 \pm 3.96*10^4$μm^3 and $3.53*10^6 \pm 3.90*10^4$μm^3 respectively; $p = 0.933$). However, the differences in egg size poorly reflected differences in levels of egg predation. In contrast, the mean volume of all eggs released during an entire spawning event differed significantly among species ($F_{2,178} = 127.82$; $p < 0.001$) and closely reflected the differences observed in levels of egg predation among species. *Ctenochaetus striatus* released significantly larger volumes of eggs than *C. bleekeri* and *T. hardwicke* during spawning events (mean ± SD: $1.24*10^{12} \pm 3.08*10^{10}$; $p < 0.001$), while the volumes of egg released by *C. bleekeri* and *T. hardwicke* did not differ significantly (mean ± SD: $9.4*10^{10} \pm 2.95*10^9$ and $3.33*10^{10} \pm 1.23*10^9$ respectively; $p = 0.889$).

Discussion

Patterns in egg predation among spawning aggregation sites

Spawning aggregations are a critical focus for conservation and fisheries management of coral reef fish populations (Rhodes & Sadovy 2002). However, little is known of the effect of egg predation on reproductive behaviour and how it impacts the effective liberation of propagules away from the reef. The present study is the first to quantify rigorously the proportion of spawning rushes attacked by planktivorous reef fishes among resident reef fish SASs. Levels of predation on the spawning rushes of *Ctenochaetus striatus* differ among front and back reef locations with higher levels of predation at reef front SASs. However, no patterns were observed for *Chlorurus bleekeri* and *Thalassoma hardwicke*. *Abudefduf vaigiensis* attacked the majority of spawning rushes and were the most abundant egg predator at front reef SASs. This provides strong evidence that egg predator distribution and abundance influenced spatial patterns of egg predation for *C. striatus*. The current findings support a number of studies that show levels of predation are determined by predator abundance on coral reefs (Connell 1996, Connell & Kingsford 1998, Holbrook & Schmitt 2003, Holmes & McCormick 2006). This study demonstrates the importance of local community dynamics in shaping levels of egg predation for *C. striatus*.

The reported variation in egg predation among SASs in the present study, which resulted from variations in egg predator assemblages, highlights the need to measure egg predation at an appropriate spatial scale (Shapiro et al. 1988; Sale 1998). Previous studies report varying levels of egg predation among spawning aggregation sites (Robertson 1983, Colin & Bell 1991), however the number of SASs within the study area are often not reported. Levels of target egg predation from previous studies are highly variable. Predation on the eggs of *Thalassoma cupido* were 42% of 213 spawning rushes (Moyer 1987). In comparison, 0.6% of 7448 spawning rushes by six spawning species were attacked during 77.5 hours of observations at a single SAS at Johnston Atoll (Sancho et al. 2000) and egg predation was not observed during many spawning aggregations of up to 20,000 *Acanthurus bahianus* at a single SAS in south-western Puerto Rico (Colin & Clavijo 1988). Furthermore, making within-species comparisons of egg predation among SASs, by comparing levels of egg predation among studies, are difficult due to the infrequent overlap of species among studies. Consequently, the relative importance of target egg predation is poorly understood and likely to have been influenced by site level processes resulting from a lack of replication among SASs. The present study highlights the importance for future studies to control for the effects of target egg predator distribution and abundance.

Patterns in egg predation among spawning species

The current findings demonstrate that levels of egg predation vary among spawning species. Previous studies also report large differences in levels of egg predation among spawning species within the same spawning aggregation site (Colin & Clavijo 1988, Sancho et al. 2000). Although the reasons for these differences are unclear, several factors may be important. Sancho et al. (2000) provided preliminary evidence that species with larger eggs suffer greater rates of target egg predation. However, differences in egg size among *C. striatus*, *C. bleekeri* and *T. hardwicke* in this study do not closely reflect the differences in the levels of egg predation among spawning species. Alternatively, differences in the total volume of eggs released during an entire spawning aggregation are more representative of differences in egg predation among species. Such heterogeneity in reproductive output per spawning aggregation is likely to result from differences in spawning behaviour. The spawning rushes by *C. striatus* are predominantly performed in group synchrony resulting in large visible clouds (Robertson 1983). In contrast, *C. bleekeri* and *T. hardwicke*, primarily pair spawn in a haphazard manner (see

Colin & Bell 1991 for a detailed description of *T. hardwicke* spawning behaviour). Multiple gamete clouds released in rapid succession by *C. striatus* may be more visible to target egg predators and offer greater profitability than the spawning rushes of *C. bleekeri* and *T. hardwicke*. Robertson (1983) provided similar reasoning for intra-specific differences in predation rates between group and pair spawns of *Acanthurus nigrofuscus* and *C. striatus*. Such logic is also supported by optimal foraging theory, whereby predators are expected to switch prey types only when the alternative prey source offers a net energetic advantage (Schoener 1971). In addition, the release of gametes away from the relative safety of the reef substrate is a ubiquitous trait of all known broadcast spawners (Johannes 1978, Colin & Bell 1991). Larger gamete clouds released by *C. striatus* may provide an added benefit to egg predators by providing enough eggs for multiple egg predators to prey upon eggs simultaneously. Therefore, feeding in larger groups rather than individually may reduce their individual probability of being preyed upon. A better understanding of the relationship between rates of egg predation and prey characteristics for a range of spawning species will provide insight into the factors which influence rates of egg predation among spawning species.

Spawning and egg predator functional response

Results from this study do not support the prediction that rates of predation will asymptote with increasing egg availability. At front reef SASs rates of rushes attacked increased linearly with rates of spawning intensity. This may be the result of an aggregation response by egg predators that caused rates of egg predation to increase with increasing spawning intensity. However increases in egg predator densities large enough to account for the indefinite increase in egg predation levels were not observed and are therefore unlikely. From observations of egg predator behaviour during predation bouts at *C. striatus* aggregations, it was evident that egg predators attacked gamete clouds more selectively. That is, they fed more briefly on each gamete cloud when gamete clouds were released more rapidly, targeting clouds when eggs were likely to be at highest densities. Consequently, overall egg survivorship may have been promoted through the limited handling time of the egg predators (Robertson 1983). The data presented here may be an artefact of measuring egg predation as rushes attacked rather than actual egg mortality. To date, every study that has quantified egg predation has quantified the spawning rushes attacked (Robertson 1983, Moyer 1987, Sancho et al. 2000), which does not account for shifts in egg predator behaviour. To clearly demonstrate if swamping occurs during synchronised spawning it is imperative to quantify egg mortality, which is a logistically difficult task. At back reef SASs, where egg predators are less abundant and levels of egg predation are lower, there was no relationship between egg predation and spawning intensity. Clearly spawning at back reef SASs at this study location conveys greater immediate egg survival from targeted egg predation. Knowledge of actual egg mortality associated target egg predation will make evident the actual cost of spawning at front reef SASs compared to back reef SASs.

Effects of target egg predation on spawning site selection

Egg predation is hypothesised to be an important determinant for resident spawning site selection (Johannes 1978, Lobel 1978). However, the large variation in levels of predation among SASs suggests target egg predation may not be a factor in spawning site selection for *C. striatus* at seven SASs used in the present study. Evidence shows that front reef sites clearly have an increased risk of egg predation. Therefore if minimising egg predation was a factor in SAS selection, it would be expected that the reef front would not be used for spawning. This is further supported by the common use of spawning aggregation sites by species that suffer both high and negligible rates of egg predation. Finally, if *C. striatus* use egg predator swamping to ensure offspring survival, as the present data suggests, SASs may be selected based on alternative criteria (such as propagule dispersal) regardless of egg predator density. However, the present data must be interpreted with caution since this study only quantified target egg predation. Non-target egg predation also occurs once gamete clouds have dispersed down-current of a spawning aggregation (Colin & Bell 1991) and this mortality is difficult to quantify accurately. Spawning aggregation sites are hypothesised, in conjunction with water current flows, to reduce the risk of egg predation and promote propagule dispersal (Johannes 1978, Lobel 1978). While there is some evidence to suggest spawning sites do favour off-reef transport of eggs (Hensley et al. 1994), it is still unknown if SAS selection minimises non-target egg predation or promotes propagule dispersal (Sancho et al. 2000).

In summary, the present study demonstrates that levels of target egg predation differ at SAS among reef zones and among spawning species. Target egg predation may not pose a significant challenge to some broadcast spawning species. However, for other species target egg predation may be an important source of propagule mortality which is influenced by egg predator distribution and abundance. The observed patterns in egg predation among SASs and spawning species at Kimbe Bay during the study period do not support the egg predation hypothesis. By spawning in synchrony *C. striatus* may ensure a portion of offspring survive immediate predation, however a quantitative assessment of actual egg mortality in relation to spawning intensity is required. It is of great importance for fisheries management and conservation to increase our understanding of the effects of egg predation on reproductive behaviour, and to assess the contribution of target egg predation to the high levels of mortality experienced by reef fishes during the dispersal life phase. Therefore, comparable studies on transient spawning species (e.g. many groupers and snappers) would provide insight into the role of egg predation on spawning aggregation dynamics of commercially important species.

Chapter 3

Egg predators aggregate at resident reef fish spawning aggregation sites

---

Introduction

Predator abundance is fundamentally linked to fluctuations in prey abundance (Krebs 1994). As such, fluctuations in prey abundance (Yang 2004, Yang & Naeem 2008), can have a cascade of bottom-up consequences for consumer populations (Schmidt & Ostfeld 2003). In response to variations in the prey abundance, generalist predators have evolved to switch prey preference when the consumption of alternative prey offers greater profitability (Sinclair & Krebs 2002). Previous studies demonstrate that a switch to feed on more abundant prey can alter predator abundance within a locality through: (1) an increase in resident predator abundance (Cushing 1987) or, (2) a temporary aggregative response (Sears et al. 2004). Since the decision to switch prey preference is a trade-off between energetic gains and potential costs in relation to the original prey source (Schoener 1971), examining the numerical response of consumers will indicate the relative importance of alternative prey and will provide information necessary to understand the dynamics of prey consumption.

Changes in predator density either through an aggregative response or through increased density of residents can greatly influence predator-prey interactions and functional response models (Nachman 2006). In many natural systems large fluctuations in prey availability result from synchronised reproductive events such as mast fruiting events in trees (Curran 2000), mass coral spawning events (Hall & Hughes 1996) and reef fish spawning aggregations (Robertson 1983). It is hypothesised that these reproductive behaviours have evolved from increased offspring survival that result from ‘swamping’ of predators. As such, predator swamping is the consequence of a Type II functional response resulting from rapid increases in prey density (through synchronised reproduction) and limited prey consumption through fixed predator handling time or satiation (Oaten & Murdoch 1975). However, the spatial distribution of predators must be accounted for in order to measure the effectiveness of this reproductive strategy and construct realistic models that describe prey consumption (Nachman 2006).

Many reef-associated fishes aggregate to spawn and this provides a pulse of energy rich eggs that may be available to planktivorous egg predators (Chapter 2). In the tropics, 243 species from 29 families have been found to spawn at highly localised and traditionally used spawning aggregation sites (SASs) (approximately 100 m^2) (Warner 1988, Domeier & Colin 1997, Claydon 2004), with many of these species being large and commercially important (e.g. groupers and snappers). Many species synchronise spawning at these sites by forming breeding groups that make successive rapid spawning rushes toward the water’s surface to release their gametes into the prevailing current (Robertson 1983). At the apex of the spawning rush eggs are at higher densities and have 20% – 25% greater energy content than alternative planktonic prey (Kamler 1992), which may make eggs a valuable food source for egg predators. Evidence suggests that tropical waters are energy limited and density dependent growth of planktivores is directly related to food availability (Forrester 1990, Jones & McCormick 2002). Thus, it may be expected that recently spawned eggs will influence egg predator abundance and foraging behaviour. Alternatively, it has been suggested that spawning species may select SASs with reduced resident egg predator abundances to minimise egg predation and promote offspring survival (Shapiro et al. 1988). However no studies have systematically compared egg predator abundances at SASs with other non-spawning aggregation locations. How the release of eggs as a pulsed prey source influences egg predator resident densities and movement patterns at SASs is still poorly understood.

This study tests the prediction that SASs will have higher densities of resident egg predators and/or egg predators will actively aggregate to exploit the energetically rich prey pulse. This prediction was examined in two ways. Firstly, the densities of egg predator species were compared among SASs and structurally similar non-spawning aggregation sites outside of spawning periods. Secondly, to determine if egg predators aggregate at SASs during spawning periods, the change in egg predator density between spawning and non-spawning periods at SASs and non-SASs was quantified. To determine the distance travelled to aggregate and feed on the pulsed resource, a movement study was conducted on tagged individuals of a key egg predator species

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 four small inshore platform reefs (Kume, Hanging Gardens, Mayas and Limuka) (Fig 1.4). The reefs are located less than 800 m from shore and are separated by deep passages of water (≈ 80 m deep). Each reef contains multiple SAS's (Fig 1.5 and 1.6). Previous work shows that the surgeonfish, *Ctenochaetus striatus*, form large spawning aggregations (up to 2000 individuals) once per day per SAS prior to dusk at this study location (Claydon 2005).

Recently spawned gametes by *C. striatus* are known to suffer high levels of predation (Robertson 1983). Spawning events by *C. striatus* at this study site occur between 1400 h and ~1800 h (dusk) and are typified by an hour of pre-spawning courting behaviour, followed by 10 to 15 minutes of intense synchronised spawning rushes that release visible gamete clouds near the water's surface (personal observation). It is estimated that on average 1,240,000 mm^3 of eggs are released during a *C. striatus* spawning aggregation and up to 80% of spawning rushes are attacked (Chapter 2).

An estimate of spawning frequency was obtained from two months of daily observations of *C. striatus* spawning and associated egg predator activity from a previous study at this study location (see Chapter 2). These data were used also to identify the species of egg predators monitored during this study. These include the damselfishes *Abudefduf vaigiensis*, *Acanthochromis polyacanthus*, *Amblyglyphidodon curacao*, *Chromis viridis*, *C. ternatensis*, *C. xanthura*, the wrasse *Thalassoma hardwicke*, and the triggerfish *Melicthys vidua*.

Spatial and temporal distribution of egg predators

Monitoring sites of a known area (ranging 31.6 to 152.2 m^2) were established at nine SAS's used by *C. striatus*, Kume 2 (K 2) and 5 (K 5); Hanging Gardens 1 (HG 1),3 (HG 3),6 (HG 6); Mayas 1 (M 1) and 4 (M 4); Limuka 2 (L 2) and 5 (L 5) (Fig. 1.5 and 1.6). Nine non-SASs were also established for comparison and these were sites where reef fish spawning did not occur, but which had similar reef exposure, coral cover, topography and size, and were approximately 50 m from a monitored SAS's. Data from monitoring of *C. striatus* spawning aggregations from Chapter 2 were used to document the frequency of spawning events at SASs at this study location. Spawning activity data at L 2 and L 5 were not collected for logistical reasons. A diver quantified the density and identity of egg predators during the morning when spawning was known not to occur (between 0800 and 1200 hrs) at all 18 sites over a one week period. To test whether the density of resident egg predators was influenced by the presence of spawning aggregations, fish densities were compared between SASs and non-SASs. The equality of the resident assemblages of egg predators between SAS's and non-SASs was tested using one-way MANOVA (with Pillai's trace test statistic). Assumptions of multivariate homogeneity of variance and normality were examined prior to analysis (Quinn & Keough 2002).

To determine whether egg predators only aggregated at SASs during periods of *C. striatus* spawning, a diver quantified egg predator density and identity in SASs and non-SASs over a two month period (factor: 'spawning status') during periods of spawning and at the same afternoon periods when no spawning occurred. Egg predator densities between spawning and non-spawning periods within a site were used to calculate the change in egg predator density associated with spawning (factor: 'spawning activity'). To determine whether there was an aggregative response in the absence of spawning activity (i.e. aggregating in anticipation of spawning activity), the change in egg predator density between spawning periods and non-spawning periods in the morning (between 0800 and 1200 hrs) (factor: 'spawning activity') were also determined. The changes in density of each egg predator species among 'spawning status' (SASs and non-SASs) and 'spawning activity' (difference between spawning and afternoon non-spawning periods; spawning and morning non-spawning periods) treatments were analysed using two-way MANOVA (with Pillai's trace test statistic). Data were log(x+1) transformed to meet the assumptions of multivariate homogeneity of variance and normality (Quinn & Keough 2002). To examine the significant difference in 'spawning status' found by MANOVA, data from 'spawning activity' treatments were pooled and the change in egg predator density at SASs and non-SASs were analysed for each species using multiple one-way ANOVAs. To prevent an increase in the Type I error rate with multiple univariate tests, α was set at the 0.01 level.

