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

https://doi.org/10.25903/2sjs%2Dfc53

TITLE PAGE

The structure and dynamics of spawning aggregations of coral reef fish

Thesis submitted by

John Alexander Brightman CLAYDON Bsc(hons), MappSc

In April 2005

For the degree of Doctor of Philosophy
In Marine Biology
Within the School of Marine Biology and Aquaculture
James Cook University

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STATEMENT ON CONTRIBUTION OF OTHERS

This project was funded by a number of parties: Bernard Dyer paid university fees; time in the field was co-sponsored by the Mahonia na Dari Research and Conservation Centre and Max Benjamin of the Walindi Plantation Resort, Kimbe Bay, Papua New Guinea under the Mahonia na Dari Researcher in Residence Fellowship; The Nature Conservancy paid for flights to Papua New Guinea.

Editorial assistance was given by my PhD supervisors, Geoff Jones and Mark McCormick.

ACKNOWLEDGMENENTS

There are a large number of people without whom this project would never have happened. Firstly, I would like to thank Bernard Dyer for his unfaltering financial support. Max Benjamin, of the Walindi Plantation Resort, Kimbe Bay, New Britain, Papua New Guinea, for access to boats, workshops, fuel, and wonderful food, without which fieldwork would have been impossible. The Mahonia na Dari Research and Conservation Centre, Kimbe Bay, for granting me the position of Researcher in Residence, logistical support, housing me and allowing me to carry out my studies. The Nature Conservancy, both for financial and logistical support. My supervisors, Mark McCormick and Geoff Jones, for their help, expertise and encouragement.

I also wish to thank all those that helped me in the field: Charlotte, Costa, Nina, Sarah, Miguel, Vanessa, Nat, and Jo. I hope it wasn’t too distressful. Thanks to all my friends from Walindi, Mahonia and TNC – my work would have suffered were it not for the “wealth” of Shannon’s local knowledge. A very special thanks to Francis who is sadly no longer with us.

I wish to thank all my neglected friends and family who still tolerate me despite woefully inadequate effort on my part (I can’t blame it all on temperamental phone lines, sorry, Moo). Thanks to Mike for continuing to house me whenever I made it back to Townsville.

Finally, a very special thanks to my long-suffering parents and their tireless emotional and financial support. Your understanding throughout a decade of tertiary education is greatly appreciated.

ABSTRACT

The broad objective of this thesis is to improve the general understanding of the structure and dynamics of spawning aggregations of coral reef fish The specific aims are to identify and characterise: (1) the species of coral reef fishes that formed spawning aggregations, (2) the locations where spawning aggregations were formed, (3) the periodicity with which these aggregations were formed, and (4) individuals' patterns of migration to spawning aggregation sites. All fieldwork was conducted on the inshore reefs of Kimbe Bay, New Britain, Papua New Guinea (5^{o}30'S 150^{o}6'E).

Spawning aggregations of reef fish were located by intensively searching areas of reef on snorkel at all times of the day from before dawn to after dusk. After >2,000hours of observations made between June 2001 to May 2004, 37 species from 6 families were observed forming spawning aggregations at 38 sites spread over 7 reefs. All species were relatively large (none <10cm max T.L.) and all but one species spawned pelagically. There was no relationship between a species' population density and whether it formed spawning aggregations, nor was spawning aggregation formation itself a density dependent phenomenon, with aggregations ranging in size from 3 to 2000 individuals. Most spawning aggregation sites were used by multiple species, with a maximum of 27 species spawning aggregatively at one site of <10x10m.

A selection of spawning aggregation sites were monitored on 3 reefs in order to establish the periodicities with which different species spawned. Of the 13 species for which such periodicities could be established, spawning occurred year round, and all but one species spawned during all 4 lunar quarters. Spawning occurred more often during high tides, but no species spawned predictably more often during either ebb or flood tides. Aggregative spawning was seen at times ranging from dawn (05:45hrs) to dusk (18:00hrs). However, each species had a fixed diel interval during which it spawned. For all species this interval spanned no more than 6 hours, but for most it was less than 2. For the one species with enough data for analysis, *Ctenochaetus striatus*, this diel spawning interval differed significantly between sites within reefs.

The physical and biotic characteristics found at spawning aggregation sites of *Ctenochaetus striatus* were compared to those found at alternative sites. Within spawning aggregation sites, characteristics that varied temporally were compared between times of spawning and times of no spawning. It was predicted that spawning aggregations would be formed at sites and times with characteristics that limited predation on both spawning adults and their pelagically spawned eggs. Characteristics predicted to reduce predation on eggs included: seaward projecting margins of reef, steep slopes, currents flowing rapidly off-reef (as measured by purpose-built devices), and low densities of planktivores. Characteristics predicted to reduce predation on adults included: topographically complex substratum with a large number of holes providing refuge from predators, and low densities of piscivorous fish. The only physical feature consistently distinguishing spawning aggregation sites from alternative locations was that they were found on margins of reef that projected seawards, rather than flatter or concave margins. However, many seaward projections were not used as spawning aggregation sites, and any potential anti-predatory benefit from this feature was likely to be outweighed by: (1) the greater biomasses of planktivores found at spawning aggregation sites, (2) the frequently observed predation on recently spawned eggs, and (3) certain species of egg predator being attracted to spawning aggregation sites at times of spawning. Spawning aggregations were not formed at distinctive sites with regard to current speed or direction, and there was no difference between the currents at times of aggregative spawning and those at other times within sites.

Individuals' patterns of migration from home ranges to spawning aggregations were documented following an extensive tagging program of *Ctenochaetus striatus*. Tagged individuals were consistently resighted within limited home ranges (max. diameter averaging <13m). Tagged individuals were seen in spawning aggregations on a total of 549 occasions at 13 sites on 3 reefs. The maximum distance migrated was 291m. No tagged individuals were witnessed spawning at more than one site. Most resighted individuals migrated to the spawning aggregation site that was closest to their home range. However, the few individuals that migrated to sites further away always spawned at sites where the spawning aggregation was larger than that found closest to their home range. Neither the size nor the sex of individuals limited migration distance. However, males migrated more frequently than females, and larger females migrated more frequently than smaller ones. Migration distance did not affect the frequency with which individuals spawned.