Movement study

A monitoring study of the movement of tagged *A. vaigiensis* was conducted at Hanging Gardens and Lumika, with one SAS and non-SAS per reef (Fig 1.5 and 1.6). Non-SAS is defined as above. *A. vaigiensis* were the focus of this study because the species was found to be a dominant predator of *C. striatus* gametes (Chapter 2). SASs were ~100 m from non-SASs (20 m further than the greatest distance travelled by any tagged individual). Fish collection was confined to a 10 m stretch of reef crest inside SASs and non-SASs and fish were caught by herding individuals into a fence net. While underwater, each fish was determined for gender and fork length, and uniquely tagged by sewing coloured beads into the musculature on the dorsal and ventral region (Barlow 1987, Claydon 2005). Using this method it was possible to identify individually fish. Twenty-nine fish from each SAS and non-SAS were tagged initially. However, not all tags were retained by fish; this was evident by observations of wounds and scars in the precise tagging location in many fish. This was confirmed further by frequently witnessing the tags being targeted by *T. lunare*, *T. hardwicke*, *H. hortulanus* and *B. undulatus*. Subsequently, more fish were tagged when less than ten tagged individuals were resighted. To determine movement of tagged individuals in relation to SAS and spawning activity, surveys for tagged *A. vaigiensis* were conducted in SASs and non-SASs: (1) during spawning events; (2) when spawning did not occur at SAS, but during the same diel period when spawning usually occurred at that site. Visual surveys of tagged *A. vaigiensis* were performed by a diver who began inside the site and swam outward along the crest of the entire reef. The positions of tagged individuals were recorded in relation to markers placed every 10 m along the reef crest and radiating away from the initial tagging site. The behaviour of tagged fish was also recorded using focal point sampling (Martin & Bateson 1993). Behaviours were categorised either as: feeding on eggs, feeding on plankton, swimming, hiding or interacting. Feeding on spawn is clearly distinguished by a change in behaviour and bite rate, as individuals actively attacked and fed on visible gamete clouds released by spawning *C. striatus*. The daily frequency of *C. striatus* spawning activity at SASs during the tagging study was also recorded.

The mean proportions of tagged *A. vaigiensis* resighted were compared among treatments (Spawning status = SASs and non-SASs: Spawning activity = spawning event and non-spawning event: Distance from SAS = 10 m increments) using a three-way ANOVA. Residual analysis indicated data did not violate assumptions of homogeneity of variance and normality (Quinn & Keough 2002).

Results

Spawning frequency

Spawning events by *C. striatus* were not observed every day that SASs were monitored for spawning activity (Fig 3.1). The occurrence of *C. striatus* spawning aggregations ranged between 22% and 66% of days that SASs were monitored.

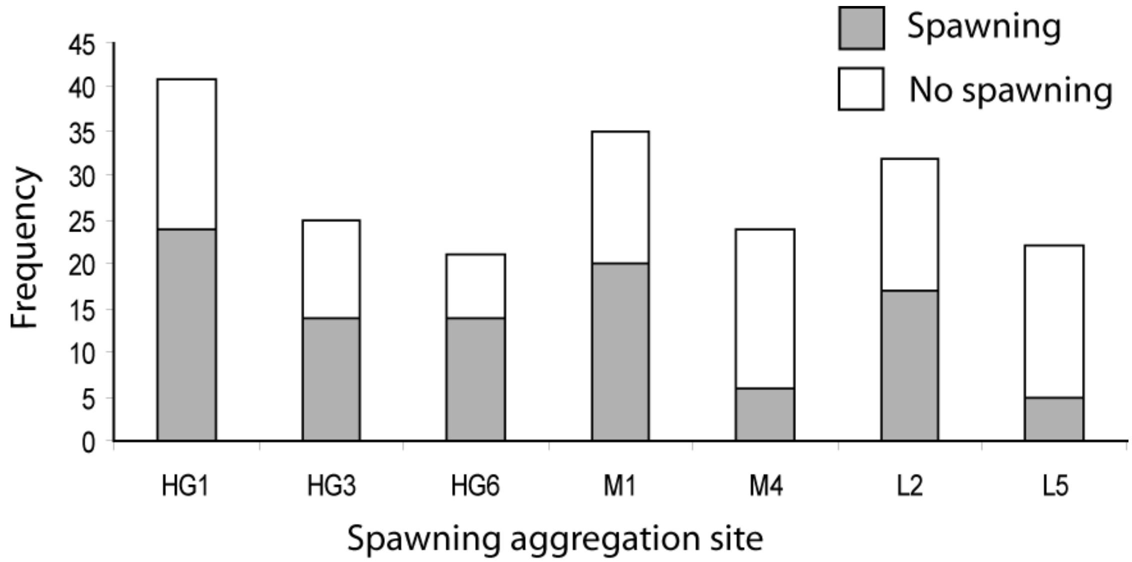

Figure 3.1 Frequency of days of *Ctenochaetus striatus* spawning activity and no spawning activity at seven SASs. Total frequencies per SAS are days of sampling effort. Site labels are Hanging Gardens 1 (HG 1),3 (HG 3),6 (HG 6); Mayas 1 (M 1) and 4 (M 4); Limuka 2 (L 2) and 5 (L 5).

Egg predator densities

To determine if the consumption of eggs influenced resident egg predator densities, egg predator assemblages were compared among SASs and non-SASs during the morning periods (between 0800 and 1200 hrs) when *C. striatus* spawning is known not to occur at the study SASs. Species assemblage of resident egg predators did not differ significantly among SASs and non-SASs (one-way MANOVA; Pillai's trace $_{8,9}$ = 1.33, p = 0.35; Fig 3.2).

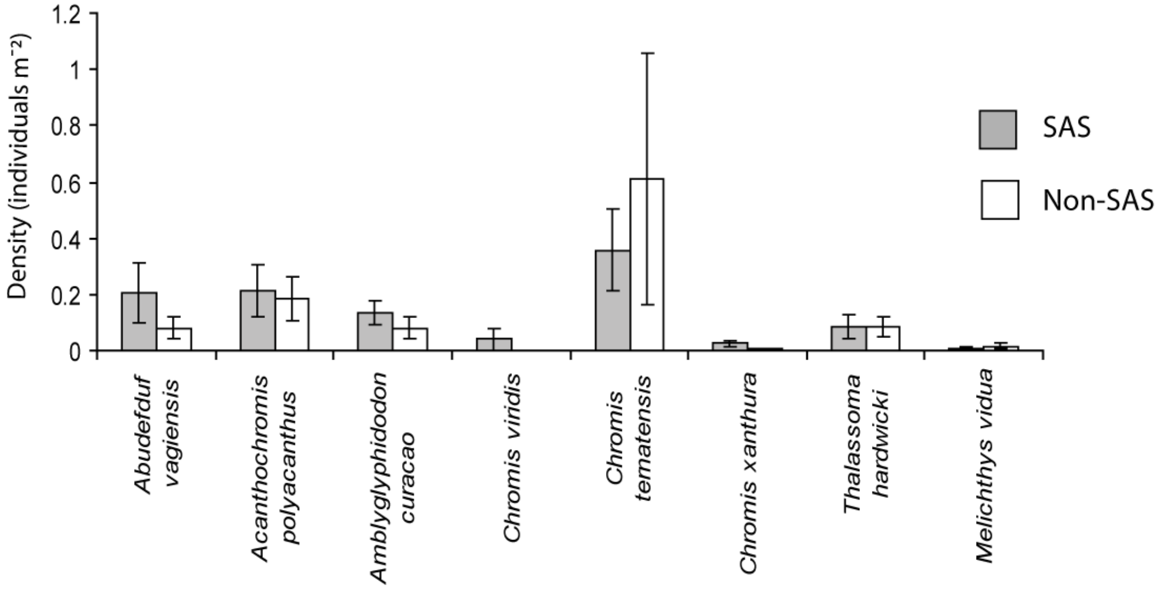

Figure 3.2 Resident egg predator densities at SASs and non-SASs (n = 9) during periods when *Ctenochaetus striatus* did not form spawning aggregations (i.e. before noon).

To determine if egg predators aggregated to feed on *C. striatus* eggs during spawning events, changes in egg predator densities among spawning and non-spawning periods were compared among SASs and non-SASs. Changes in egg predator density differed significantly among SASs and non-SASs (factor 'spawning status') (two-way MANOVA, Pilla's trace $_{8,22}$ = 2.46, p = 0.04, Fig 3.3). The egg predator *A. vaigiensis* was the only species that had significantly different changes in density among SASs and non-SASs (one-way ANOVA, $F_{1,31} = 7.39$, $p < 0.01$) (Fig 3.3A). At SASs, the mean change in *A. vaigiensis* density increased during *C. striatus* spawning events. The changes in densities of *A. polyacanthus*, *A. curacao*, *C. viridis*, *C. ternatensis*, *C. xanthura*, *T. hardwicke* and *M. vidua* did not differ among SASs and non-SASs. (Fig 3.3 B, C, D, F, G and H respectively).

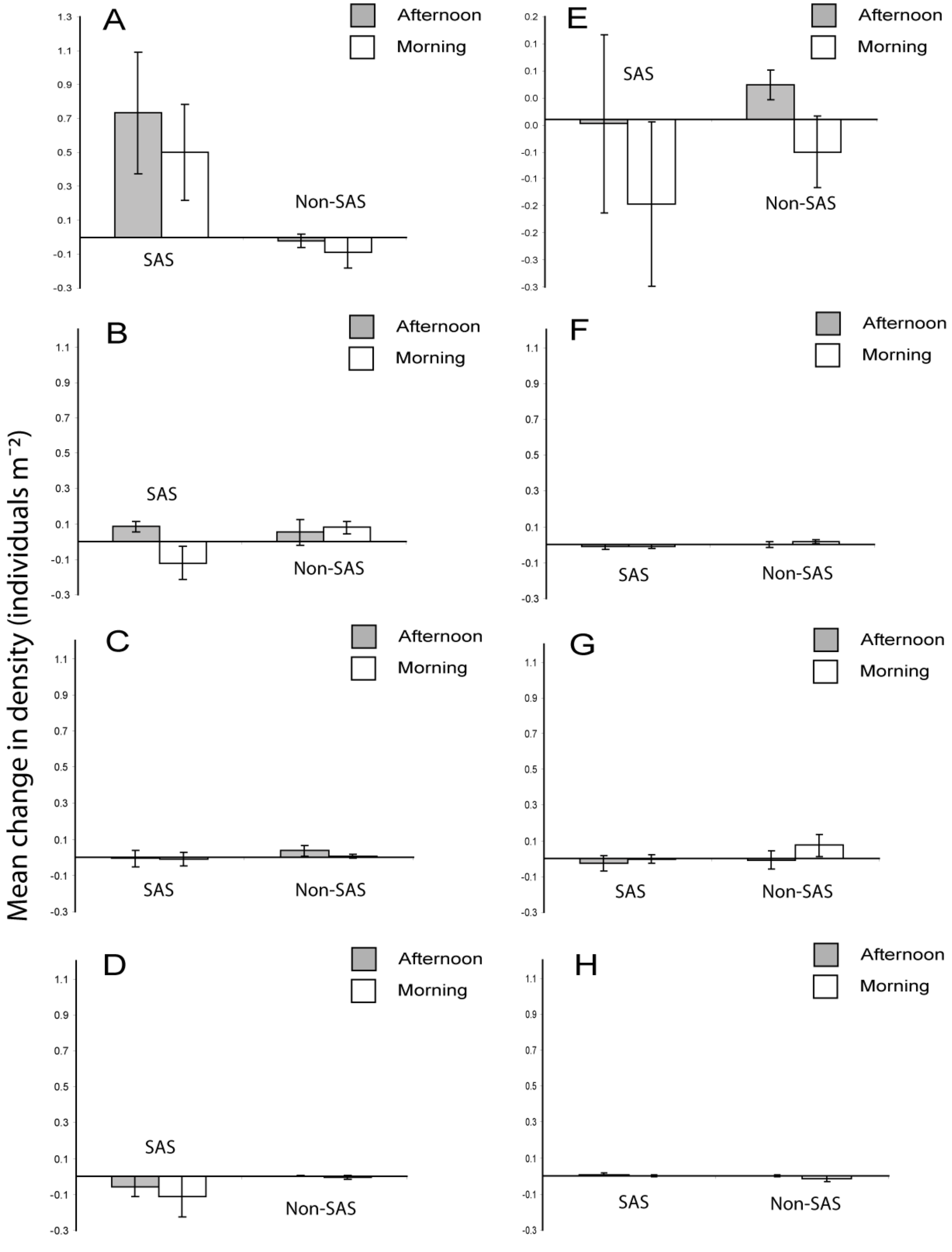

Figure 3.3 Mean change in density between spawning periods and non-spawning periods in the afternoon, and spawning and non-spawning periods in the morning, for eight egg predator species at SASs and non-SASs. (A) *Abudefduf vagiensis*; (B) *Acanthachromis polyacanthus* (C) *Amblyglyphidodon curacao* (D) *Chromis viridis* (E) *Chromis ternatensis* (F) *Chromis xanthura* (G) *Thalassoma hardwicke* (H) *Melicthys vidua*.

Movement study

Over the duration of the movement study, 153 *A. vaigiensis* were tagged at SASs and 103 individuals were tagged at non-SASs. At SASs, there were 116 re-sightings during 12 *C. striatus* spawning events and 331 re-sightings during 14 non-spawning events. Similarly, at non-SASs there were 121 re-sightings during 11 spawning events and 139 re-sightings during nine non-spawning events. The greatest proportions of individuals were resighted within 20 m from their originally tagged location at both treatment and control sites. Tagged fish from SASs were never observed in non-SASs and vice versa. Interestingly, the proportion of tagged *A. vaigiensis* resighted differed significantly among spawning periods and the distance from the SAS (three-way ANOVA interaction $F_{5, 372} = 2.51$; $p = 0.028$) at SASs (Fig 3.4). The proportion of tagged *A. vaigiensis* at SASs increased during spawning events by 20% within SASs, compared to periods without spawning activity. In the 1 to 10 m zone adjacent to the SAS, the proportion of resighted individuals declined by 21.3% compared to periods without spawning. At distances greater than 10 m from SASs, no differences were observed between spawning and non-spawning periods at SASs. The proportions of re-sighted tagged individuals at non-SASs were less than that at SASs and did not differ with spawning periods (Fig 3.4).

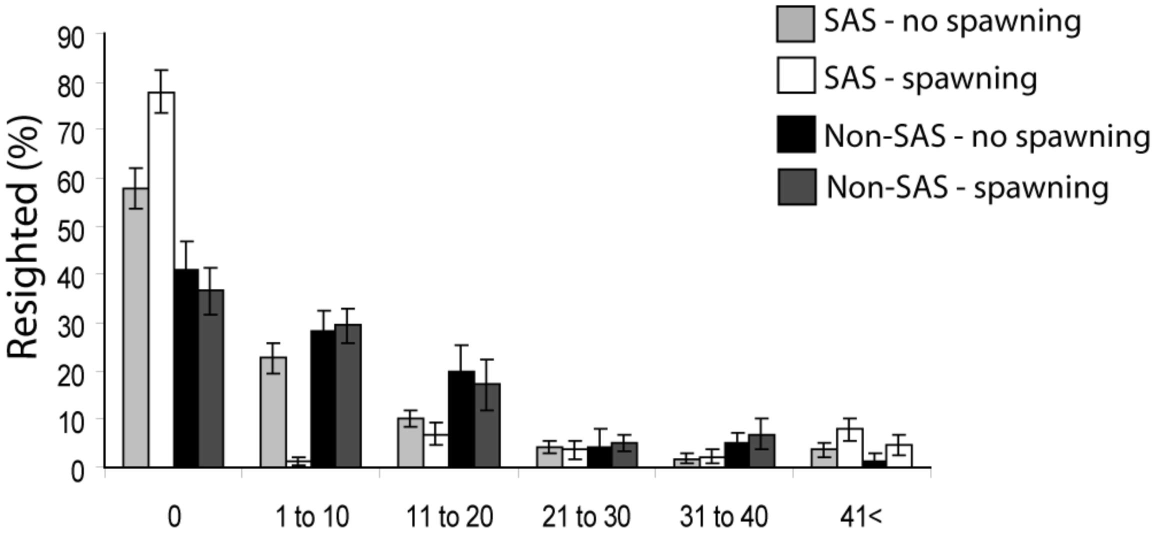

Figure 3.4 Mean (± SE) proportions of resighted tagged *Abudefduf vaigiensis* at SASs and non-SASs during *Ctenochaetus striatus* spawning events and periods with no spawning.

Egg predation

Observations of tagged *A. vaigiensis* behaviour confirm that fishes that aggregated within SASs during a spawning event feed exclusively on recently released *C. striatus* gametes. All re-sighted individuals within SASs (39) fed on gametes during spawning events. In addition, the behavioural budgets of tagged *A. vaigiensis* during periods when spawning did not occur and at non-SASs did not differ significantly (Fig 3.5).