The notion that spawning aggregations are formed at intrinsically beneficial sites and times is not supported by the results of this study. Strong theoretical arguments are proposed that question the mechanisms by which such adaptation could arise. It is concluded that the sites and times of spawning aggregation formation in *Ctenochaetus striatus* in Kimbe Bay are not adaptive beyond their clarity as cues that enable conspecifics from home ranges with limited or no overlap to synchronise spawning in space and time. Patterns of spawning aggregation formation and migration suggest that tradition plays a more significant role than resource assessment in determining where and when individuals spawn. The use of small species of aggregative spawners as biological models has the potential to greatly enhance understanding of spawning aggregation formation in certain species of commercially exploited reef fish.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Background:

Many marine animals migrate to breeding sites at predictable locations and times to form conspecific breeding aggregations. A multiphyletic array of animals are known to display this behaviour, including mammals (e.g. gray whales, Jones et al. 1984), reptiles (e.g. olive ridley turtles, Plotkin et al. 1997), fishes (e.g. salmonids, Groot & Margolis 1991), crustaceans (e.g. Christmas Island red crabs, Adamczewska & Morris 2001), molluscs (e.g. cuttlefish, Hall & Hanlon 2002), and even polychaetes (e.g. the palolo worm, American Samoa, Caspers 1984). The scale of these migrations ranges from occurring daily over distances of less than a kilometre (e.g. some fish, see Domeier & Colin 1997) to annual migrations over thousands of kilometres (e.g. gray whales, Jones et al. 1984). However, we are still in the early stages of understanding why, where and when breeding aggregations occur.

Spawning aggregations of fish are well known phenomena to fishermen in all of the world's fished oceans. The spatial and temporal predictability of spawning aggregations along with the predictably high yields from low fishing effort (high catch per unit effort) make them attractive targets for fishermen (Johannes 1978, 1981). A wide variety of coral reef fishes are known to form spawning aggregations (see Chapter 2, Domeier & Colin 1997, Claydon 2004, and SCRFA 2004), and while the size of these spawning aggregations and their migration distances may be smaller than those of pelagic and anadromous fishes, such aggregations are dramatic features of coral reef environments. Many spawning aggregations of coral reef fish have been exploited by commercial and artisanal fishermen for centuries (Johannes & Riepen 1995). However, recent increased fishing effort along with the efficiency of modern gears is believed to be threatening the existence of these ecologically important phenomena (Sadovy 1994, Aguilar-Perera & Aguilar-Davilá 1996, Sadovy 1996). Accordingly, interest in and research on spawning aggregations of reef fish have grown over recent years. Whilst this research has primarily been conducted in the context of management of commercially exploited species, understanding the fundamental basis of why, where and when spawning aggregations occur is likely to apply to all species.

1.1.1 Definition of spawning aggregations

For the purposes of this dissertation the definition of spawning aggregations proposed by Claydon (2004) has been adopted: - *spawning aggregations are any temporary aggregations formed by fishes that have migrated for the specific purpose of spawning*. Detailed justification for this definition is given in Chapter 2.

1.1.2 Gaps in knowledge of spawning aggregations:

Randall & Randall (1963) conducted the first study on spawning aggregations of coral reef fish. Since then, over 240 species of reef fishes from 29 families have been documented forming spawning aggregations (see Table 2.1, Chapter 2). However, spawning aggregations of reef fish remain poorly understood. For the majority of these species, little is known of their reproductive behaviour beyond the fact that they have been recorded forming spawning aggregations. Relatively few publications have dealt directly with spawning aggregations of reef fish, and a disproportionate number of the species known to form spawning aggregations come exclusively from two sources, Johannes (1981) and Squire & Samoilys (unpubl.).

A number of factors have hindered progress into research on spawning aggregations. Research has focussed on commercially important species, and primarily concentrated on just two: the Nassau grouper, *Epinephelus striatus*, in the Caribbean and Western Atlantic (Smith 1972, Olsen & LaPlace 1978, Colin et al. 1987, Colin 1992, Tucker et al. 1993, Aguilar-Perera 1994, Carter et al. 1994, Aguilar-Perera & Aguilar-Davilá 1996, Bolden 2000, Whaylen et al. 2004), and, to a lesser extent, the common coral trout, *Plectropomus leopardus*, in the Indo-Pacific (Samoilys & Squire 1994, Samoilys 1997, Zeller 1998, Fulton et al. 2000). Most commercially important species form spawning aggregations for a few days only once a month over a limited spawning season, and spawn at dusk or during the night (see Chapter 2, Domeier & Colin 1997, and Claydon 2004). Individuals of some species are known to migrate to spawning aggregation sites from home ranges over 100km away (Carter et al. 1994, Bolden 2000). Thus, annually, there are few days over which data can be collected from spawning aggregations themselves. Spawning itself may occur at times of the day/night that are most difficult to document. When not forming spawning aggregations, the populations of fish are spread over large and usually undefined areas of reef. The study of spawning aggregations of commercially important species is logistically difficult, potentially expensive and data inefficient. Accordingly, studies rarely focus on more than one species at more than one spawning aggregation site.

Whilst the study of spawning aggregations of smaller more frequently spawning fish that migrate shorter distances is logistically easier, research has concentrated on spawning aggregations of just one such species: the bluehead wrasse, *Thalassoma bifasciatum* (Warner & Hoffman 1980, Warner 1988b, Fitch & Shapiro 1990, Warner 1990b, a, 1995), in the Caribbean and Western Atlantic. Spawning aggregations of this species are better understood than those of any other coral reef fish, yet rarely have lessons learned from *T. bifasciatum* or other smaller-bodied aggregative spawners been employed to improve the understanding of their larger commercially important counterparts or *vice versa*. This is in part due to the artificial distinction between species that form “transient” and “resident” spawning aggregations (Domeier & Colin 1997). These terms merely denote the scale of migrations and the frequency with which spawning aggregations are formed, yet “transient” and “resident” spawning aggregations are often wrongly perceived as two different phenomena (see Chapter 2 and review in Claydon 2004).

One fundamental question that remains unanswered is: how widespread is spawning aggregation formation? Whilst this question can be answered in terms of the number of species of reef fish known to form spawning aggregations globally, it is usually not possible to answer this question in terms of the number of species that form spawning aggregations within a single reef system, single reef or even small area within a reef. Nor can this question be answered in terms of the number of individuals involved or the spatial distribution of spawning aggregation sites. Our understanding is further limited by not knowing how widespread spawning aggregation formation is as a trait amongst conspecifics both within and between populations.

1.1.3 Hypotheses relevant to thesis:

A number of hypotheses have been proposed to explain why spawning aggregations are formed, and where and when they are formed (see Chapter 2 and Claydon 2004). Whilst largely complementary, these hypotheses can be separated into those that identify the intrinsic benefits of spawning in aggregations and those that identify the intrinsic benefits of the location and timing of spawning. Although hypotheses are explored in greater detail in the relevant chapters, it is useful to present a brief overview of the hypotheses that form the conceptual framework of this thesis.

Most of the hypotheses pertinent to this thesis describe strategies that reduce the predatory threats to spawning adults and their eggs during reproductive activities. Spawning in aggregations is proposed to limit this predation by means of predator satiation/saturation: the more potential prey (i.e. the larger the aggregation), the less likely any prey item (either an egg or an adult) will be consumed (Johannes 1978). Additionally, the location and timing of aggregative spawning are believed to reduce predation on spawning adults and/or their eggs in a number of ways:

- spawning at sites and times of reduced predator densities and/or predatory efficiency (Shapiro et al. 1988);
- spawning at sites where the substratum affords spawning adults greater refuge from predation (Shapiro et al. 1988);
- spawning at sites and times where and when currents sweep pelagically spawned eggs more rapidly away from reefs and into waters of reduced planktivore densities (Johannes 1978, Lobel 1978);
- spawning at sites and times coinciding with faster currents that disperse gamete clouds more rapidly and reduce the efficiency with which planktivorous fish can prey on eggs.

Alternatively, the location and timing of spawning may have no intrinsic advantages beyond their clarity as cues that synchronise aggregative spawning (Lobel 1978, Moyer & Zaiser 1981, Colin & Clavijo 1988, Colin & Bell 1991). The benefits of spawning in aggregations may include reduced predatory threats by means of predator satiation/saturation, increased mate choice, and the facilitation of important social interactions, such as those proposed to enable more informed decisions concerning sex change amongst sequential hermaphrodites (Shapiro et al. 1993). Due to a lack of comparative studies, most hypotheses remain largely untested, being supported anecdotally or merely by speculation (see Chapter 2 and Claydon 2004).

1.2 Thesis outline

The broad objective of this dissertation is to improve the general understanding of the structure and dynamics of spawning aggregations of reef fish. The specific aims are to identify and characterise (1) the species of reef fish forming spawning aggregations, (2) the locations where these aggregations are formed, (3) the times when they are formed, and (4) individuals' patterns of migration to spawning aggregation sites. The thesis contains a literature review chapter (Chapter 2), 4 data chapters that address the specific aims of the thesis (Chapters 3 to 6), and a general discussion that synthesises general themes and concepts arising from the thesis as a whole, and discusses directions for future research (Chapter 7). The outlines to data chapters are as follows:

Chapter 3: Spawning aggregations: species, location, and timing

The first data chapter identifies the species forming spawning aggregations on the inshore reefs of Kimbe Bay, New Britain, Papua New Guinea, the sites where these aggregations are formed, and the periodicity with which species form them. This chapter investigates the prediction that spawning aggregations are more likely to be formed by larger, pelagically spawning species found in larger more dense populations. Whether the temporal patterns of aggregative spawning fit a pattern dictated by synchrony with environmental variables or by a species-specific trade-off between piscivory and planktivory is also investigated. Identifying the location and timing of spawning aggregation formation was essential in order to proceed with subsequent chapters.

Chapter 4: Spawning aggregations sites: physical and biotic characteristics

This chapter attempts to characterise spawning aggregation sites with regard to physical and biotic parameters. Specifically, this chapter investigates the role of predation on the location and timing on aggregative spawning, testing 2 hypotheses:

1. The physical characteristics of spawning aggregation sites help to reduce predation on spawning adults and their eggs.
2. Aggregative spawning occurs at sites and times where and when the densities of predators (of both spawning adults and eggs) are low.

The degree to which the reef projected seawards, the incline of the reef slope, the potential refuge from predation (topographic complexity and number of holes in the substratum), and coral cover were compared between spawning aggregation sites and alternative sites. Similarly, the abundance of piscivores and planktivores was also compared between spawning aggregation sites and alternative sites, but also compared within sites between times when spawning aggregations were formed and at times of no such aggregations.

Chapter 5: Spawning aggregation formation and currents

This chapter continues on from Chapter 3, investigating the role of currents in the timing and location of aggregative spawning. Specifically, this chapter investigates whether aggregative spawning occurs at sites and times coinciding with currents that reduce the loss of pelagically spawned eggs to planktivorous predators. Currents were measured using low-tech purpose built devices. The speed and direction of currents were compared both between spawning aggregation sites and alternative sites and between times of aggregative spawning and times of no spawning within spawning aggregation sites themselves.

Chapter 6: Patterns of migration to spawning aggregations

This chapter investigates individuals' patterns of migration to spawning aggregations. Specifically, the influence of an individual's size and sex, the distance of its home range from spawning aggregation sites, and the size of the spawning aggregation are investigated. Four hypotheses were tested:

1. Individuals with home ranges closer to spawning aggregation sites will migrate more frequently than those with home ranges further away.
2. Larger individuals are able to migrate further and more frequently than smaller individuals
3. Males migrate more frequently to spawning aggregations than females
4. Individuals will migrate further to spawn in aggregations with greater numbers of conspecifics.

This was achieved by tagging over 400 individuals of the surgeonfish, *Ctenochaetus striatus*, on three reefs and then documenting individuals' home ranges, the locations where individuals spawned in aggregations, and the frequency with which they spawned.

Fieldwork was carried out on the inshore reefs of Kimbe Bay (5^o30'S 150^o6'E), New Britain, Papua New Guinea (see Figures 2.1 to 2.7). All maps of reefs were constructed from aerial photographs taken from a helicopter in 2004. Data was primarily collected using snorkel or SCUBA. In total, over 2000 hours of observations were made, spanning 190 days between June 2001 to May 2004, and ranging from before dawn to after dusk.

1.3 Publications arising:

Whilst Chapters 3 to 6 have been submitted for peer-reviewed publication, the following paper arising during the PhD project has been published, and is reproduced in full in the Appendices:

Claydon, J. A. B. 2004 Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanography and Marine Biology: An Annual Review* **42**, 265-302.

CHAPTER 2: SPAWNING AGGREGATIONS: REVIEW OF THE LITERATURE

2.1 Introduction

Migration in marine animals is a well-documented phenomenon. For many of these animals, such migrations culminate in the formation of conspecific breeding aggregations, such as the mass egg-laying *arribadas* formed by olive ridley turtles (Eckrich & Owens 1995, Plotkin et al. 1997), the aggregations formed by anadromous salmonids returning to breed in home streams (Groot & Margolis 1991), and the aggregations formed by giant cuttlefish that migrate to the same location to spawn (Hall & Hanlon 2002). Despite being typically regarded as site-attached, sedentary and territorial (Sale 1971, Robertson & Lassig 1980, Fautin & Allen 1992, Patton 1994, Munday et al. 1997), many species of coral reef fishes have also been documented migrating to form breeding aggregations (Domeier & Colin 1997, Claydon 2004). Artisanal fishing in the tropics has exploited some spawning aggregations for centuries (Johannes & Riepen 1995), and studies date back to Randall & Randall (1963). However, research has only recently focussed on spawning aggregations since the recorded disappearance and reduction in size of aggregations targeted by commercial fishing (Sadovy 1994, Aguilar-Perera & Aguilar-Davilá 1996, Sadovy 1996). Whilst the majority of literature concerns these commercially important species, many species of coral reef fishes that are not fished commercially also form spawning aggregations (see Domeier & Colin 1997).