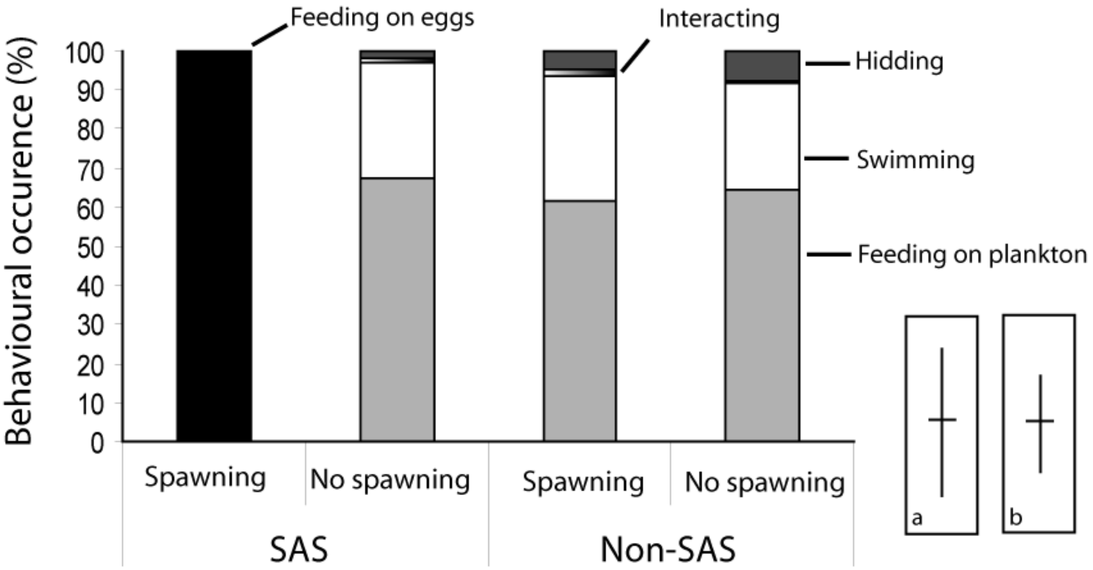

Figure 3.5 Behaviour of tagged *Abudefduf vaigiensis* at SAS and non-SASs during and not during *Ctenochaetus striatus* spawning aggregations. Tukey's 95% confidence limits are inset for comparison of (a) feeding on plankton and (b) swimming at SASs during periods of no spawning and at non-SASs.

Discussion

The present study is the first to rigorously examine egg predator distribution and abundances and movement patterns among multiple SASs. This study demonstrates that resident reef fish SASs have similar egg predator densities as non-SAS reef locations, which conflicts with the hypothesis by that SASs may be selected by spawners for reduced egg predator abundances (Shapiro et al. 1988). Furthermore, Chapter 2 demonstrated that *C. striatus* did not show preference for SASs based on levels of target egg predation among SASs. These findings suggest SASs used by *C. striatus* were not chosen solely based on the presence of egg predators. In addition, of the known egg predator species only *A. vaigiensis* migrated small distances to feed on *C. striatus* gamete clouds. Only one other study has examined movements of an egg predator, the whale shark, *Rhincodon typus* at Gladden Spit in Beliz, in relation to SASs (Heyman et al. 2001). However, no information was given on *R. typus* movements during periods of no spawning, therefore it is not possible to determine if *R. typus* aggregated specifically for the purpose of preying on pelagic eggs. These findings demonstrate that egg predator movements are important in shaping predator-prey dynamics at SASs and are an important cost in the trade-offs that determine the reproductive success of pelagic spawners.

A key finding of this study was the relatively small distance of 10 m that *A. vaigiensis* migrated to feed on *C. striatus* eggs despite the potential for large energetic gains that can be observed and heard (at least by the principle investigator) from much greater distances. Optimal foraging theory predicts that egg predators will only aggregate and prey on eggs if the net energy gain outweighs the risk of predation (Schoener 1971). Previous work reports relatively high rates of piscivory on spawning species at SASs (Sancho et al. 2000). Therefore, egg predators that feed near the water's surface away from the relative safety of benthic shelter may also be exposed to similarly high levels of piscivory. During the course of this study several predation attacks by *Caranx* sp., *Plectropomus* sp. and *Epinephalus* sp., were observed, however it was difficult to determine if these were focused at spawners or egg predators. Previous experimental work demonstrates that predation risk is an important factor in shaping foraging behaviour in fish (Godin 1986). The increased threat of predation from piscivores at SASs may be a factor influencing aggregation of *A. vaigiensis*. In addition, competition with conspecifics already migrated from less than 10 m may reduce egg availability for fish migrating from greater distances. Egg predators that are located greater than 10 m from SASs may not aggregate due to increased competition for limited quantities of eggs and the increased threat of piscivory. Optimal foraging theory also explains the lack of aggregation by smaller bodied species such as *A. polyacanthus*, *A. curacao*, *C. xanthura*, *C. ternatensis* and *C. viridis*, that are expected to be more vulnerable to predation as a consequence of their small body size (Sogard 1997). Finally, the lack of aggregation by larger bodied *T. hardwicke* and *M. vidua* may be a consequence of their inability to consume sufficient quantities of eggs to warrant aggregating. Labrids and blastids use manipulation and ram-suction prey capture methods to primarily feed on benthic items (Wainwright 1988, FerryGraham et al. 2002). This feeding method may allow relatively opportunistic consumption of small planktonic eggs, as previously documented for *M. vidua* (Sancho et al. 2000), however may not facilitate the required level of egg consumption (and therefore energetic gain) to warrant migrating to feed and compete for eggs.

Although distances migrated by *A. vaigiensis* were within their normal home ranges, movements were sufficient to change localised densities within SASs. Such changes in density have been shown to have a number of influences on predator-prey dynamics. A decrease in localised consumer density immediately adjacent to the resource pulse will decrease the predation pressure on alternative prey (Holt 2008). However, since the distances migrated by *A. vaigiensis* were small, and *C. striatus* spawning events are short in duration, the effects of changes in consumer density on alternative planktonic prey are likely to be minimal.

An increase in densities of predators consuming resource pulses may also influence rates of prey consumption which have been shown to influence predator-prey functional responses (Oaten & Murdoch 1975). Synchronised spawning rushes by *C. striatus* are proposed to 'swamp' egg predators and promote offspring survival

(Robertson 1983) as a result of a Type II functional response (Claydon 2004). It was suggested in Chapter 2 that as spawning intensity increased, egg predators became more selective and spent less time preying on each gamete cloud. The evidence from this study suggests the aggregative behaviour of *A. vaigiensis* may influence rates of egg predation and the effectiveness of a ‘swamping’ strategy. Future attempts to model a Type II functional response of egg predation at reef fish SASs should account for changes in egg predator density that result from aggregation.

Previous studies show that increases in food availability influence reef fish density via growth rates (Forrester 1990). Despite the large amounts of food energy made available for egg predators during a resident spawning events, the results from this study show the availability of eggs as a food resource did not influence resident egg predator density. The increased threat of piscivory at SASs may prevent some egg predators, particularly small bodied egg predators, from preying on sufficient quantities of eggs to alter their abundances (Sancho et al. 2000). However, this does not explain the similar densities of *A. vaigiensis* among SASs and non-SASs, which are known to attack 70% of *C. striatus* gamete clouds (Chapter 2). Models of predator responses to resource pulses predict resident predator abundance is closely linked to the size and frequency of a resource pulse (Holt 2008) and recent empirical work supports this prediction (Yang & Naeem 2008). Spawning events of *C. striatus* at the present study site were observed to range from 22% to 66% of days monitored among SASs. This level of *C. striatus* spawning activity may be insufficient to support increased densities of resident egg predator species, despite the high energetic value of the prey source. Infrequent *C. striatus* spawning events at a SAS, or the distribution of spawning effort among multiple

SASs to minimise frequent use of individual SASs may be a behavioural adaptation to promote reproductive success.

In summary, this study demonstrates that the egg predator *A. vaigiensis* travelled small distances within their normal home ranges to prey on eggs at *C. striatus* SASs. However, this pulsed prey source was insufficient to alter resident egg predator abundances. Factors proposed to prevent greater predation on *C. striatus* eggs and therefore greater numerical responses were the increased threat of piscivory at SASs, competition among egg predators and insufficient frequency of *C. striatus* spawning. An understanding of the energy consumed by egg predators during a spawning event in relation to their energetic intake from alternative planktonic prey will provide greater insight into the significance of this prey source for egg predators. The change in foraging behaviour and aggregative response by *A. vaigiensis* suggests there is an energetic advantage in preying on eggs (Schoener 1971), and investigation of the energetic response of egg predation is warranted.

Chapter 4

Benefits of eating eggs at resident reef fish spawning aggregation sites depend on your gender

---

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 through increased 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 which has evolved to maximise reproductive success over an individuals expected life span (Stearns 1992). Therefore, 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 waters (Forrester 1990, Jones & McCormick 2002). Manipulative experiments that artificially increased food availability to reef fishes show that growth in juveniles (Jones 1986) and adults (Jones & McCormick 2002), and reproduction are tightly regulated by food availability (Jones & McCormick 2002). Because sexual maturity (Roff 1984) and mortality schedules (Gust et al. 2002) are related to size in fishes, increased food availability can also increase the size of a breeding population. 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 (except 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 more than two 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 fish 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 (Chapter 2). In the tropics, 243 species from 29 families have been found to spawn at highly localised spawning aggregation sites (SASs) (Domeier & Colin 1997, Claydon 2004), many of which spawn gametes pelagically. At these sites, breeding groups make rapid spawning rushes toward the waters 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% – 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 have been shown to aggregate to feed on spawners' gamete clouds at (SASs) (Chapter 2). Therefore, it may be expected that eggs released at SASs 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 if feeding on eggs at reef fish spawning aggregation sites influenced the life history traits of a key egg predator, the damselfish *Abudefduf vaigiensis*. Specifically, I examined how this predator of nutrient-rich eggs allocated energy to growth, condition and reproduction.

Materials and Methods

Study site, sampling locations and study species

This study was conducted in Kimbe Bay, West New Britain Province, Papua New Guinea (5° 30'S, 150° 05'E) on two small inshore platform reefs (Hanging Gardens, and Limuka) (Fig 1.3 and 1.4). The reefs were less than 800 m from shore and separated by deep passages of water (≈ 80 m deep). Sampling was conducted at two SASs and one non-SAS on Hanging Gardens Reef, and one SAS and one non-SAS on Limuka Reef. Non-SASs were locations on the reef where reef fish spawning did not occur, however were of a similar size, had similar reef exposure, coral cover, and topographic complexity and were over 100 m from SAS's.

At the studied SASs the surgeonfish *Ctenochaetus striatus* is known to form large spawning aggregations (up to 2000 individuals) a maximum of once per day per SAS between 1400hrs and dusk (~1800 hrs) (Claydon 2005). Spawning events by *C. striatus* are typified by an hour of pre-spawning courting behaviour, followed by 10 to 15 minutes of intense synchronised spawning rushes that release visible gamete clouds near the water's surface (personal observation). It is estimated that on average 1,240,000 mm^3 of eggs are released during a *C. striatus* spawning aggregation (Chapter 2). SASs used by *C. striatus* at this study location were identified initially in 2001 (Claydon 2005), and were still in use in March 2008, seven years later (personal observation).

Recently spawned gametes by *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 (Chapter 2). Previous work has shown that they attack 70% of the gamete clouds released by *C. striatus* (Chapter 2). A movement study of *A. vaigiensis* showed most tagged individuals at SASs and non-SASs did not move greater than 40 m, and the greatest movement observed was < 80 m. In order to determine if differences in *A. vaigiensis* life history traits resulted from the consumption of *C. striatus* eggs or another site-related effect, the damselfish *Pomacentrus moluccensis*, was used in comparison because this species is known not to consume *C. striatus* eggs (personal observation) and are relatively site attached (Beukers et al. 1995).

Egg predation and fish collection

Egg predation was quantified in October 2007 with behavioural observations at SASs and non-SASs during *C. striatus* spawning events. Scan observations of *A. vaigiensis* and *P. moluccensis* were performed by placing all individuals within a SAS into one of several behavioural categories that represented their entire range of behaviours (Martin & Bateson 1993). Behavioural categories were: (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 (Chapter 2). For *A. vaigiensis* at SASs, scan observations were performed for the duration of a *C. striatus* spawning event (n = 30 spawning events). At non-SASs scan observations were performed for the same duration when *C. striatus* spawning events were occurring at

SASs (n = 13 spawning events). In the same way, scan observations for *P. moluccensis* were performed at SASs (n = 8) and non-SASs (n = 6).

During November 2007 fish were collected from each SAS immediately after a *C. striatus* spawning event, when possible. However, for logistical reasons collections were also made the morning after a spawning event. Collections of *A. vaigiensis* (n = 59 from SASs and n = 47 from non-SASs) and *P. moluccensus* (n = 40 from SASs and n = 39 from non-SASs) were made using a fence net, spear gun and clove oil. 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 four hours prior to processing. Fishes were weighed (0.01 g) and measured (0.1 mm) (*A. vaigiensis*, fork length; *P. moluccensis*, standard length), and the heads of each fish were 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 SASs collected immediately after a *C. striatus* spawning event (n = 4) revealed 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). Annual growth bands for a number of tropical pomacentrid species have been shown to be deposited annually (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 inside and outside SASs using analysis of covariance (ANCOVA). Length data were natural log transformed to meet assumptions of homogeneity of slopes and normality (Quinn & Keough 2002).

The effects of egg predation on body condition were determined using three condition indices for both *A. vaigiensis* and *P. moluccensis*. An indication of a fish's relative weight, or fatness, at one point in time was determined using length versus gutted body weight plots. Slopes were compared among SASs and non-SASs using ANCOVA. Length data were natural log transformed to meet assumptions of ANCOVA (Quinn & Keough 2002). The relative weight of the liver, or hepatosomatic index (HSI) (Kao et al. 1997) 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 * 100/WB, where WL = preserved liver weight and WB = gutted body weight (McCormick 2003). Liver vacuolation in fishes is indicative of lipid and glycogen storage within the liver (Theilacker 1978, Pratchett et al. 2004). To quantify liver vacuolation, livers were prepared histologically following the methodology of (Pratchett et al. 2004).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 40x magnification. The mean was then calculated using the six estimates from the liver of each fish. For each species, mean HSI data from replicate sites and compared among SASs and non-SASs using one-way

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

Reproductive output of female *A. vaigiensis* and *P. mollucensis* at a single point in time were determined using the relative weight of the gonad (gonadosomatic index: GSI). The state of maturation of preserved ovaries were recorded and weighed to the nearest 0.001 g then divided by gutted body weight. Mean GSI values of fishes from SASs and non-SASs were examined for both species using one-way ANOVA. Assumptions of ANOVA were examined using residual analysis (Quinn & Keough 2002).

Results

Egg predation

Only *A. vaigiensis* at SASs fed actively on eggs during *C. 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-SASs fed on eggs during the same period. As a consequence of a change in foraging behaviour, smaller proportions of *A. vaigiensis* behaviour was spent swimming (6.6%) and feeding on plankton (5.1%) at SASs during *C. striatus* spawning aggregations. This corresponds to 61.9% more overall feeding behaviour (feeding on eggs and plankton) for *A. vaigiensis* at SASs compared to non-SASs. In contrast, *P. moluccensis* were never observed feeding on eggs at SASs (92 fish) or non-SASs (61 fish) (Fig 4.1).

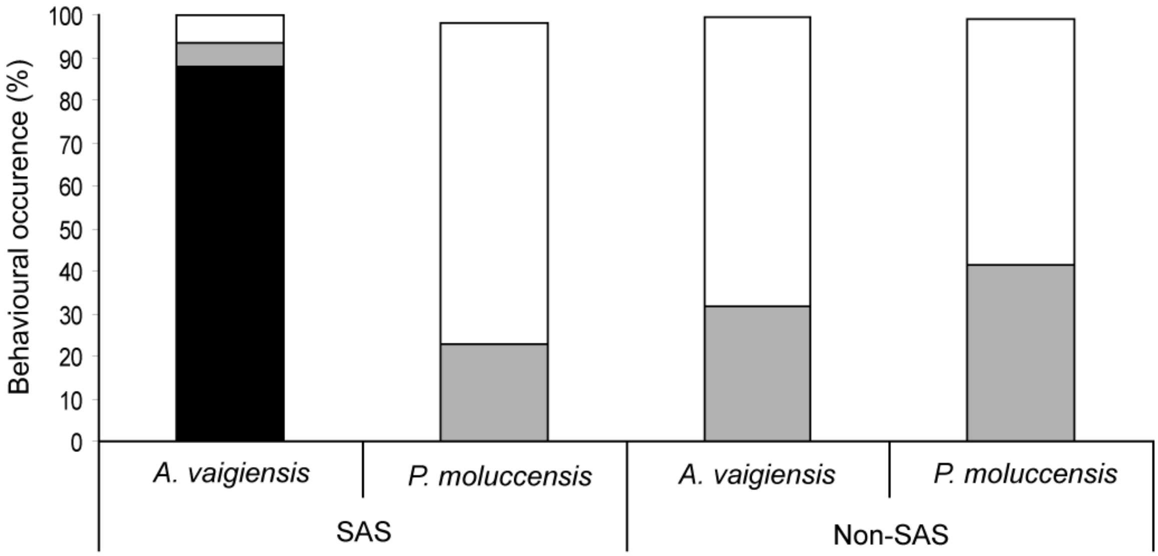

Figure 4.1 Mean occurrence of behaviours of *Abudefduf vaigiensis* and *Pomacentrus moluccensis* at spawning aggregations sites (SASs) and non-SASs during *Ctenochaetus striatus* spawning aggregations. Behavioural categories: black, feeding on gamete clouds; grey, feeding on plankton; white, swimming.

Condition

Length versus weight relationships, as a measure of condition, 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* among SASs and non-SASs (Fig 4.2 and 4.3). Similarly, there was no significant difference in the relative 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* among SAS and non-SASs.

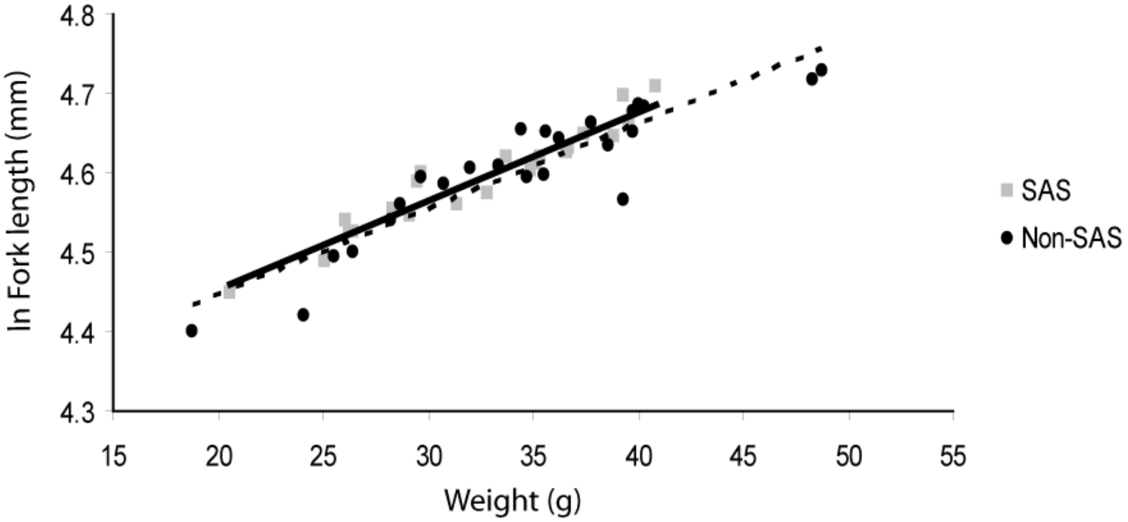

Figure 4.2 Length (ln of fork length) versus weight (g) as a measure of relative condition of female *Abudefduf vaigiensis* from SASs and non-SASs. Solid line is SAS and broken line is non-SAS.

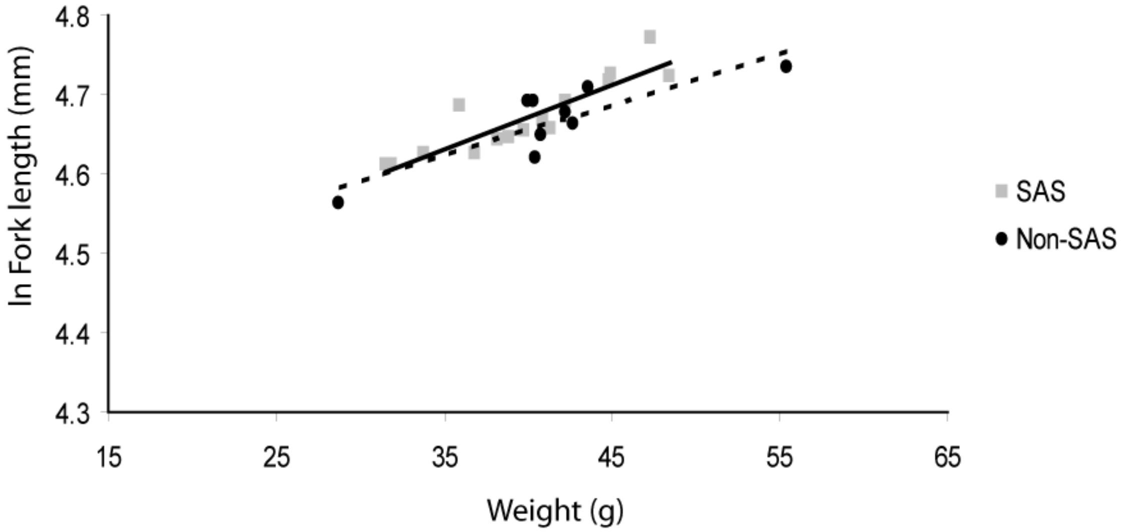

Figure 4.3 Length (ln of fork length) versus weight (g) as a measure of relative condition of male *Abudefduf vaigiensis* from SASs and non-SASs. Solid line is SAS and broken line is non-SAS.

The mean proportion of hepatocyte vacuolation differed significantly in female (one-way ANOVA, $F_{1,26} = 13.787$, $p < 0.001$) and male (one-way ANOVA, $F_{1,19} = 6.5718$, $p = 0.019$) *A. vaigiensis* among SASs and non-SASs (Fig 4.4). The mean proportion of hepatocyte vacuolation for *A. vaigiensis* was 19.4% ± 2.2% (SE) in females and 14.6% ± 3.0% in males from SASs in comparison to 6.9% ± 0.7% (SE) in females and 6.1% ± 1.1% (SE) in males from non-SASs (Fig 4.4). In contrast, there was no significant difference in the mean proportion of hepatocyte vacuolation in female (one-way ANOVA, $F_{1,33} = 0.322$, $p = 0.527$) or male (one-way ANOVA, $F_{1,12} = 1.181$, $p = 0.298$) *P. moluccensis* among SASs and non-SASs. In addition, HSI was not significantly different for female (one-way ANOVA, $F_{1,18} = 4.091$, $p = 0.058$) or male (one-way ANOVA, $F_{1,21} = 2.582$, $p = 0.123$) *A. vagiensis* among SASs and non-SASs, however there was a general trend for both females and males from SASs to have relatively heavier livers at SASs compared to non-SASs (Fig 4.5). Similarly, there was no significant difference in HSI of female (one-way ANOVA, $F_{1,20} = 1.726$, $p = 0.203$) or male (one-way ANOVA, $F_{1,12} = 0.275$, $p = 0.609$) *P. moluccensis* among SASs and non-SASs.

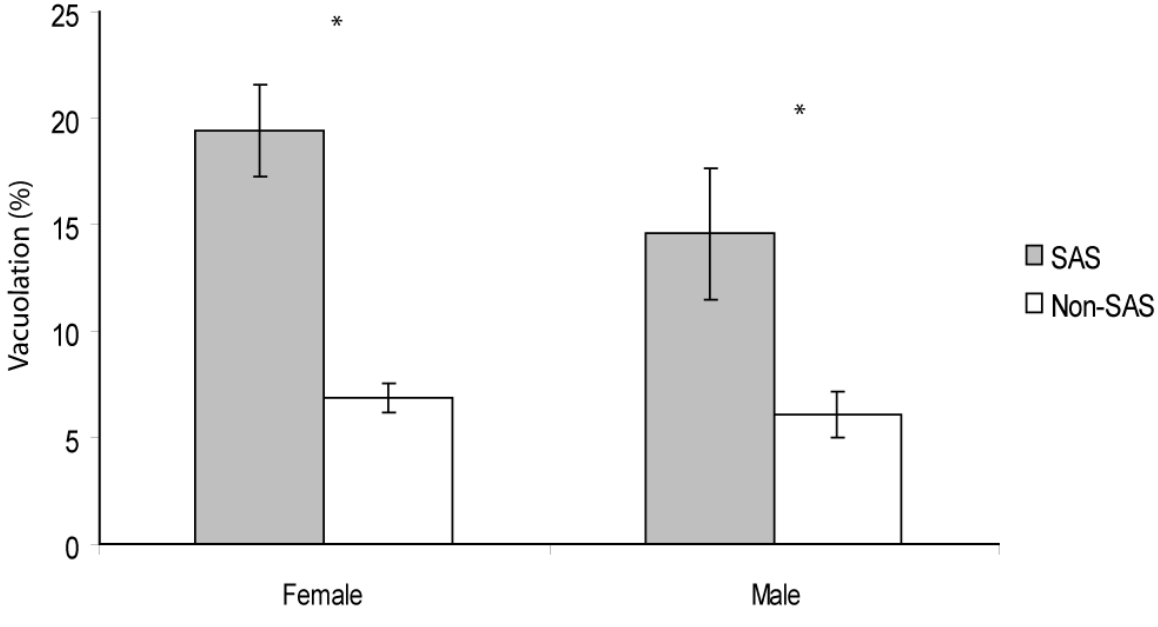

Figure 4.4 Hepatocyte vacuolation (%) of female and male *Abudefduf vaigiensis* from SASs and non-SASs. * denotes statistically significant difference.

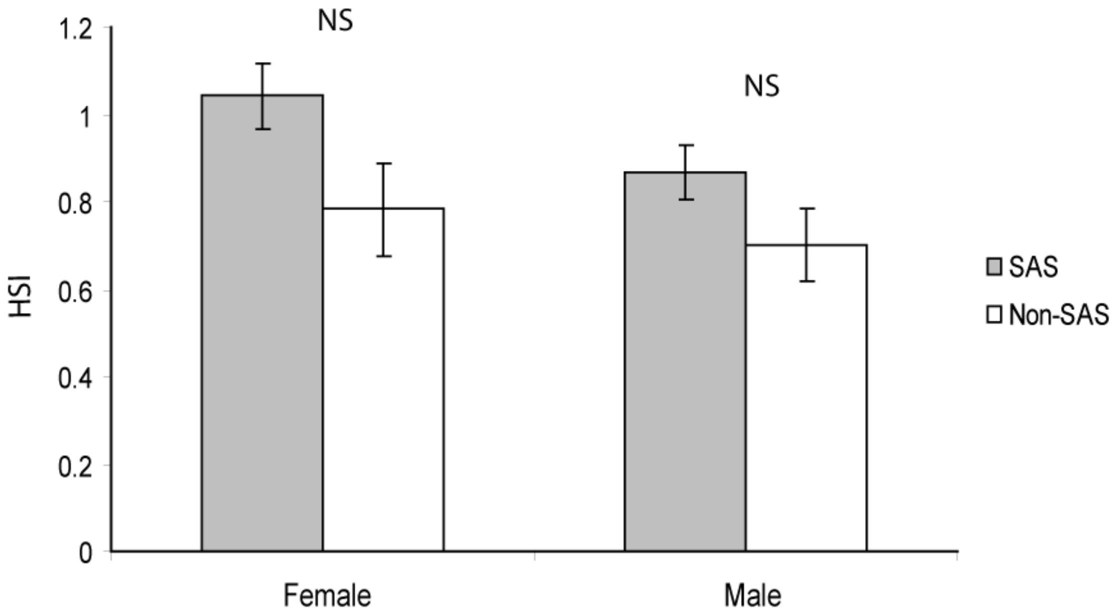

Figure 4.5 Hepatosomatic index (HSI) of female and male *Abudefduf vaigiensis* from SASs and non-SASs. NS denotes non-significant difference.

Growth

The *A. vaigiensis* collected at the present study location were remarkably short-lived, with ages ranging from two to four years (Fig 4.6 and 4.7). Male *A. vaigiensis* that fed on eggs at SASs had significantly different growth histories compared to males from non-SASs (ANCOVA, $F_{1,24} = 6.156$, $p = 0.021$) (Fig 4.6). The difference in growth histories was predominantly in the two year class, with the older three and four year class fish being of a similar length. No significant difference was found in the growth histories of female *A. vaigiensis* among SASs and non-SASs (ANCOVA, $F_{1,50} = 3.311$, $p = 0.075$) (Fig 4.7). 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 among SAS and non-SASs.

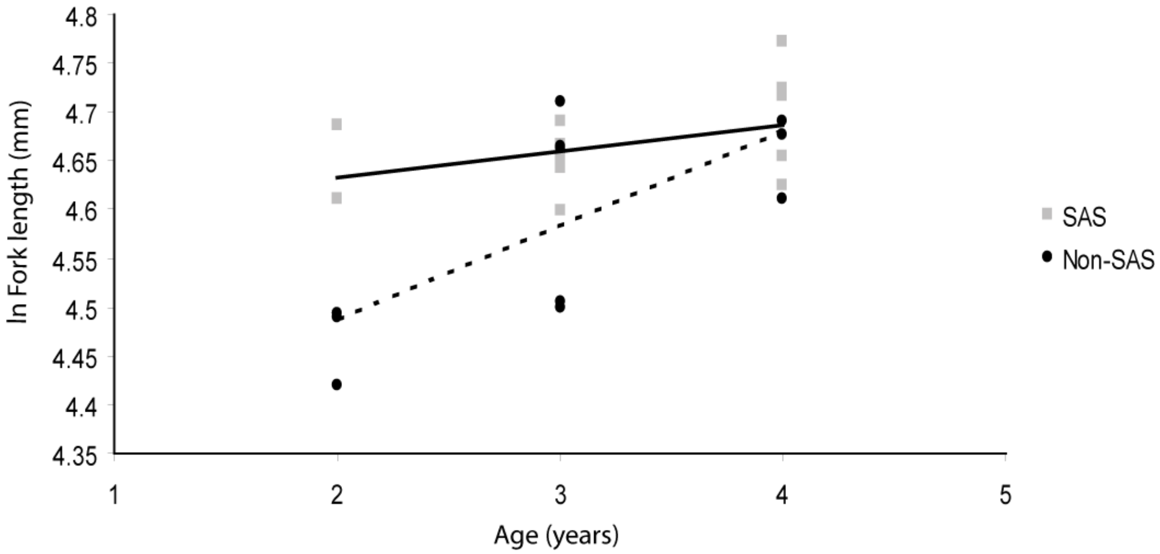

Figure 4.6 Length (ln of fork length) versus age (years) relationships of male *Abudefduf vagiensis* collected from SASs and non-SASs. Solid line is SAS and broken line is non-SAS.

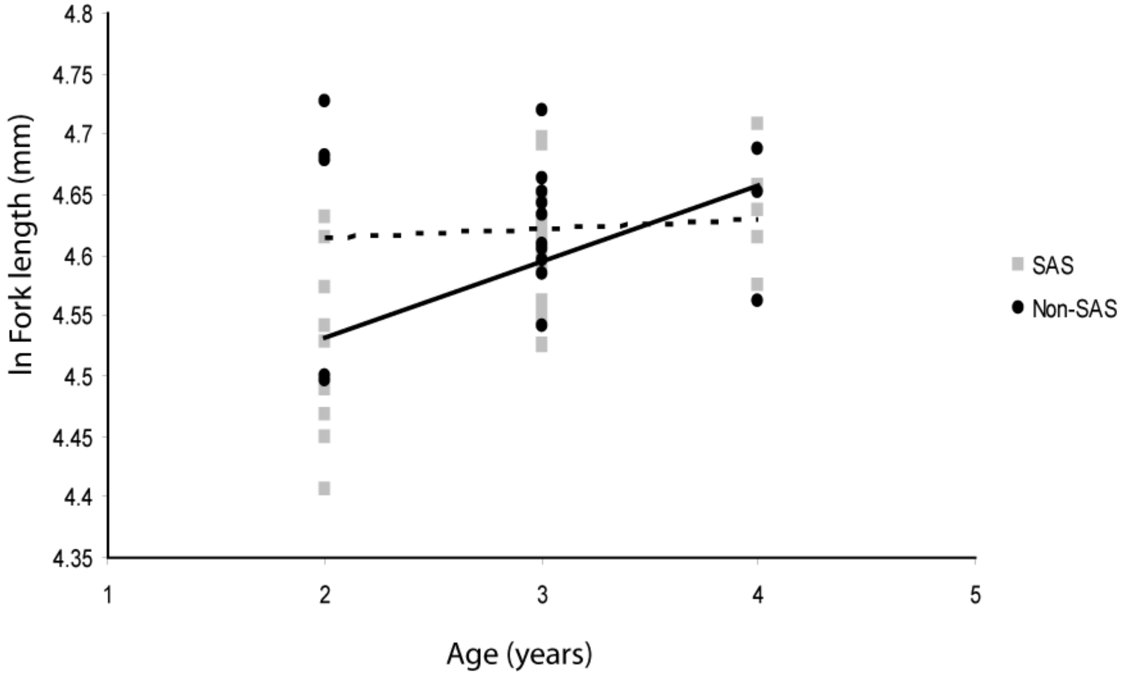

Figure 4.7 Length (ln of fork length) versus age (years) relationships of female *Abudefduf vaigiensis* collected from SASs and non-SASs. Solid line is SAS and broken line is non-SAS.