The broad aim of this chapter is to present a review of the literature that addresses spawning aggregations of coral reef fishes. The specific objectives of this review are to: (1) define spawning aggregations of coral reef fish (2) identify which species of coral reef fish form spawning aggregations, (3) identify any unifying characteristics these species may have, (4) critically assess the hypotheses explaining why, when and where spawning aggregations are formed. Extensive descriptions of individual species will not be made as this has been performed comprehensively by Domeier and Colin (1997).

2.2 What are spawning aggregations?

Defining spawning aggregations is problematic and to some extent arbitrary. In a review by Domeier and Colin (1997) a spawning aggregation was defined as "a group of conspecific fish gathered for the purpose of spawning with fish densities or numbers significantly higher than those found in the area of aggregation during non-reproductive periods". Albeit a practical and broadly accepted definition, it may be unnecessarily restrictive. It is based around the assumption that aggregative spawners will be present in greater numbers or higher densities than at non-reproductive times, and will exclude species whose behavioural ecology contradicts this assumption. Whether species are categorised as forming spawning aggregations by this definition will also vary greatly depending on the scale at which fish densities and numbers are measured. The scale of measurement will need to be appropriate for each species in question. In order to circumvent these complications and for the purposes of this thesis, a more simple definition has been adopted: - *spawning aggregations are any temporary aggregation of fish that have migrated for the specific purpose of spawning*.

Domeier & Colin (1997) identified two types of spawning aggregation: resident and transient. Resident aggregations are typified by smaller species of locally abundant populations from the same reef (e.g. *Thalassoma bifasciatum*). Transient aggregations are typified by commercially important species of disperse populations that migrate between reefs (e.g. *Epinephelus striatus*). However, this distinction is somewhat artificial. All spawning aggregations are “resident” in that all the constituent individuals migrating to an aggregation are, by definition, “resident” to the spawning aggregation’s catchment area. All spawning aggregations are “transient” because the aggregations are formed briefly during a period of reproductive activity, and dissipate afterwards. The distinction between “resident” and “transient” *in sensu* Domeier and Colin (1997) is simply a matter of scale and whether species migrate between reefs or not. In fact, the same species could be said to form a “transient” spawning aggregation at one site, but a “resident” one at another. This could arise simply because the former’s catchment area consists of multiple, small, connected reefs (separated by small distances and shallow depths), whilst the latter’s catchment area consists of one large reef isolated by great distance and depth from any others. This, not unlikely, scenario helps to illustrate that whilst the terms "resident" and "transient" may serve to create an artificial distinction between spawning aggregations, they are not intrinsically different. Whether "resident" or "transient" and regardless of the scale of the migration or the periodicity of spawning aggregation formation, the underlying processes are identical: fish migrate to form temporary aggregations for the specific purpose of spawning.

In addition to defining spawning aggregations, it is also necessary to define what group of fishes are classed as *coral reef fishes*. This is also problematic, but for the purposes of this thesis, coral reef fishes are defined as both "those fishes that have obligate associations with coral reef biota" (Choat & Bellwood 1991) and those that are reef-associated, *sensu* Choat and Bellwood (1991).

2.3 Which species spawn in aggregations?

2.3.1 Phylogenetic distribution

Globally, 243 species of reef fish from 29 families have been identified as forming spawning aggregations (see Table 2.1). The highest numbers of aggregatively spawning species are found in the Serranidae, Labridae, Scaridae, Lutjanidae, and Acanthuridae (see Table 2.1 and Figure 2.1a). However, spawning aggregation formation appears to be an uncommon characteristic relative to the total numbers of coral reef species within these families (see Figure 2.1b). Similarly, most species known to form spawning aggregations are found within families represented by proportionally few aggregative spawners (see Figure 2.1b). Whilst all coral reef species of Chanidae spawn in aggregations, this family is only represented by one such species (see Table 2.1 and Figure 2.1b).

Table 2.1. Species of coral reef fish known to form spawning aggregations (updated from Claydon 2004).

ACANTHURIDAE

Acanthurus bahianus[1,2,3]
Acanthurus coeruleus[1,2,3]
Acanthurus guttatus[4]
Acanthurus lineatus[5,6,7,8]
Acanthurus mata[5]
Acanthurus nigricauda[9]
Acanthurus nigrofuscus[6,7]
Acanthurus nigroris[10,11]
Acanthurus olivaceus[9]
Acanthurus triostegus[6,8,12,13]
Acanthurus xanthopterus[9]
Ctenochaetus striatus[6,7,13]
Ctenochaetus strigosus[10,11]
Naso brevirostris[5,9]
Naso hexacanthus[5]
Naso lituratus[14]
Naso lopezi[15]
Naso unicornis[14]
Naso vlamingii[9]
Zebrasoma flavescens[10,11]
Zebrasoma scopas[13]
Zebrasoma veliferum[9]

ALBULIDAE

Albula vulpes[5]

BALISTIDAE

Canthidermis sufflamen[16]
Pseudobalistes flavimarginatus[17]

CAESIONIDAE

Caesio teres[18]
Pterocaesio digramma[19]

CARANGIDAE

Caranx bartholomaei[16]
Caranx ferdau[5]
Caranx ignobilis[5]
Caranx latus[16]
Caranx lugubris[16]
Caranx melampygus[5]
Caranx ruber[16]
Caranx sexfasciatus[15]
Caranx tille[15]
Decapterus macarellus[16]
Elagatis bipinnulata[5]
Gnathanodon speciosus[5]
Megalaspis cordyla[9]
Selar boops[5]
Selaroides sp.[15]

CHAETODONTIDAE

Chaetodon auriga[9]
Chaetodon ephippium[9]
Chaetodon kleinii[9]
Chaetodon lineolatus[9]
Chaetodon melannotus[9]
Chaetodon ornatissimus[10,11]
Chaetodon rafflesi[9]
Chaetodon semeion[9]
Chaetodon trifasciatus[9]
Chaetodon unimaculatus[9]
Chaetodon vagabundus[9]
Heniochus singularis[9]
Heniochus varius[9]

CHANIDAE

Chanos chanos[5]

EPHIPPIDAE

Platax orbicularis[9]

GERREIDAE

Gerres argyreus[5]
Gerres erythrourus[5]
Gerres oblongus[5]

HAEMULIDAE

Diagramma pictum[9]
Haemulon album[20]
Plectorhinchus chaetodonoides[9]
Plectorhinchus chrysotaenia[9]
Plectorhinchus flavomaculatus[9]
Plectorhinchus gibbosus[9]
Plectorhinchus lineatus[9]
Plectorhynchus obscurus[5]
Plectorynchus goldmani[5]

Table 2.1 continued.