Reproduction

Female *A. vaigiensis* from SASs had significantly more ovarian tissue relative to body weight (GSI) than females from non-SASs (one-way ANOVA, $F_{1,49}$ = 4.861, p = 0.032) (Fig 8) despite females having a range of reproductive conditions from both locations. The mean GSI of female *A. vaigiensis* from SASs was 9.77 (± 1.08) compared to 6.57 (± 0.76) from non-SASs (Fig 4.8). In comparison, male GSI in *A. vaigiensis* did not differ among SASs and non-SASs (one-way ANOVA, $F_{1,25}$ = 0.665, p = 0.422) (Fig 4.8). The mean GSI of female (one-way ANOVA, $F_{1,21}$ = 0.489, p = 0.492) and male (one-way ANOVA, $F_{1,10}$ = 1.207, p = 0.298) *P. moluccensis* did not differ significantly among SAS and non-SASs.

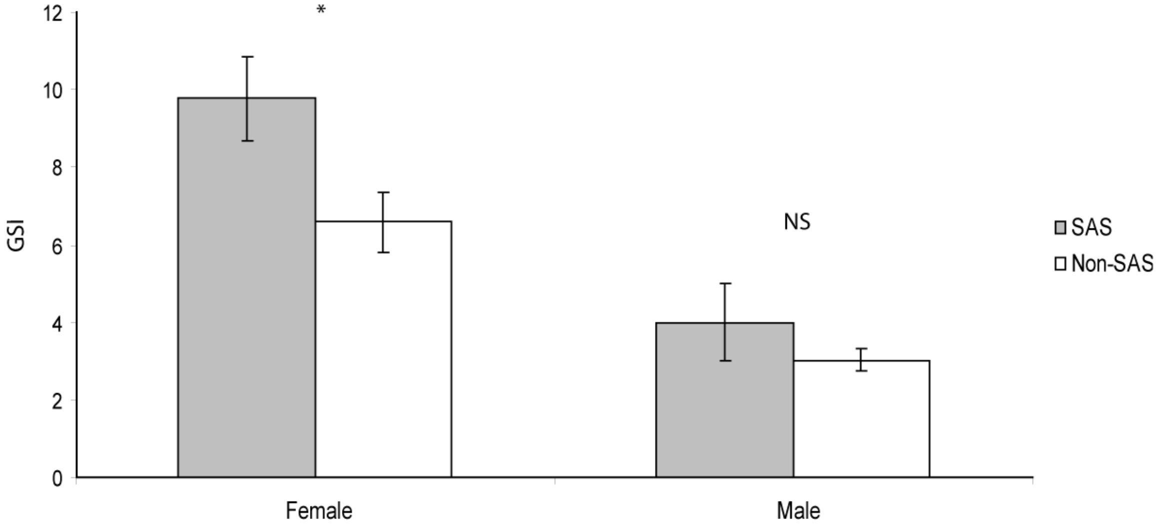

Figure 4.8 Gonadosomatic index (GSI) of female and male *Abudefduf vaigiensis* and from SASs and non-SASs. * denotes statistically significant difference, NS denotes statistically non-significant difference.

Discussion

Identifying sources of variation in food availability on coral reefs and how reef fish make trade-offs in energy allocation between growth and reproduction is fundamental to understanding population dynamics. This study is the first to quantitatively examine the trophic link between eggs liberated at reef fish spawning aggregation sites and predators of the eggs. Tis study showed that egg predation did not influence overall body condition of *A. vaigiensis*. Both males and females however, provisioned greater energy to liver storage in vacuoles. From there, males allocated excess energy to growth, while females allocated greater energy to reproduction. This study reveals the importance of eggs as a food source for the egg predator community and the potentially greater contribution they make, relative to conspecifics from other reef locations, to the reproductive output of the population. Moreover, these findings highlight the importance of determining sex-specific differences in energy allocation when examining energetic mechanisms of population dynamics.

Interestingly, *A. vaigiensis* that fed on eggs at SASs did not allocate energy to overall body condition rather energy was allocated to liver storage. Liver vacuoles serve as stores for glycogen and lipids (Pratchett et al. 2001, Hoey et al. 2007) which may be used for growth (Watanabe 1982) or the production of vitellogenin during vitellogenesis (Mommsen & Walsh 1988). Furthermore, liver vacuoles are the first point of energy storage but during increased levels of food intake excess energy may be directed to adipose tissues (specialised connective tissues for fat storage) (Mommsen & Walsh 1988). Egg consumption at SASs did not influence the relative weight of *A. vaigiensis*, a measure of fat storage in adipose tissues, which suggests that the amount of excess energy consumed was within the sum of all metabolic requirements of *A. vaigiensis*.

The findings from this study differ from the only previous study that unequivocally quantified the effects of a natural variation in food availability on growth and reproduction of a sexually mature tropical reef fish. Seasonal variation in the standing algal crop at low latitudinal Caribbean reefs influenced both the growth and reproduction in female *Scarus iserti* (Clifton 1995). These results may differ from the allocation of energy to gonadal tissues in female *A. vaigiensis* for several reasons. Firstly, in the parrotfish study the four to six month duration that increased food levels were available may have resulted in levels of food that were not limiting for *S. iserti*. Therefore, females would not have been required to make trade-offs between growth and reproduction. This also suggests that the energy consumed by *A. vaigiensis* at SASs was less than their total physiological requirements. Alternatively, the life history strategy of *S. iserti* a protogynous sequential hermaphrodite, may have influenced how initial phase females allocated energy to growth and reproduction. Little is known of the life history of *A. vaigiensis* in terms of sex change, but since there is little divergence in size at age plots among sexes in this study, it is unlikely that *A. vaigiensis* is a sequential hermaphrodite. Direct comparisons in energy allocation between gonochores and sequential hermaphrodites are problematic due to the differences in their life history strategies. Therefore any differences in patterns of energy allocation should be interpreted with caution. In protogynous hermaphroditic fishes, size is a major determinate of sex change (size-advantage model) and ultimately increased reproductive value is enhanced as a result of changing sex (Munday et al. 2006). Sizes at age plots demonstrate the variability in energy allocation to growth among individuals in scarids (Choat & Robertson 2002). Therefore energy allocation to either growth and/or reproduction may vary greatly among individual *S. iserti,* and may be the consequence of a number of factors, including social interactions (Munday et al. 2006). The disparity among the findings from the present study and previous work emphasises the poor understanding of the link between natural fluctuations in food and energy allocation in sexually mature reef fish. Factors such as temperature (Vondracek et al. 1988), habitat (Munday 2001, Hoey et al. 2007), conspecific density (Forrester 1990) and mating systems (Schultz & Warner 1989) have been shown to influence how individuals allocate energy to growth and reproduction. Therefore, a greater understanding of the interaction between these factors with natural fluctuations in food availability and their influence on demographic parameters is essential for accurate population estimates.

Theory predicts trade-offs in energy allocation between growth and reproduction evolved to maximise reproductive success (RS) over an individual's expected lifetime (Stearns 1992). The present findings show that males that fed on eggs allocated more energy to growth while reproductive output (GSI) remained similar to fishes that did not feed on eggs. In male demersal spawning fish, body size has been shown to play an essential role in RS. Previous studies show that females give mating preference to larger males (Cote & Hunte 1989, Cole & Sadovy 1995), and larger males have higher clutch survivorship (Cote & Hunte 1989). The present data suggests that male *A. vaigiensis* trade immediate RS (if any), for socially mediated future RS. In addition, size is closely linked with age of reproduction in reef fish (Jones & McCormick 2002). Therefore, male *A. vaigieanis* at SASs may also reach sexual maturity at a younger age than conspecifics from non-SAS locations. Collectively, the present data suggests male *A. vaigiensis* from SASs may contribute greater to the breeding population and may out compete males from non-SASs to reproduce. In contrast to males, female *A. vaigiensis* allocated greater energy to reproduction relative to females that did not consume eggs. These results suggest female *A. vaigiensis* trade any increases in fecundity associated with growth through increased body size (Jones & McCormick 2002), and therefore future RS, for immediate RS. 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 RS. 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 six months that coincide with the dry season (Srinivasan & Jones 2006). In addition, this study shows that *A. vaigiensis* have a relatively short life span of four years compared to over 20 years for several pomacentrid species from low latitudes (Fowler & Doherty 1992, Meekan et al. 2001). Such characteristics suggest *A. vaigiensis* at this study location have an r-selected life history strategy. This 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.

In summary, this study demonstrates the importance of the trophic link between pelagic spawners and planktivorous egg predators, and how energy allocation differs with gender. Evidence suggests that energy is allocated by females according to their life history strategy, while for males energy allocation may be influenced by social factors. Most importantly, this study shows that natural variations in food supply influence demographic parameters in reef fish. The life history strategies of reef fishes are likely to vary among species and across environmental gradients (Choat & Robertson 2002). Therefore, more work is needed to determine the link between natural variations in food supply and life history strategies in reef fishes, particularly for commercially important species. Finally, protection of commercially exploited reef fish spawning aggregations has received increasing attention in recent years as a fisheries management measure to protect spawning biomass (Sadovy & Domeier 2005). The current findings demonstrate that protecting spawning aggregations will also benefit trophically linked reef fishes.

Chapter 5

Maternal effects of fish egg consumption on the offspring of a damselfish egg predator

---

Introduction

Variations in prey availability in energy limited systems greatly influence predator population dynamics (Krebs 1994). During periods of increased prey availability female fecundity is a major contributor to numerical responses in predator species, however the ability of females to alter offspring quality is receiving increasing recognition as an important factor in cohort success (Plaistow & Benton 2009). Offspring phenotype is primarily determined by parental genotype (Miles et al. 2007), however maternal provisioning may also significantly affect offspring phenotype (Marshall & Uller 2007). Females can influence the phenotype of their young through altering size, energy reserves or biochemical composition (Bernado 1996). Theory predicts that in energy limited systems females will make trade-offs between the quantity and quality of offspring to maximise their contribution to future generations (Marshall & Uller 2007). Therefore, fluctuations in prey availability are expected to greatly influence the dynamic between fecundity and offspring quality through altering energy limitations. Since offspring mortality is generally not random with selection for offspring life history traits dependent on the environment they experience (Vigliola & Meekan 2002), understanding how increases in prey availability influence maternal trade-offs between offspring quality and quantity is fundamental to determining how prey fluctuations influence population dynamics.

In tropical marine fishes, increased fecundity may increase the probability of offspring survival, however evidence suggests larval morphologies also have an important role in selective mortality experienced after hatching. Back calculation of juvenile growth rates has shown that rapid growth during early development enhances later survival (Shima & Findlay 2002). In addition, larval body size is an important function of swimming ability (Fisher et al. 2000) and therefore is thought to enhance prey acquisition and predator avoidance (Sogard 1997), while increased yolk sac provisioning has been shown to buffer larvae from starvation in low food environments (Donelson et al. 2009). Previous studies show fecundity and maternally induced variations of larval progeny life history traits are influenced by changes in food availability (Kerrigan 1997, McCormick 2003, Gagliano & McCormick 2007, Donelson et al. 2008). Supplementally fed female reef fish have shown increases in the number (Gagliano & McCormick 2007, Donelson et al. 2008), body size (Donelson et al. 2008), and yolk sac provisioning (Gagliano & McCormick 2007, Donelson et al. 2008) of larval offspring. However, no studies have reported a trade-off between larval quantity and quality with alterations in food availability in tropical reef fish. This is most likely due to the majority of studies being conducted on the damselfish, *Pomacentrus amboinensis*, which produces offspring with a high degree of phenotypic variability regardless of the maternal environment (bet-hedging strategy) (Gagliano & McCormick 2007). In addition, work conducted on the brooding damselfish, *Acanthachromis polyacanthus*, tested theoretical food levels with artificial diets (Donelson et al. 2008). How variations in natural food types influence the maternal provisioning of the number and quality of offspring is still poorly understood (but see McCormick 2003).

Previous studies show that eggs consumed at reef fish spawning aggregation sites are an important pulsed food source for planktivorous egg predators (Chapter 3). To date, 32 species of reef associated obligate and facultative planktivores have been reported to actively attack the visible gamete clouds of aggregative pelagic spawning reef fishes (Robertson 1983, Moyer 1987, Colin & Clavijo 1988, Colin & Bell 1991, Sancho et al. 2000, Chapter 2). Egg predators have also been reported aggregating to exploit recently spawned eggs at reef fish SASs (Heyman et al. 2001, Chapter 2) and the energetic benefits of this pulsed resource are known to influence reproduction of females of the damselfish, *Abudefduf vaigiensis* (Chapter 3). How female egg predators subsequently partition energy from this food resource among their offspring is currently unknown and is the focus of this study. The obvious focal candidate for this study was the damselfish *A. vaigiensis*, however guarded nesting sites were inaccessible at the study location were egg predation had previously been documented (Chapters 2 and 3). Subsequently, breeding pairs of the known egg predator *A. polyacanthus* were monitored for breeding activity, however too few clutches were laid at SASs to provide meaningful results. Therefore this study was conducted using breeding pairs of *A. polyacanthus* housed in aquaria. The aim of this study was to compare the fecundity and larval life history traits of larvae from parents fed a control diet (consisting of a crustaceous plankton diet) with those of parents fed a control diet partially substituted with fish eggs (and identical to the control diet in energy content), and a control diet supplemented with fish eggs (greater energy content than the control).

Materials and Methods

Study species and fish collection

The damselfish, *Acanthachromis polyacanthus*, is a demersal spawning species that unlike most coral reef fishes, lack a dispersive planktonic larval stage. After hatching parents defend their young which stay in close proximity to the nesting site for up to 45 days (Kavanah 2000). During October 2006, 20 breeding pairs of *A. polyacanthus* were collected with a fence net at Orpheus Island, Great Barrier Reef (GBR), Australia. Fish pairs were transported to James Cook University Marine and Aquaculture Research Facility Unit and held in separate 70 litre aquaria. Each aquarium contained a nesting shelter constructed with three small house bricks and was supplied with recirculating water (~ 1L/minute) and constant gentle aeration.

Field collections of *A. polyacanthus* (n = 21) were made also from the same field location with a spear gun to quantify the energetic value of their stomach contents (see next section). Fish were placed immediately on ice and stored for up three hours prior to the removal of the stomach. Stomach contents were removed and weighed (0.001g), and stored at -12 ˚C prior to freeze drying for bomb calorimetry energy analysis.

Dietary treatments

Dietary treatments were designed to represent a range of food levels that egg predator damselfish are likely to consume at SASs and non-spawning aggregation reef locations. Previous work suggests damselfish food intake ranges from 0% - 8% of body weight (bw) per day (Booth & Hixon 1999, Booth & Alquezar 2002). The quantity of eggs consumed by egg predators is also likely to vary in the field, however evidence suggests the damselfish egg predator, *Abudefduf vaigiensis*, consume between 51% and

80% (n = 4 specimens) of their stomach volume in eggs during a single *Ctenochaetus striatus* spawning event (Chapter 4). Therefore dietary rations were formulated within this range and contained just a natural plankton diet as a control (Ocean Plankton Hikari, predominantly *Acetes* spp, 6.8% protein and 1.5% fat) or a natural plankton diet and fish eggs. Hydrated fish eggs were collected from the ripe gonads of *Scomboromorsus queenslandicus* caught during their spawning season from the inshore waters of the GBR. Eggs of *S. queenslandicus* have a similar size and morphology to reef-associated fishes (personal observation). Rations containing fish eggs contained 0.25 g of fish eggs per parent (0.5g per breeding pair) that occupied a volume within 80% of the total stomach volume of *A. polyacanthus*.

The energetic compositions of the plankton diet, fish eggs, and the stomach contents of field-caught *A. polyacanthus*, were determined to ensure energy of the plankton diet were similar to the natural diet of *A. polyacanthus* and to calculate isocaloric levels for dietary treatments 1 and 2. Energy contents were determined using bomb calorimetry of freeze dried samples (analysis conducted by the Pig and Poultry Production Institute, Nutrition Research Laboratory, Roseworthy, South Australia, Australia). Due to the small volumes of stomach contents, samples were pooled for energy analysis. The energy contents of *A. polyacanthus* stomachs were 19.56 kJ/g, which were similar to the mean (± SE) energy contents of the plankton diet of 18.29 ± 0.19 kJ/g. The mean (± SE) energy contents of the eggs of *S. queenslandicus* were 26.42 ± 0.19 kJ/g.

Breeding pairs were assigned randomly to a dietary treatment so that each treatment had five replicate breeding pairs. Dietary treatments were: (1) a control plankton diet (6% of body weight (bw) per day) (mean energy consumed per day ± standard deviation, 9.38 kJ ± 0.38 kJ); (2) plankton diet substituted with fish eggs (mean energy consumed per day ± standard deviation, 9.83 kJ ± 0.85 kJ); and (3) plankton diet supplemented with fish eggs (mean energy consumed per day ± standard deviation, 11.03 kJ ± 1.95 kJ). A fourth dietary treatment consisting of the control plankton diet fed at 2% bw per day was also fed to breeding pairs (n = 5), however only two breeding pairs laid egg clutches and were therefore excluded from analysis.

Reproductive output, progeny traits and parental condition

On the day a clutch was laid on the nesting substrate a digital photograph was taken and the numbers of embryos counted. Samples of 20 embryos were then haphazardly sampled from the clutch with forceps. Individual embryos were digitally photographed under a stereo dissector (Image Tool, UTHSCSA, San Antonio, USA) and an estimate of the mean volume of each embryo was calculated from calibrated photographs following (Donelson et al. 2008).

To assess embryonic development and larval characteristics, individual embryos were placed into separate 20 ml glass vials which were housed individually in separate 2 L aquaria (n = 20 per parental pair). Water flow was passed over the surface of each embryo through a glass pipette to prevent oxygen depletion at the boundary layer of the embryo surface (Green 2004). Water flow was supplied at the rate of approximately 50 μL per 1-1.5 seconds. On the day of hatching nonn-anesthetised larvae were removed from their aquaria and digitally photographed (dorsal view) under a stereo dissector (Image Tool, UTHSCSA, San Antonio, USA). From calibrated photographs the length of the larvae (notochord length), diameter of the eye, and area of the endogenous yolk sac were calculated (Donelson et al. 2008).

To determine survival time on endogenous reserves, measured larvae were then placed into individual aquaria and monitored daily for unfed survival. Starvation is thought to be a major contributor to larval mortality (Leis & McCormick 2002), therefore this methodology imitates this natural source of mortality. At the termination of the feeding experiment, male and female breeding pairs were measured (± 0.1 mm, fork length) and weighed (± 0.1 g). Parental condition or relative "fatness" was determined by comparing length-weight relationships among dietary treatments (Jakob et al. 1996).

Statistical analysis

Length versus weight relationships of parental pairs and fecundity versus length relationships of females were compared among dietary treatments with analysis of covariance (ANCOVA). Data were analysed for homogeneity of slopes and normality prior to analysis (Quinn & Keough 2002). The effects of maternal diet on offspring morphologies were examined using multivariate analysis of variance (MANOVA) and a canonical discriminant analysis (CDA). Vector length and direction indicate the importance of each larval trait in discriminating among dietary treatments (McCormick & Makey 1997) and 95% confidence limits were plotted around dietary treatment centroids (Seber 1984). Data were examined for multivariate normality prior to analysis.. To further explore the significant effect found by MANOVA, embryo volume, larval length and larval yolk sac volume were compared with two-factor nested ANOVAs, where parental replicates were nested as random factors within dietary treatments. Assumptions of ANOVA were tested with residual analysis. A multiple sample Cox-Mantel survival analysis, which computes a X^2 value based on scores assigned to survival times, was used to determine the effect of maternal diet on survival of unfed offspring.

Results

Parental condition and reproductive output

Dietary treatments did not significantly influence parental condition (ANCOVA, $F_{2,23}$ = 3.419, p = 0.0501) (Fig 5.1). However, parents fed diets containing eggs (diets 2 and 3) tended to be heavier relative to their length than parents fed a diet without eggs (diet 1).

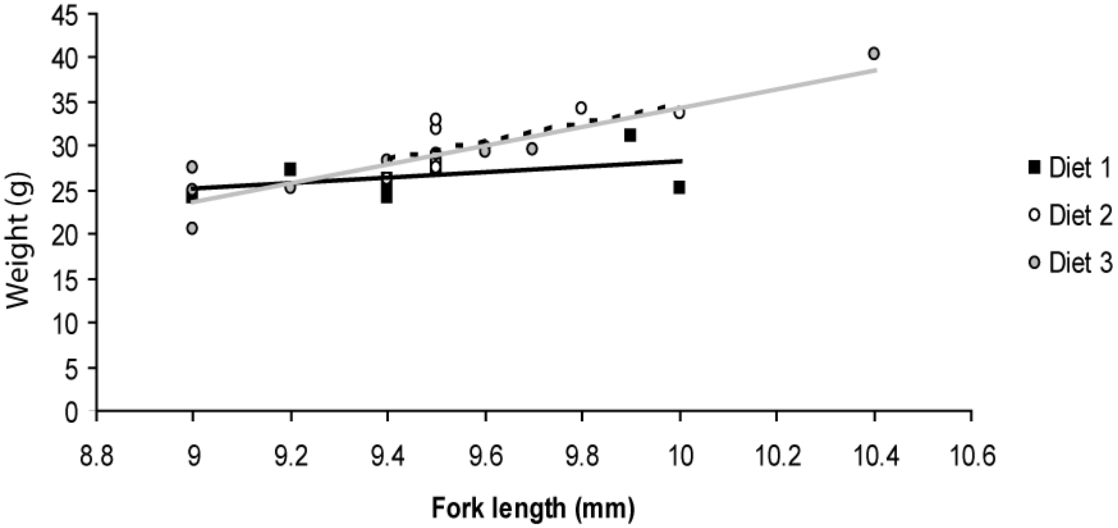

Figure 5.1 Length vs weight relationship of *Acanthachromis polyacanthus* parents fed diets 1,2 and 3. Full line = Diet 1, broken line = Diet 2, Grey line = Diet3.

Female fecundity differed significantly among dietary treatments (ANCOVA, $F_{2,8}$ = 4.835, p = 0.042) (Fig 5.2). Females fed diets 1 and 2 did not produce significantly different numbers of embryos, while females fed diet 3 produced significantly more embryos than mothers fed diets 1 and 2.

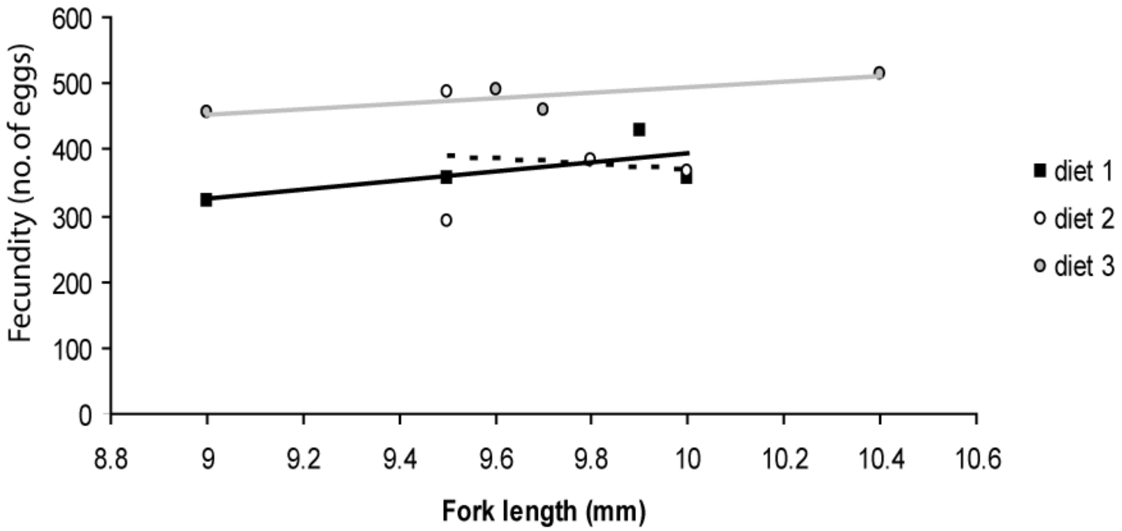

Figure 5.2 Fecundity (number of eggs) laid on nesting substrates by females *Acanthachromis polyacanthus* fed diets 1, 2 and 3. Full line = Diet 1, broken line = Diet 2, grey line = Diet3.

Progeny morphologies

Maternal diet had a significant effect on offspring life history traits (MANOVA, Pillai's trace, $F_{10,290} = 11.91$, $p < 0.001$). The CDA summarises the nature of the differences in offspring life history traits found by MANOVA (Fig 5.3). There was a clear separation between the diet that did not contain fish eggs (diet 1) and diets containing fish eggs (diets 2 and 3) along the first canonical variate, which explained 77% of the model variance. Mothers fed diets 2 and 3 tended to produce larger embryos, and larvae that had greater sensory development and larger yolk sacs. Diets 2 and 3 are separated along the second canonical variate (17% of the variance) which shows that mothers fed diet 3 produced larvae with greater unfed survival.

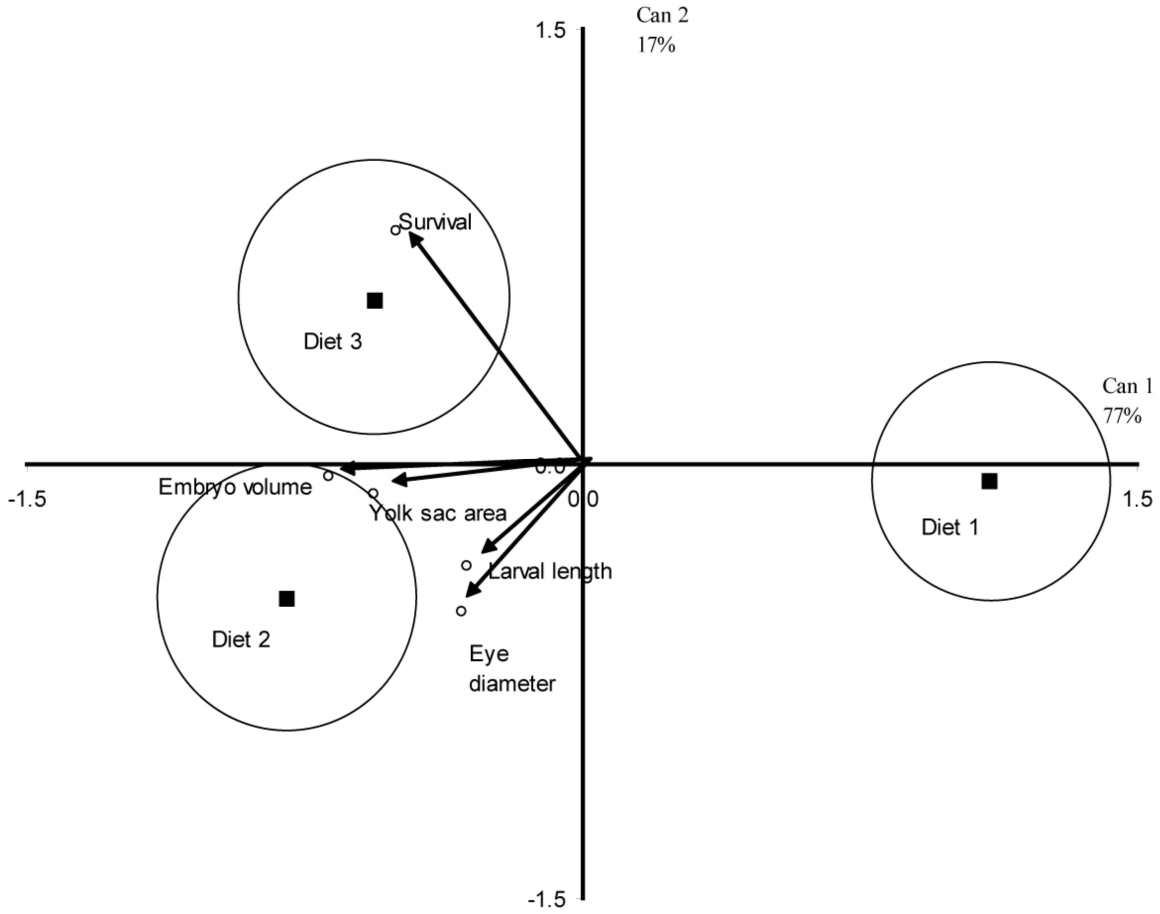

Figure 5.3 Canonical discriminant analysis of life history traits of larval progeny of female *A. polyacanthus* fed diets 1 to 3. Centroids with 95% confidence limits are displayed.

Despite multivariate statistics suggesting that there were strong influences of maternal diet on juvenile attributes, univariate statistics did not support these trends. The high variation in offspring morphologies attributable to differences among parental pairs lead to no significant difference in embryo size, larval length, larval eye diameter or yolk sac provisioning being found among maternal diet treatments (Table 5.1, Fig 5.4). Between 22 and 42% of the variation in larval morphology, depending upon the attribute considered, was accounted for by differences in females nested within diets. Furthermore, 52 to 72% of the variability in larval morphology was explained by differences in the attributes of individual juveniles within parental groups (Table 5.1). However, there was a general trend for females fed diet 1 to produce the smallest embryos and larvae, with reduced eye development and yolk sac provisioning. In contrast, females fed diet 2 tended to produce the largest embryos and larvae with increased eye development and large yolk sac provisions. Finally, females fed diet 3 generally produced smaller embryos and larvae with less developed eyes compared to females fed diet 2, but generally larger than females fed diet 1 (Fig 5.4). Interestingly, yolk sac provisioning in the offspring of mothers fed diets 2 and 3 were generally similar despite the difference in energy contents of these diets (Fig 5.4c).

Table 5.1 Summary of nested ANOVA examining effects of parental diet and parental pairs (parental pairs as a random factor nested within dietary treatment) on offspring embryo volume, larval length, eye diameter, and yolk sac area.

Dependent variable	Factor	df	MS	F	p	% variance
Embryo volume	Diet	2	4.260	2.755	0.111	9.8
	Parents(diet)	10	1.541	6.387	<0.001	30.3
	Error	229	0.241			69.9
Larval length	Diet	2	10801	1.825	0.208	6.2
	Parents(diet)	10	6813	6.301	<0.001	26.0
	Error	174	1081			67.8
Eye Diameter	Diet	2	371.1	3.332	0.075	15.4
	Parents(diet)	10	128.1	6.017	<0.001	22.5
	Error	172	21.3			62.1
Yolk sac area	Diet	2	0.436	1.502	0.273	5.8
	Parents(diet)	10	0.297	13.194	<0.001	42.3
	Error	174	0.022			52.0

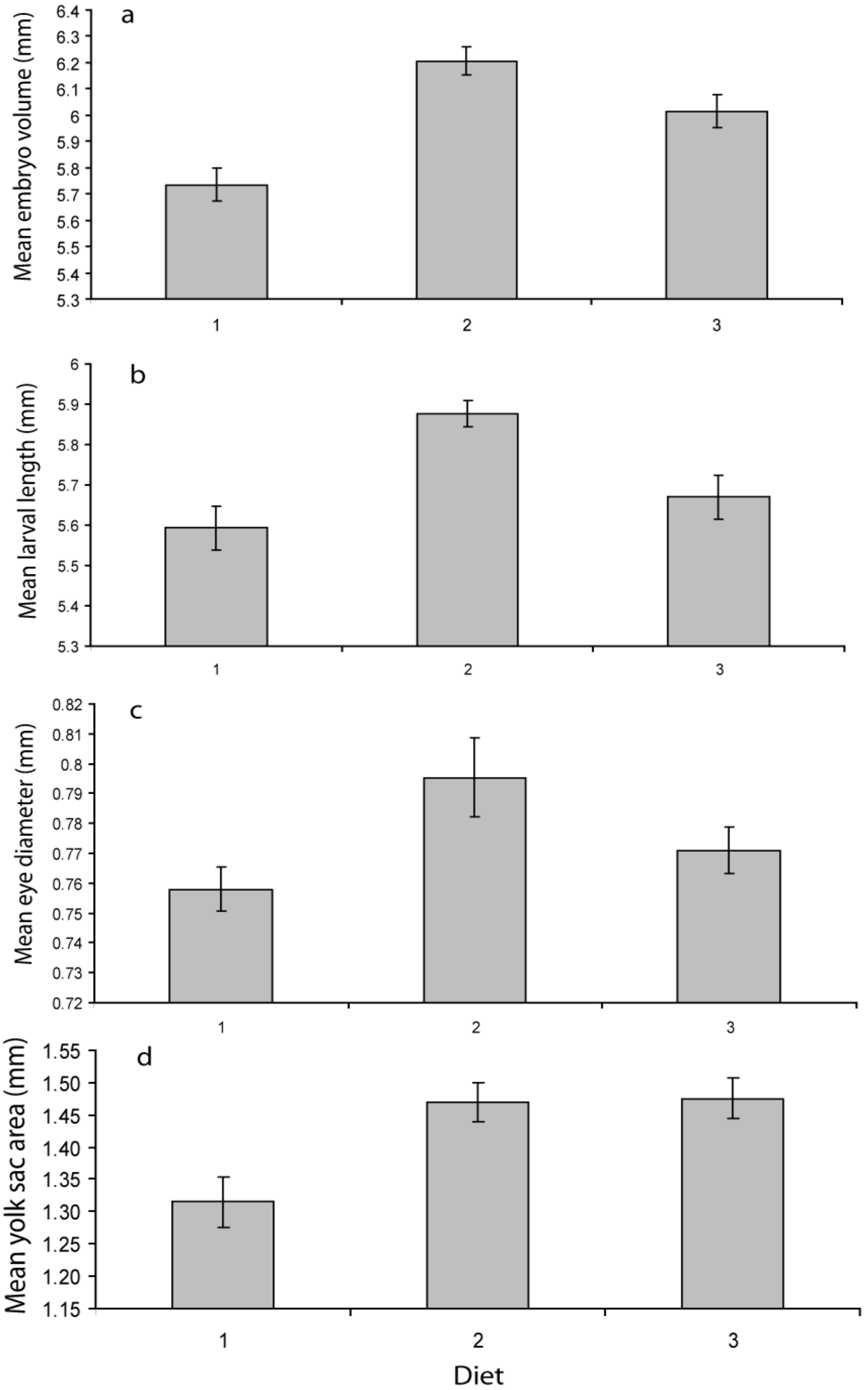

Figure 5.4 Mean embryo volume (a), larval length (b), eye diameter (c), and yolk sac area (d) (± SE) (immediately after hatching) of progeny from female *Acanthachromis polyacanthus* fed diets 1, 2 or 3.