HEMIRAMPHIDAE

Rhynchorhamphus goergii[5]

KYPHOSIDAE

Kyphosus bigibbus[15]
Kyphosus cinerascens[15]
Kyphosus vaigensis[15]

LABRIDAE

Bodianus loxozonus[9]
Cheilinus chlorourus[9]
Cheilinus fasciatus[9]
Cheilinus undulatus[9]
Choerodon anchorago[5]
Cirrhilabrus punctatus[9]
Clepticus parrae[2]
Coris aygula[9]
Coris gaimard[10,11]
Epibulus insidiator[9]
Halichoeres hortulanus[9]
Halichoeres prosopeion[9]
Halichoeres tenuisipinis[21]
Hemigymnus melapterus[9]
Lachnolaimus maximus[15]
Macropharyngodon ornatus[9]
Oxycheilinus unifasciatus[10,11]
Pseudocoris yamashiroi[22]
Stethojulis interrupta[21]
Stethojulis trilineata[23]
Thalassoma amblycephalum[21]
Thalassoma bifasciatum[23,24,25,26]
Thalassoma hardwicke[23]
Thalassoma lutescens[22]
Thalassoma purpureum[9]
Thalassoma quinquevittatum[22]

LETHRINIDAE

Lethrinus atkinsoni[9]
Lethrinus crocineus[27]
Lethrinus harak[5]
Lethrinus lentjan[5]
Lethrinus mahsena[27]
Lethrinus miniatus[5]
Lethrinus nebulosus[1,28,29]
Lethrinus olivaceus[15]
Lethrinus xanthochilus[15]
Monotaxis grandoculis[5]

LUTJANIDAE

Aprion virescens[5]
Lutjanus adetii[30]
Lutjanus analis [31,32,33,34,35,36]
Lutjanus apodus[37]
Lutjanus argentimaculatus[5]
Lutjanus argentiventris[38]
Lutjanus bohar[5,14]
Lutjanus campechanus[39]
Lutjanus carponotatus[9]
Lutjanus cyanopterus[40]
Lutjanus gibbus[5,14]
Lutjanus griseus[36]
Lutjanus jocu[40,41]
Lutjanus kasmira[9]
Lutjanus malabaricus[5]
Lutjanus novemfasciatus[38]
Lutjanus rivulatus[30]
Lutjanus sanguineus[27]
Lutjanus sebae[5]
Lutjanus synagris[42]
Lutjanus vitta[15]
Macolor niger[43]
Ocyurus chrysurus[37]
Symphorichthys spilurus[5]
Symphorus nematophorus[5]

MONACANTHIDAE

Amanses scopas[9]
Oxymonacanthus longirostris[9]

MUGILIDAE

Crenimugil crenilabis[5,44]
Liza macrolepis[5,45]
Liza vaigiensis[5]
Mugil cephalus[15]
Neomyxus leuciscus[15]
Valamugil seheli[45]

MULLIDAE

Mulloidichthys flavolineatus[15]
Mulloidichthys vanicolensis[9]
Parapeneus bifasciatus[10,11,15]
Parapeneus multifasciatus[10,11]
Pseudupeneus maculatus[45]

Table 2.1 continued.

MURAENIDAE

Unidentified sp.[47]

OSTRACIIDAE

Ostracion meleagris[10,11]

POMACANTHIDAE

Centropyge bicolor[9]
Pomacanthus imperator[9]
Pomacanthus sexstriatus[9]
Pygoplites diacanthus[9]

POMACENTRIDAE

Chromis cinerascens[9]
Chromis viridis[48]

PRIACANTHIDAE

Heteropriacanthus cruentatus[15]
Priacanthus hamrur[9]

SCARIDAE

Bolbometopon muricatum[14]
Calotomus carolinus[10,11]
Cetoscarus bicolor[9]
Chlororus gibbus[5]
Chlorurus bleekeri[9]
Chlorurus frontalis[15]
Chlorurus sordidus[9,49]
Hipposcarus harid[46,50]
Hipposcarus longiceps[9]
Scarus altipinnis[9]
Scarus chameleon[9]
Scarus dimidiatus[9]
Scarus forsteni[9]
Scarus frenatus[9]
Scarus ghobban[9]
Scarus globiceps[9]
Scarus iseri[23,46,51]
Scarus microrhinos[9,22]
Scarus niger[9]
Scarus oviceps[9]
Scarus prasiognathos[15]
Scarus psittacus[10,11]
Scarus rubroviolaceus[9]
Scarus schlegeli[9]
Sparisoma rubripinne[23,51,52]

SCOMBRIDAE

Scomberomorus commersoni[5]
Acanthocybium solandri[5]
Grammatorcynus bicarinatus[5]
Rastrelliger kanagurta[15]

SERRANIDAE

Anyperodon leucogrammicus[9]
Cephalopholis argus[15]
Cephalopholis boenak[15]
Cephalopholis cruentata[53]
Cephalopholis miniata[15]
Cephalopholis sexmaculata[15]
Cephalopholis sonnerati[15]
Cephalopholis urodeta[15]
Epinephelus adscencionis[54]
Epinephelus chlorostigma[27]
Epinephelus coioides[15]
Epinephelus corallicola[15]
Epinephelus cyanopodus[15]
Epinephelus fulvus[15]
Epinephelus fuscoguttatus[5]
Epinephelus guttatus[3,31,54,55,56,57,58,59,60,61]
Epinephelus itajara[3,31,65]
Epinephelus lanceolatus[15]
Epinephelus maculatus[15]
Epinephelus malabracus[9]
Epinephelus merra[5]
Epinephelus multinotatus[15]
Epinephelus ongus[15]
Epinephelus polyphekadion[14]
Epinephelus spilotoceps[15]
Epinephelus striatus[53,62,63,64,65,66,67,68,69,70]
Epinephelus trimaculatus[15]
Epinephelus tukula[27]
Gracila albomarginata[9]
Mycteroperca bonaci[41,65,66,71]
Mycteroperca microlepis[67,72,73,74]
Mycteroperca phenax[67,72,73,74]
Mycteroperca tigris[66,75,77]
Mycteroperca venenosa[57,58,65,66,67,70,71,76,77]
Paranthias furcifer[71]
Plectropomus areolatus[78]

Table 2.1 continued.

SERRANIDAE continued

Plectropomus laevis[15]
Plectropomus leopardus[5,78,79,80]
Plectropomus maculatus[15]
Plectropomus oligacanthus[15]
Pseudanthias pleurotaenia[9]
Pseudanthias tuka[9]

SIGANIDAE

Siganus argenteus[5]
Siganus canaliculatus[5,29]
Siganus guttatus[15]
Siganus lineatus[5]
Siganus puellus[15]
Siganus punctatus[5]
Siganus sutor[27]
Siganus randalli[15]
Siganus spinus[5]
Siganus vermiculatus[15]

SPARIDAE

Acanthopagrus australis[81]
Acanthopagrus berda[82]
Pagrus auratus[15]

SPHYRAENIDAE

Sphyraena barracuda[5]
Sphyraena genie[5]

Note: [1]Colin 1985; [2]Colin & Clavijo 1988; [3]Colin 1994; [4]Craig 1998; [5]Johannes 1981; [6]Robertson 1983; [7]Myrberg et al. 1988; [8]Randall et al. 1990; [9]Squire and Samoilys unpubl.; [10]Sancho et al. 2000a; [11]Sancho et al. 2000b; [12]Randall 1961a; [13]Randall 1961b; [14]Johannes et al. 1999; [15]SCRFA 2004; [16]Whaylen et al. 2004; [17]Gladstone 1994; [18]Bell & Colin 1986; [19]Thresher 1984; [20]Claro & Lindeman 2003; [21]Nakazono 1979; [22]Colin & Bell 1991; [23]Randall & Randall 1963; [24]Warner & Robertson 1978; [25]Warner & Hoffman 1980; [26]Warner 1988; [27]Robinson et al. 2004; [28]Ebisawa 1990; [29]Hasse et al. 1977; [30]Johannes & Hviding 2000; [31]Schroeder 1924; [32]Rojas 1960; [33]Craig 1966; [34]Claro 1981; [35]Mueller 1994; [36]Domeier et al. 1996; [37]Lindeman et al. 2000; [38]Sala et al. 2003; [39]Moe 1963; [40]Domeier & Colin 1997; [41]Carter & Perrine 1994; [42]Reshetnikov & Claro 1976; [43]Myers 1989; [44]Helfrich & Allen 1975; [45]Johannes & Yeeting 2001; [46]Colin & Clavijo 1978; [47]Kuiter & Debelius 1994; [48]Lewis 1997; [49]Yogo et al. 1982; [50]Gladstone 1996; [51]Colin 1978; [52]Colin 1996; [53]Sala et al. 2001; [54]Colin et al. 1987; [55]Burnett-Herkes 1975; [56]Garciá-Moliner 1986; [57]Beets & Friedlander 1992, 1998; [58]Bullock et al. 1992; [59]Shapiro & Rasotto 1993; [60]Shapiro et al. 1993; [61]Sadovy et al. 1994a; [62]Smith 1972; [63]Carter 1988a; [64]Carter 1988b; [65]Carter 1989; [66]Fine 1990; [67]Colin 1992; [68]Tucker et al. 1993; [69]Aguilar-Perera 1994; [70]Carter et al. 1994; [71]Fine 1992; [72]Gilmore & Jones 1992; [73]Coleman et al. 1996; [74]Koenig et al. 1996; [75]Sadovy et al. 1994b; [76]Olsen & LaPlace 1979; [77]Bannerot 1984; [78]Johannes 1988; [79]Samoilys & Squire 1994; [80]Samoilys 2000; [81]Pollock 1984; [82]Sheaves et al. 1999.