Offspring survival

Survival schedules of larval progeny differed significantly among parental dietary treatments ($X^2 = 38.08$, df = 2, $p < 0.001$) (Fig 5.5). Parents fed diet 1 produced larvae that first suffered mortality five days after hatch (DAH), progeny of parents fed diet 2 first suffered mortality 6 DAH and progeny from parents fed diet 3 suffered first mortality 7 DAH. Total mortality of larvae from parents fed diets 1 and 2 occurred ten DAH while larvae of parents fed diet 3 had the greatest survival with 100% mortality eleven DAH (Fig 5.5).

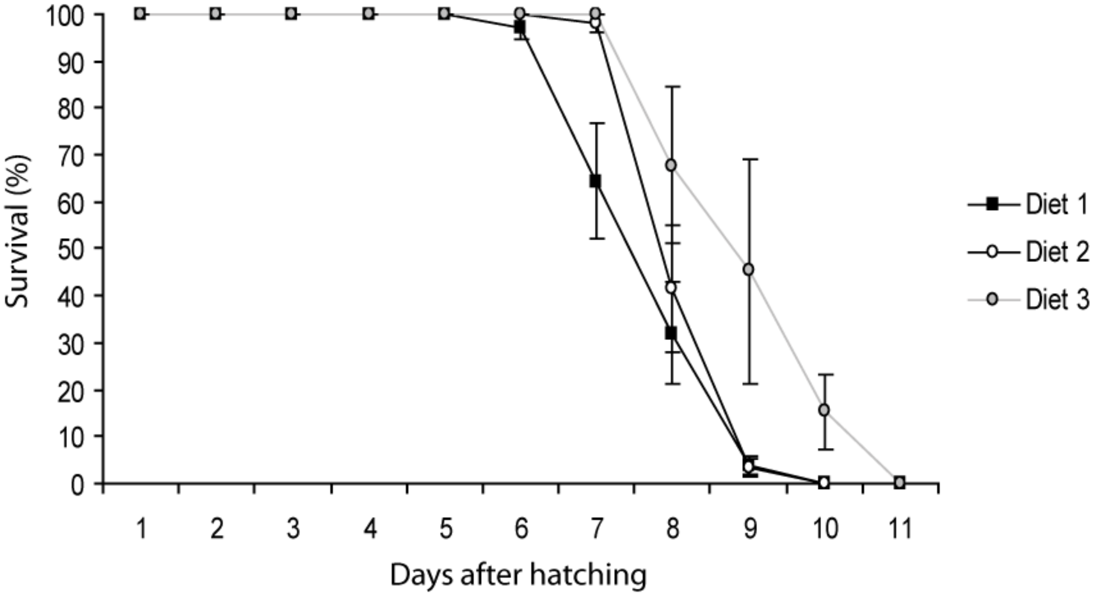

Figure 5.5 Mean proportional survival (± SE) of unfed larval progeny of *A. polyacanthus* females fed diets 1, 2 and 3.

Discussion

The findings of this study suggest that increased energy intake in *A. polyacanthus*, that results from the consumption of fish eggs, may be associated with a trade-off between offspring morphology (quality) for increased fecundity. Previous work shows that female egg predators at reef fish spawning aggregation sites have increased energy stored within their livers and increased fecundity, suggesting egg predation does increase energy intake (Chapter 3). Furthermore, mothers fed eggs as a component of their diet tended to produce larger young with greater provisioning, even though maternal energy intake was not altered. Mothers fed the higher energy diet containing eggs (diet 3) tended to produce smaller embryos and larvae with reduced eye development, however with similarly provisioned yolk sacks, compared to offspring from mothers fed diet 2. This corresponded to significantly greater unfed larval survival in larvae of mothers fed diet 3. Due to the nested design and low power of this factorial experiment (with parental replicates as a random factor), trends in offspring morphologies were not statistically significant. However, the findings from this study demonstrate similar findings to recent studies on reef fishes examining the role of maternal nutrition on larval progeny (Gagliano & McCormick 2007, Donelson et al. 2008, Donelson et al. 2009). Recent work has shown that *A. polyacanthus* larvae with increased yolk sac provisioning had increased survival when exposed to low food environments, but survived equally well as poor condition larvae in high food environments (Donelson et al. 2009). The current study suggests that larval progeny that are produced by females that have increased energy intake, as a result of consuming eggs, may potentially have greater survival under conditions of variable food availability. Female egg predators may therefore make a greater contribution to the next generation not only through the quantity of young produced but also the quality of their young.

The fecundity versus offspring size trade-off is a well established parameter of maternal provisioning that has evolved in food limited environments (Bernado 1996). Mothers are expected to make trade-offs in the quantity and quality of offspring based on the environment she experiences in order to promote offspring fitness and ultimately her fitness (anticipatory maternal effect hypothesis) (Marshall & Uller 2007). In this study mothers fed diet 2 tended to produce larger offspring, however females fed the highest energy food source, diet 3, traded larval size for gains in offspring quantity without compromising the provision of yolk to offspring. Size is thought to be an important determinant in mitigating the high rates of mortality during the larval phase (Miller et al. 1988). Therefore, mothers fed diet 3, which consequently produced smaller offspring, may have compensated for the increased risk of mortality by producing more young. This may be particularly beneficial for *A. polyacanthus* which are capable of further reducing the risk of predation through parental care after hatching (Kavanagh 2000). The production of smaller young while maintaining equally high levels of yolk reserves may have been the mechanism that promoted longer unfed larval survival. Since body size/mass (log of mass) is positively correlated with metabolic activity (log of metabolic activity) (Withers 1992), lower metabolic activity in the smaller embryos and larvae coupled with relatively high yolk sac provisioning may have promoted longer unfed survival. Previous research suggests that increased yolk sac provisioning buffer larval fish from starvation (Heming & Buddington 1988) and may act to promote survival in a fluctuating environment, therefore promoting female fitness regardless of future food levels.

The differences in life history traits of larvae produced by mothers fed isocaloric diets 1 and 2 suggest eggs in diet 2 may have contained nutrients capable of influencing offspring traits. Most vertebrates require essential nutrients that can not be biosynthesised and must be obtained through the diet (Clements & Raubenheimer 2006). While there is some evidence that essential nutrients are limited in the natural environment (Jones & McCormick 2002), interpreting biological significance from the present findings should be done with caution. Since the control diet in this study was not identical to that of planktivores in their natural environment, the addition of fish eggs may have simply increased the level of essential nutrients required for normal reproduction and maternal provisioning. However, the eggs consumed by damselfish at reef fish spawning aggregation sites have the exact nutrient profile necessary for their own reproduction and are known to be rich in essential fatty acids and amino acids capable of influencing fecundity and maternal provisioning (Sargent et al. 1999). Traditionally, the dynamics of life history parameters are framed within a context of energy acquisition and expenditure and very little work is available on the role of essential nutrient availability for consumer species. Increased essential nutrients have been shown to enhance reproduction and maternal provisioning in the natural diets of the zebra finch (*Taeniopygia guttata*) (Royal et al. 2003) and the limitation of essential nutrients have been proposed to describe patterns in reproduction in wrasses (*Thalassoma bifasciatum*) (Schultz & Warner 1991). Examining the role of essential nutrient availability in the natural environment and their role in energetic processes, particularly reproduction and maternal provisioning, may be a novel research avenue that may help elucidate the processes that influence population dynamics.

Ultimately, maternal provisioning by egg predators at reef fish spawning aggregation sites will be determined by the level of egg consumption that is likely to vary temporally and spatially. This study therefore demonstrates the possible outcomes for maternal provisioning that are likely to occur under such variation. Previous work has shown that the consumption of eggs at reef fish spawning aggregation sites influences the reproductive output of egg predators (Chapter 3). This study highlights the potential additional impact the consumption of eggs may have on larval quality and survival. Furthermore, it has been suggested that egg predators may also consume the sperm of spawning males during attacks on gamete clouds (Robertson 1983). The consumption of sperm may have additional nutritional benefits not examined in the present study. While studying life history processes in the laboratory provides useful insight into causal mechanisms (Schultz & Warner 1991), a true understanding of the effects of egg predation at reef fish spawning aggregation sites on egg predator progeny through maternal provisioning will require hypothesis testing in the field studies.

Chapter 6

General discussion

This thesis advances our understanding of the ecology of resident reef fish spawning aggregations and of the effects of a natural food fluctuation on reef fish population dynamics. For the resident spawners, the present study shows that levels of target egg predation vary greatly among SASs and among spawning species, and may be an important source of propagule mortality for some species. For the egg predators, the eggs released by synchronised group spawners can be a valuable food source. However, the presence of this high energy food source does not lead to densities of egg predators that are higher than other areas of reef of similar topography and aspect. For at least one key egg predator, spawning aggregations provide an important food source which increases their growth and reproductive output. Laboratory manipulations suggest that maternal provisioning of the nutrients gained through egg consumption may also influence offspring fitness. Collectively, these findings suggest that egg predators at reef fish SASs will potentially make a greater contribution to successive generations relative to conspecifics from other reef locations. Previously, spawning aggregations have been viewed as important ecological events for the spawning species, however this thesis demonstrates that they are also an important for egg predators. Furthermore, this study agrees with previous manipulative studies that suggest food is a limiting resource capable of altering demographic processes in coral reef fish populations.

Spawning aggregation site selection and egg predation

A unique and ubiquitous feature of reef fish spawning aggregations is their spatial predictability. The reasons why pelagic spawners use the same SASs across generations is not fully understood. The minimisation of egg predation, and hence the promotion of offspring survival, is one key hypothesis proposed for the selection of SASs (Claydon 2005). Warner (1988) demonstrated that SASs were selected based on an original assessment of the spawning environment and the selected sites were traditionally passed on through generations in a resident spawning wrasse. This suggests that the factors responsible for the promotion of offspring survival will not change greatly among generations at these sites. However, the distribution and abundance of egg predator species do change through time (Williams 1991), the density of egg predators correlated strongly with levels of egg predation (Chapter 2), and SASs and non-SASs with similar physical attributes had similar densities of known resident egg predators (Chapter 3). Therefore, it is unlikely that egg predator abundance is important in the selection of SASs. The high variability in target egg predation among SASs in this study also supports this conclusion. A true test of the egg predation hypothesis, however, must measure target egg predation at SASs and non-SASs. This will require an artificial release of gametes to mimic a spawning event. It would therefore be necessary to compare any artificial methodology against natural egg predation during a spawning event in order to detect any confounding effects. In addition, it is recommended that future studies examining the role of egg predation on SAS selection focus also on non-target egg predation. Non-target egg predation cannot be accurately quantified because egg predators feed down current of a spawning aggregation after gamete clouds are no longer visible (Colin & Bell 1991). Therefore, non-target egg predation must be determined by measuring current flows and will require the assumption that gametes carried towards the reef may be preyed upon. Ideally, measurements of non-target egg predation should be conducted over the entire spawning season (if seasonal) at SASs and non-SASs to determine if the immediate fate of the eggs is important in SAS selection. This study does not support the hypothesis that target egg predation is important in SAS selection, however target egg predation and non-target egg predation must be measured in conjunction with control treatments to determine if the immediate fate of the eggs is important in the evolution of SAS selection.

Food availability and population processes

The importance of food availability in shaping animal population demographics is well demonstrated (Krebs 1994). In tropical marine fish populations the current evidence suggests that food is a limited resource and has a fundamental influence on populations via numerical and energetic processes (Jones & McCormick 2002). The findings of this thesis generally did not support previous manipulative experiments on the role of food availability on numerical processes. There was an aggregation response by one species of egg predator, but generally the release of eggs at SASs did not influence the numbers of resident egg predators (Chapter 3), despite observations of frequent egg predation (Chapter 2). The findings from this thesis do, however, support previous studies on the role of food availability on energetic processes in coral reef fishes. This study demonstrates that the consumption of eggs influences the condition (lipid storage) of adults, growth of males, and reproductive output of female egg predators. A previous study on the response of the parrotfish *Scarus iserti* to natural variation in food availability also supports the finding of this thesis (Clifton 1995). Furthermore, females that consumed eggs and consequently had increased energy intake tended to produce larger embryos, and larvae with larger yolk sac provisioning, which may influence post-hatch survival. These findings also agree with a previous study that found the consumption of coral propagules influenced maternal provisioning in a coral reef damsel-fish during the annual synchronised coral spawn on the Great Barrier Reef (McCormick 2003). Finally, evidence from this study suggests that females that consume the eggs of pelagic spawners produce offspring that are more capable of surviving during periods of low food availability, and supports similar findings in previous manipulations of maternal nutrition (Gagliano & McCormick 2007, Donelson et al. 2008). Collectively, these findings suggest that natural variations in food availability for reef fishes have the potential to influence the size of the breeding population and its reproductive potential.

There are a number of possible reasons for an energetic response but not a numerical response by egg predators at SASs. The most likely factor is insufficient energy consumption to attract (through adult migration) and sustain greater numbers of egg predators. There is little empirical evidence that demonstrates the role of resource pulse frequency and magnitude on consumer populations in the natural environment. Mathematical models of resource pulses, however, demonstrate that the frequency and magnitude are fundamental to consumer population responses (Holt 2008). While spawning aggregations are spatially predictable, the frequency of spawning events (and therefore dietary energetic gain) at this study location may be insufficient to support higher densities of resident egg predators (Chapter 3). Furthermore, the time that eggs are available for consumption is often only a few minutes before they are carried away from the relative safety of the reef (pers. observation) and therefore becoming inaccessible to egg predators. At higher latitudes, where spawning is more seasonal, and therefore less frequent, SASs may be less likely to influence egg predator numerical processes. From the spawners' perspective, releasing gametes at SASs with a frequency great enough to support higher densities of egg predators would counter efforts to maximise reproductive success. The seemingly unpredictable use of SASs demonstrated in Chapter 3, may be a behavioural response by spawners to reduce the predictability of spawning events (and therefore an egg predator numerical response), achieved by spreading their spawning effort among multiple SASs (within a reef).

Resource pulses that involve both numerical and energetic responses tend to be greater in magnitude and duration. A pulse of marine bivalve prey (*Mytilus edulus*), resulting from an unusually large recruitment event that produced a strong cohort that persisted for 12 months, caused a number of higher order consumers to respond both energetically and numerically (Witman et al. 2003). In addition, the emergence of periodical cicadas in North American forests over a 25 day period results in the super-abundance of adult cicadas that spans hundreds of kilometres (Williams 1993) and has been documented to influence the demography of at least 15 predator bird species (Nowlin et al. 2008). The present study has shown that a small natural pulse in food availability is important in influencing reef fish populations, however, future studies examining larger scale processes are needed to advance our understanding of the role of resource availability on reef fish populations.