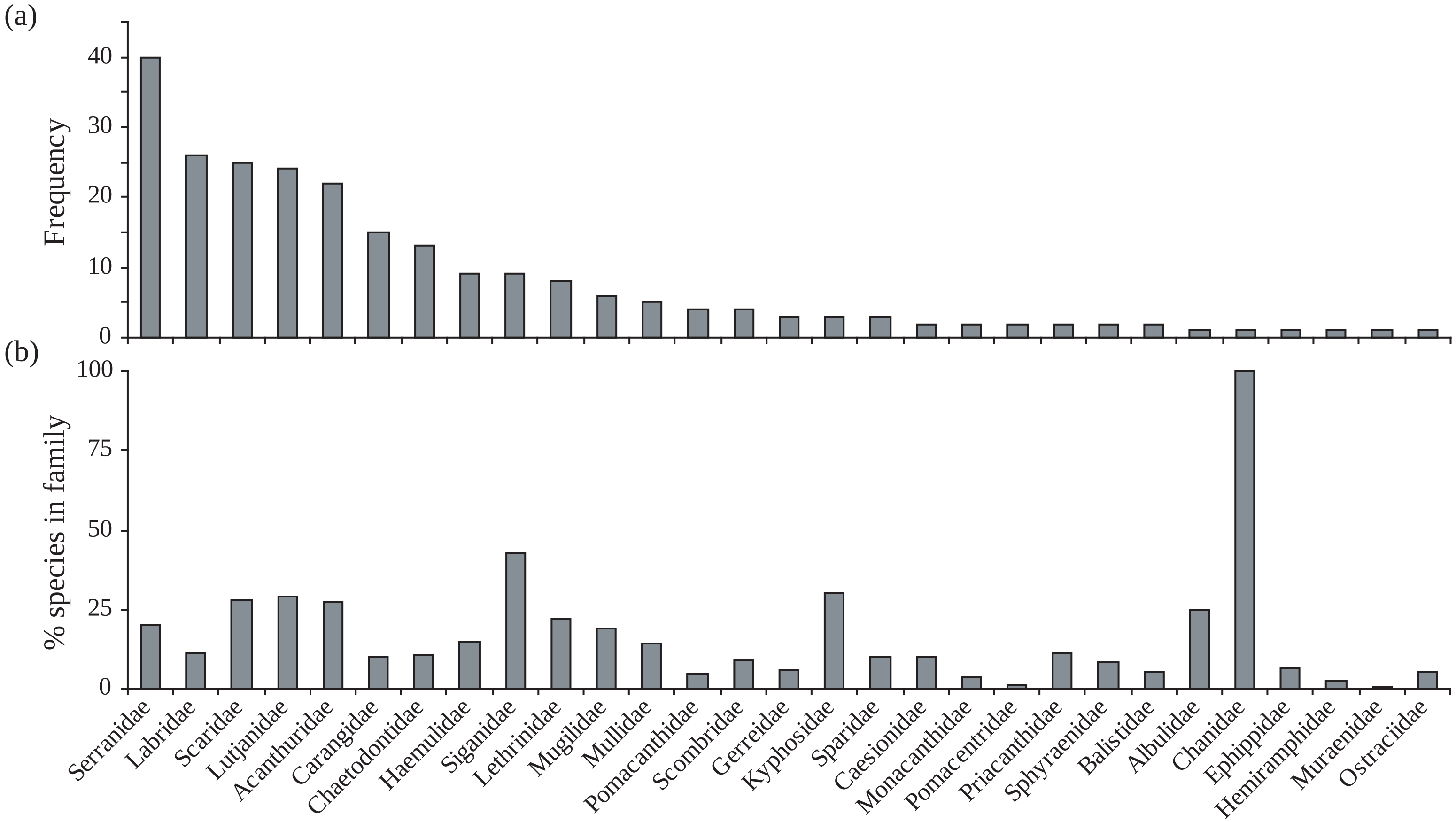

Figure 2.1.(a) The numbers of species of coral reef fishes known to form spawning aggregations from the 29 families identified in Table 2.1. (b) The percentage of coral reef fishes in each family known to form spawning aggregations. Data were compiled from Nelson (1994) and Froese & Pauly (2000).

2.3.2 Body size

Although around 50% of species forming spawning aggregations are less than 50cm in maximum total length, the relative proportion of larger reef fish spawning in aggregations is greater than that of smaller reef fish, and no species with a maximum total length of less than 10cm spawn in aggregations (see Figure 2.2). The absence of species from the smallest size class (<10cm total length) has been attributed to a hypothesised correlation between size and ability to migrate to form spawning aggregations, with smaller species being less able to afford either the energetic cost of migration (energy spent in movement, and time not spent feeding in preferred areas) or the increased risk of predation associated with migration (Domeier & Colin 1997). However, this opinion may attribute too much to the cost of migration. Many small species of fish, especially planktivorous and opportunistic scavenging species, spend the majority of the day moving. Species like the large serranids (e.g. *Epninephelus striatus*) are relatively sedentary fish and migrations will represent a considerable proportion of their energetic budget. Additionally, while many small wrasses migrate daily (e.g. *Thalassoma bifasciatum*, Warner 1995), the larger species may migrate monthly during a limited spawning season. The cumulative distances migrated annually by smaller daily spawning species can be equal to or higher than that of their larger counterparts (see Figure 2.3). Whilst the ability to migrate is an important prerequisite for spawning in aggregations, a species' size may not be a good determinant of this ability.

The prevalence of larger species may be attributable to sampling artefact. Information about spawning aggregations has originated primarily from fishermen (see Johannes 1981). Therefore, it is to be expected that most species identified as being aggregative spawners are commercially or artisanally important, and thus tend to be larger fish. More non-commercial species of aggregative spawner are likely to be identified in the future as research continues (Domeier & Colin 1997).

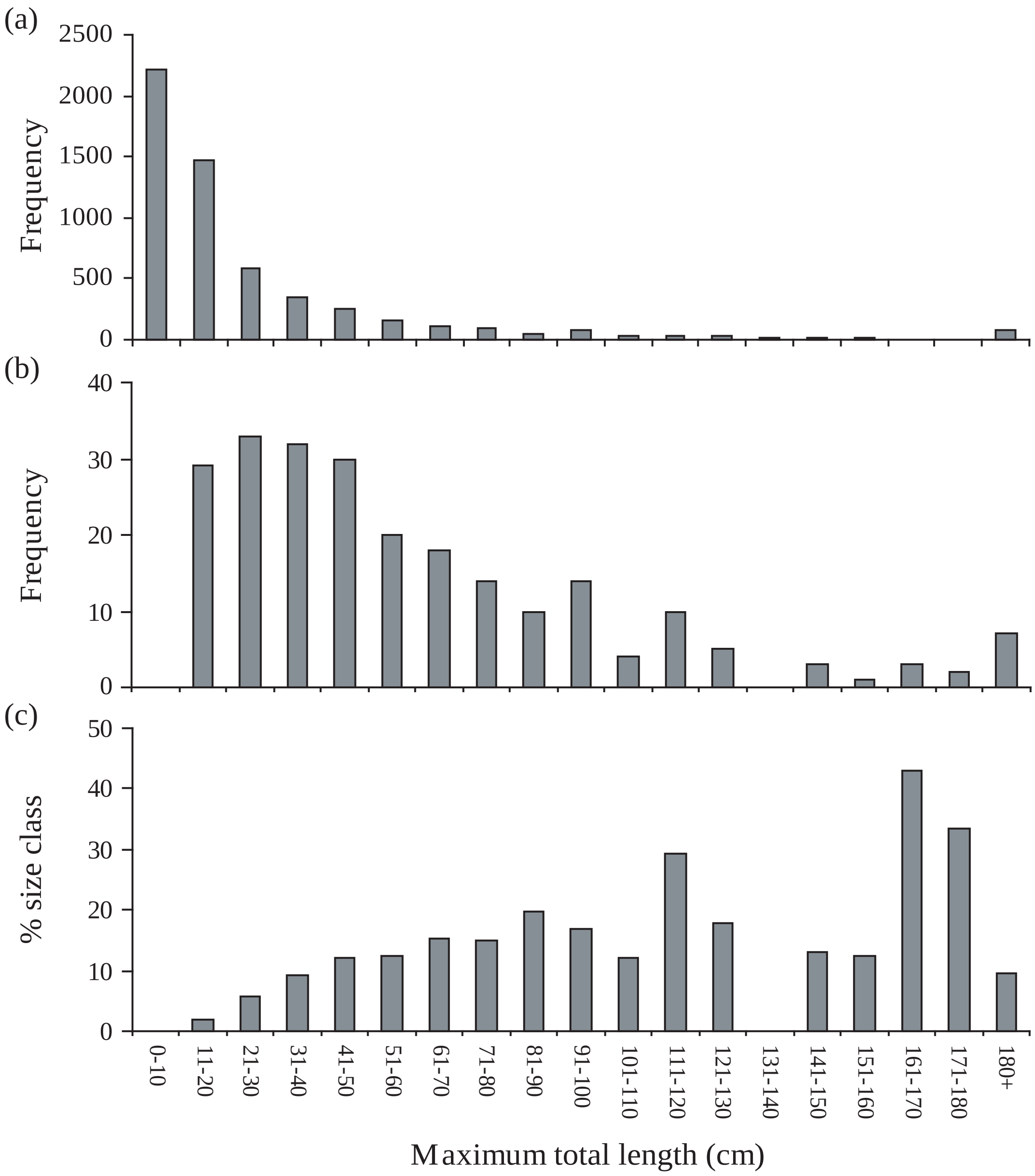

Figure 2.2.(a) Size-frequency distribution of coral reef fishes. (b) Size-frequency distribution of coral reef fishes known to form spawning aggregations. (c) The proportion of each size class represented by species known to form spawning aggregations. The total length data were compiled from sources too numerous to list, but all data can be found in Froese & Pauly (2000).