In age and size structured populations the partitioning of energy among life-history traits can have profound influences on the size of the breeding population (Jones

& McCormick 2002) that will ultimately be determined by the life-history energy allocation strategy. The differences in the way that male and female *A. vaigiensis* partitioned energy in response to feeding on eggs at SASs in the present study (Chapter 4) highlights the complexity of the interaction between variations in food availability and life-history strategies that have been reported for other taxa, including insects (Boggs 2009), and is therefore not specific to teleosts. Because energy is allocated to life-history traits that will promote reproductive success during an individuals life span (Stearns 1992), changes in demographic parameters among geographic locations, sexual ontogeny and taxa are likely to influence how energy gained from resource pulses is allocated. For example, at locations where populations are exposed to increased levels of predation, and therefore suffer higher rates of mortality (or mortality from fishing), there is a selection for individuals to reach sexual maturity at a younger age, achieve shorter maximum ages, and allocate greater energy to reproduction (Bertschy & Fox 1999). Therefore, populations with localised differences in demographics may be expected to have different allocation strategies in response to food resource pulses. In addition, at higher latitudinal locations where reproduction is seasonal (Wootton 1990) and fishes are generally longer lived (Choat & Robertson 2002) the allocation of energy may differ depending on the time of year that the resource pulse occurs. Due to the complexity of life-history strategies in fishes, the allocation of energy from pulsed resources is likely to vary greatly. Therefore, for the effective management of exploited fish populations, any incorporation of population responses to natural variations in resource availability into population models is likely to be highly specific to the focal population. Despite the well documented role of life-history strategies in shaping energy allocations in a range of taxa, including fish (Roff 1984) insects (Boggs 2009) and birds (Southwood et al. 1974), this dynamic remains largely unstudied for resource pulses in both terrestrial and marine ecosystems. Integrating theory of life-history driven allocation strategies with resource pulse dynamics is required to better understand the population responses of consumers to resource pulses.

Concluding remarks

This thesis demonstrates that egg predation at reef fish spawning aggregations is highly variable and that eggs are an important food supply for the trophically linked egg predator community. Resident spawning aggregations do not harbour greater numbers of egg predators, but provide energy rich eggs capable of altering growth, reproduction and maternal provisioning in adult egg predators. The preservation of reef fish spawning aggregations therefore will have greater effects on the reef fish populations than recognised previously. This study also demonstrates clearly that natural variations in food availability are capable of altering demographic processes in tropical reef fishes. Previously, age-based studies have found that reef fish demographics vary across small spatial scales and have been hypothesised to result from differences in food availability (Gust et al. 2002, Ruttenberg et al. 2005). This study lends support to this hypothesis by demonstrating that natural variations in food availability]alter reef fish demographics at highly localised scales. The small scale at which reef fish population processes vary emphasizes the complexity of predicting population dynamics. For effective management of reef fish populations we need to understand better the sources and quantitative effects of resource availability on population replenishment. By identifying both the locations of SASs or individuals or the groups that use them and make the greatest contributions to future generations, fisheries and conservation managers will be able to implement management protocols that are more effective at protecting exploited populations.

References

Anderson MJ (2001) A new method of non-parametric multivariate analysis of variance. Austral Ecology 26:32-46

Anderson TW, Sabado BD (1995) Correspondence between food availability and growth of a planktivorous temperate reef fish. J. Exp. Mar. Biol. Ecol. 189:65-76

Anderson WB, Wait DA, Stapp P (2008) Resources from another place and time: Responses to pulses in a spatially subsidized system. Ecology 89:660-670

Barlow GW, (1987) Spawning, eggs and larvae of the longnose filefish Oxymonacanthus longirostris, a monogamous coralivore. Env. Biol. Fish 20:183-194

Bernado JH (1996) Maternal effects in animal ecology. Am. Zool. 36:83-105

Bertschy KA, Fox MG (1999) The influence of age-specific survivorship on pumpkinseed sunfish life histories. Ecology 80:2299-2313

Beukers JS, Jones GP, Buckley RM (1995) Use of implant micro-tags for studies of populations of small reef fish. Mar. Ecol. Prog. Ser. 125:61-66

Boggs CL (2009) Understanding insect life histories and senescence through a resource allocation lens. Funct. Ecol. 23:27-37

Booth DJ, Alquezar R (2002) Food supplementation increases larval growth, condition and survival of *Acanthochromis polyacanthus*. J. Fish. Biol. 60:1126-1133

Booth DJ, Hixon MA (1999) Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. Oecologia 121:364-368

Choat JH, Robertson DR (2002) Age-based studies on coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, London, p 57-80

Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. Oceanogr. Mar. Biol. Ann. Rev. 42:265-302

Claydon J (2005) The structure and dynamics of spawning aggregations of coral reef fish. PhD Thesis, James Cook University

Clements KD, Raubenheimer D (2006) Feeding and nutrition. In: Evans BH CJ (ed) The physiology of fishes. Taylor and Francis, Baco Raton, Florida p pp 47-82

Clifton KE (1995) Asynchronous food availability on neighbouring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. Mar. Ecol. Prog. Ser. 116:39-46

Cole KS, Sadovy Y (1995) Evaluating the use of spawning success to estimate reproductive success in a Caribbean reef fish. J. Fish. Biol. 47:181-191

Colin PL, Bell LJ (1991) Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ. Biol. Fishes 31:229-260

Colin PL, Clavijo I (1988) Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, Southwestern Puerto Rico. Bull. Mar. Sci. 43:249-279

Connell SD (1996) Variations in mortality of a coral-reef fish: Links with predator abundance. Mar Biol 126:347-352

Connell SD, Kingsford MJ (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17:49-57

Côté IM, Hunte W (1989) Male and female mate choice in the redlip blenny: why bigger is better. Anim. Behav. 38:78-88

Curran LM, Leighton, M. (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecol. Monogr. 70:101-128

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249-293

Cushing JM (1987) Equilibria in systems of interacting structured populations. J. Math. Biol. 24:627-649

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60:698-726

Donelson JM, McCormick MI, Munday PL (2008) Parental condition affects early life-history of a coral reef fish. J Exp. Mar. Biol. Ecol. 360:109-116

Donelson JM, Munday PL, McCormick MI (2009) Parental effects on offspring life histories: when are they important? Biol. Lett. 5:262-265

FerryGraham LA, Wainwright PC, Westneat MW, Bellwood DR (2002) Mechanisms of benthic prey capture in wrasses (Labridae). Mar. Biol. 141:819-830

Fisher R, Bellwood DR, Job SD (2000) The development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. 202:163-173

Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. Ecology 71:1666-1681

Fowler AJ, Doherty PJ (1992) Validation of annual growth increments in the otoliths of two species of damselfish from the southern Great Barrier Reef. Aust. J. Mar. Fresh. Res. 43:1057-1068

Gagliano M, McCormick MI (2007) Maternal condition influences phenotypic selection on offspring. J. Anim. Ecol. 76:174-182

Godin J-G, J. (1986) Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). Can. J. Zool. 64:1675-1678

Green BS (2004) Embryogenesis and oxygen consumption in benthic egg clutches of a tropical clownfish, *Amphiprion melanopus* (Pomacentridae). Comp. Biochem. Physiol. A. 138:33-38

Gust N, Choat JH, Ackerman JL (2002) Demographic plasticity in tropical reef fishes. Mar. Biol. 140:1039-1052

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950-963

Heming TA, Buddington RK (1988) Yolk-absorption in embryonic and larval fishes. In: Hoar WS, Randall DJ (eds) Fish Physiology, Vol 11A. Academic Press, San Diego, p 407-446

Hensley DA, Appeldoorn RS, Shapiro DY, Ray M, Turingan RG (1994) Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. I. Dispersal over the reef platform. Bull. Mar. Sci. 54:256-270

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Mar. Ecol. Prog. Ser. 215:275-282

Hoey J, McCormick MI, Hoey AS (2007) Influence of depth on sex-specific energy allocation patterns in a tropical reef fish. Coral Reefs 26:603-613

Holbrook SJ, Schmitt RJ (2003) Spatial and temporal variation in mortality of newly settled damselfish: patterns, causes and co-variation with settlement. Oecologia 135:532-541

Holmes TH, McCormick MI (2006) Location influences size-selective predation on newly settled reef fish. Mar Ecol-Prog Ser 317:203-209

Holt RD (2008) Theoretical perspectives on resource pulses. Ecology 89:671-681

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77:61-67

Johannes RE (1978) Reproductive strategies of costal marine fishes in the tropics. Env. Biol. Fish. 3:65-84

Jones GP (1986) Food availability affects growth in a coral reef fish. Oecologia 70:136-139

Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed) Coral reef fishes- dynamics and diversity in a complex ecosystem. Academic Press, London, p 221-238

Kamler E (1992) Early life history of fish: an energetics approach, Vol 4. Chapman & Hall, London

Kao Y, Youson J, Sheridan M (1997) Differences in the total lipid and lipid class composition of larvae and metamorphosing sea lampreys *Petromyzon marinus*. Fish. Physiol. Biochem. 16:281-290

Kavanagh KD (2000) Larval brooding in the marine damselfish *Acanthochromis polyacanthus* (Pomacentridae) is correlated with highly divergent morphology, ontogeny and lift-history traits. Bull. Mar. Sci. 66:321-337

Kerrigan BA (1997) Variability in larval development of a tropical reef fish (Pomacentridae: *Pomacentrus amboinensis*): the parental legacy. Mar. Biol. 127:395-402

Kingsford MJ, MacDiarmid AB (1988) Interrelations between planktivorous reef fish and zooplankton in temperate waters. Mar. Ecol. Prog. Ser. 48:103-117

Koenig WD, and Liebhold AM (2005) Effects of periodical cicada emergences on abundance and synchrony of avian populations. Ecology 86:1876-1882.

Krebs CJ (1994) Ecology - the experimental analysis of distribution and abundance, HarperCollins College Publishers, New York

Krebs CJ (1995) Two paradigms of population regulation. Wild. Res. 22:1-10

Leis JM, McCormick MI (2002) The biology, behaviour, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, p 171 - 199

Lobel PS (1978) Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac. Sci. 32:193-207

Marshall DJ, Uller T (2007) When is a maternal effect adaptive? Oikos 116:1957-1963

Martin P, Bateson P (1993) Measuring behaviour- an introductory guide, Cambridge University Press, Canbridge UK

May RM (1972) Limit cycles in predator-prey communities. Science 177:900-902

McCormick MI (2003) Consumption of coral propagules after mass spawning enhances larval quality of a damselfish through maternal effects. Oecologia 136:37-45

McCormick MI, Makey LJ (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Mar. Ecol. Prog. Ser. 153:247-257

Meekan M, Wellington G, Axe L (1999) El Nino-Southern Oscillation events produce checks in the otoliths of coral reef fishes in the Galapagos Archipelago. Bull. Mar. Sci. 64:383-390

Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structure of coral reef damselfishes in the tropical eastern Pacific Ocean. Mar. Ecol. Prog. Ser. 212:223-232

Miles CM, Hadfield MG, Wayne ML (2007) Heritability for egg size in the serpulid polychaete *Hydroides elegans*. Mar. Ecol. Prog. Ser. 340:155–162

Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657-1670

Molony B, Sheaves M (1998) Variations in condition and body constitution in a tropical estuarine fish with year-round recruitment. Mangroves Salt Marshes 2:177-185

Mommsen TP, Walsh PJ (1988) Vitellogenesis and oocyte assembly. In: Hoar WS, Randall DJ (eds) Fish Physiology, Vol XIA. Academic Press, New York, p 347-406

Moyer JT (1987) Quantitative observations of predation during spawning rushes of the labrid fish *Thalassoma cupido* at Miyake-Jima, Japan. Jap. J. Ichth. 34:76-81

Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128:585-593

Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trend. Ecol. & Evol. 21:89-95

Nachman G (2006) A functional response model of a predator population foraging in a patchy habitat. J. Anim. Ecol. 75:948-958

Nowlin WH, Vanni MJ, Yang LH (2008) Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89:647-659

Noy-Meir I (1973) Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 425-51.

Oaten A, Murdoch WW (1975) Switching, functional response, and stability in predator-prey systems. Am. Nat. 109:299-318

Plaistow SJ, Benton TG (2009) The influence of context-dependent maternal effects on population dynamics: an experimental test. Phil. Trans. Roy. Soc. B. Biol. Sci. 364:1049-1058

Pratchett MS, Gust N, Goby G, Klanten SO (2001) Consumption of coral propagules represents a significant trophic link between corals and reef fish. Coral Reefs 20:13-17

Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sub-lethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23:352-356

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists, Cambridge University Press, Cambridge, UK

Randall JE, Randall HA (1963) The spawning and early development of the Atlantic parrotfish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48:49-60

Rhodes KL, Sadovy Y (2002) Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphekadion*, in Pohnpei, Micronesia. Env. Biol. Fish. 63:27-39

Robertson DR (1983) On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. Env. Biol. Fish. 9:193-223

Robertson DR (1992) The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale PF (ed) The ecology of reef fishes coral reefs. Academic Press, London, pp 356-386

Robertson DR, Hoffman SG (1977) Roles of female mate choice and predation in mating systems of some tropical labroid fishes. J. Comp. Eth. 45:298-320

Roff D (1984) The evolution of life history parameters in teleosts. Can. J. Fish. Aq. Sci. 41:989-1000

Royal NJ, Surai PF, Hartley IR (2003) The effect of variation in dietary intake on maternal deposition of antioxidants in zebra finch eggs. Functional ecology 17:472-481

Ruttenberg BI, Haupt AJ, Chiriboga AI, Warner RR (2005) Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. Oecologia 145:394–403

Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254-262

Sale PF (1998) Appropriate spatial scales for studies of reef-fish ecology. Aust J Ecol 23:202-208

Sancho G, Petersen C, Lobel P (2000) Predator-prey relations at a spawning aggregation site of coral reef fishes. Mar. Ecol. Prog. Ser. 203:275-288

Sano M, Shimizu M, Nose Y (1984) Food habits of teleostean reef fishes in Okinawa Island, Southern Japan. Univ. Mus. Univ. Tokyo Bull. 25:128pp

Sargent JR, Bell JG, McEvoy L, Tocher DR, Estevez A (1999) Recent developments in the essential fatty acid nutrition of fish. Aquaculture 177:191-199

Schmidt KA, Ostfeld RS (2003) Songbird populations in fluctuating environments: Predator responses to pulsed resources. Ecology 84:406-415

Schoener TW (1971) Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404

Schultz E, Warner R (1989) Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces: Labridae). Evolution 43:1497-1506

Schultz ET, Warner RR (1991) Phenotypic plasticity in life history traits of female *Thalassoma bifasciatum* (Pisces: Labridae): 2. Correlation of fecundity and growth rate in comparative studies. Env. Biol. Fish. 30:333-344

Sears ALW, Holt, RD and Polis, G.A. (2004) Feast and famine in food webs: the effects of pulsed productivity, The University of Chicago Press, Chicago

Seber GF (1984) Multivariate observations, John Wiley and Sons, New York, USA

Shapiro DY, Hensley DA, Appeldoorn RS (1988) Pelagic spawning and egg transport in coral reef fishes - a skeptical overview. Env. Biol. Fish. 22:3-14

Shima JS, Findlay AM (2002) Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. Mar. Ecol. Prog. Ser. 235:303-309

Sinclair AE, Krebs CJ (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Phil. Tran. Roy. Soc. Lon. Ser. B Biol. Sci.357:1221-1231

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129-1157

Southwood T, May RM, Hassell MP, Conway GR (1974) Ecological strategies and population parameters. American Naturalist 108:791-804

Srinivasan M (2007) Recruitment in time and space: the dynamics and distributions of reef fish populations on a low latitude coral reef. PhD Thesis, James Cook University

Srinivasan M, Jones GP (2006) Extended breeding and recruitment periods of fishes on a low latitude coral reef. Coral Reefs 25:673-682

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Theilacker GH (1978) Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull. 76:403-414

Thresher RE (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. Mar. Ecol. Prog. Ser. 10:137-145

Vigliola L, Meekan MG (2002) Size at hatching and planktonic growth determine post-settlement survivorship of a coral reef fish. Oecologia 131:89-93

Vondracek B, Wurtsbaugh WA, Cech JJ (1988) Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. Env. Biol. Fish. 21:45-57

Wainwright P (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecology 69:635-645

Warner R (1988) Traditionality of mating-site preferences in a coral reef fish. Nature 335:719-721

Watanabe T (1982) Lipid nutrition in fish. Comp. Biochem. Physiol. B Biochem. & Mol. Biol. 73:3-15

Williams DM (1991) Patterns and processes in the distribution of coral reef fish. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, p 437 - 473

Williams KS, Smith KG, Stephen FM (1993) Emergence of 13-yr periodical cicadas (Cicadidae, Magicicada): phenology, mortality, and predator satiation. Ecology 74:1143-1152

Wilson DT, McCormick MI (1997) Spatial and temporal validation of settlement marks in the otoliths of tropical reef fishes. Mar. Ecol. Prog. Ser. 153:259-271

Withers PC (1992) Comparative animal physiology, Saunders College Publishing, Orlando

Witman JD, Genovese SJ, Bruno JF, McClaughlin JW, Pavlin BI (2003) Massive prey recruitment and the control of rocky sub-tidal communities on large spatial scales. Ecol. Monog. 73:441-462

Wootton RJ (1990) Ecology of teleost fishes, Chapman and Hall Ltd, London

Yang LH (2004) Periodical cicadas as resource pulses in North American forests. Science 306:1565-1567

Yang LH, Naeem S (2008) The ecology of resource pulses. Ecology 89:619-620

Zeller DC (2002) Tidal current orientation of *Plectropomus leopardus* (Serranidae). Coral Reefs 21:183-187