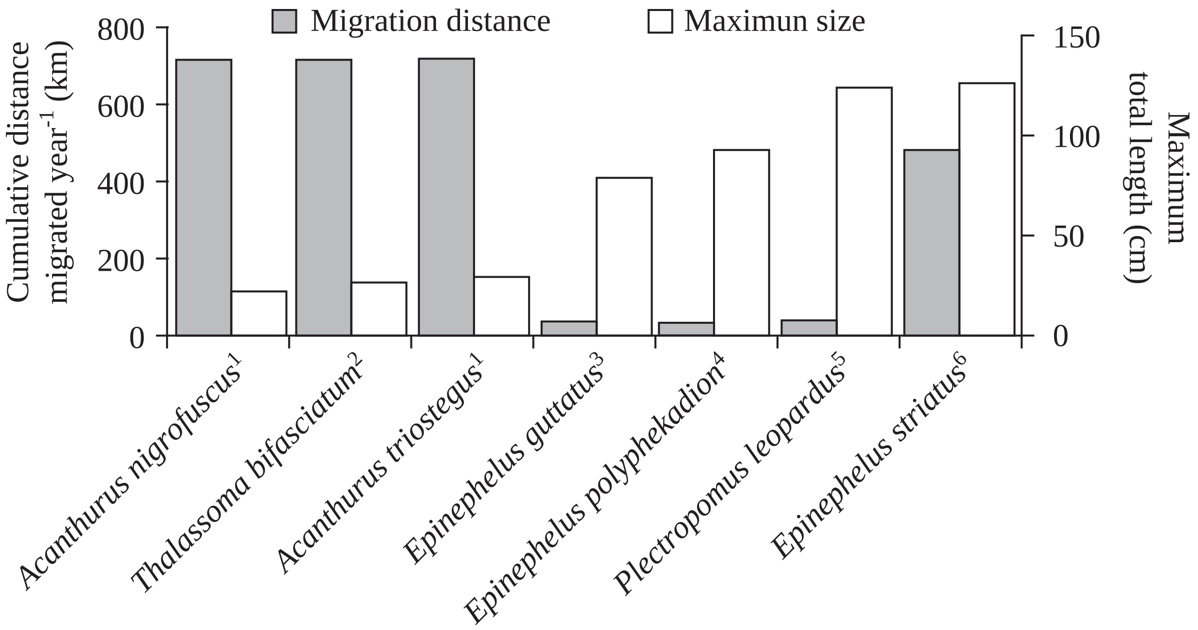

Figure 2.3. The estimated annual cumulative distance migrated by reef fishes with known migration distances to spawning aggregation sites. Cumulative distance was calculated by doubling the maximum distance that species were known to migrate to spawning aggregations, to account for return journeys, and then by multiplying this distance by the annual frequency with which species were known to form spawning aggregations. [1]Robertson (1983); [2]Warner (1995); [3]Burnett-Herkes (1975); [4]Johannes et al. (1999); [5]Zeller (1998); [6]Carter et al. (1994).

2.3.3 Spawning mode

The lack of species from the smallest size class (<10cm maximum total length) forming spawning aggregations may be more a reflection of the spawning mode of fish rather than the larger species' ability to migrate further distances under lower predation pressure. The majority of species known to form spawning aggregations spawn pelagically. Only 3 species exhibit a different mode of spawning: two Balistidae (*Canthidermis sufflamen* and *Pseudobalistes flavimarginatus*), and one Pomacentridae (*Chromis viridis*) have been documented laying demersal eggs in spawning aggregations (Gladstone 1994, Lewis 1997, Whaylen et al. 2004). Apart from the eggs spawned by the Siganidae which are negatively buoyant, adhesive, and demersal (Thresher 1991), fertilised pelagically spawned eggs are buoyant and remain in the water column.

Pelagic spawning appears to be a trait associated with larger species (Munday & Jones 1998). With the exception of the pelagically spawning Callionymidae, the majority of smaller species of reef fish are either brooders or demersal spawners (Munday & Jones 1998) and thus may be precluded from forming spawning aggregations. The only relatively small species (<15cm maximum total length) known to form spawning aggregations are members of the Labridae, Monacanthidae and Serranidae. Labridae and Serranidae are all pelagic spawners (Thresher 1984). Monacanthidae is represented by pelagic spawning and egg laying species (Thresher 1984, Nelson 1994). All three families are represented by species from a wide size range (<10cm to >100cm). The majority of small species (<10cm) come from families that are represented exclusively by small species (see Munday & Jones 1998).

The idea that pelagic spawning is a prerequisite for forming spawning aggregations appears to be supported by the conspicuous absence of all but two of the Balistidae. The Balistidae are relative large and abundant on many coral reefs but are demersal spawners (Thresher 1984, 1991). However, historically, only pelagically spawning species have been recognised as forming spawning aggregations (see Domeier & Colin 1997), and this may have inhibited species with other spawning modes from being considered. In the future, as the reproductive ecology of non-pelagically spawning species becomes better understood, more species with these modes of spawning, particularly the Balistidae, are likely to be recognised as forming spawning aggregations.

2.3.4 Population density

Although only a small proportion of all coral reef fish are known to form spawning aggregations, the species that form spawning aggregations can be among those with the highest densities within their size classes on reefs (with the exception of the smallest size classes, see Figure 2.2) and thus may represent a more common phenomenon, than is reflected by the number of species alone. A species' ability to form spawning aggregations may rely on a combination between its density and its ability to overcome the costs of migration. On average, for species that form spawning aggregations, those with lower densities will have to travel further to form a spawning aggregation of the same size. Therefore, it is to be expected that, below a species-specific threshold density, migration distance will become prohibitively high (see Figure 2.4). Thus, rare or locally uncommon species are unlikely to form spawning aggregations. This may also explain why species known to form spawning aggregations at one location may not display aggregative spawning over the whole of their geographic range (e.g. *Thalassoma bifasciatum*, Fitch & Shapiro 1990).

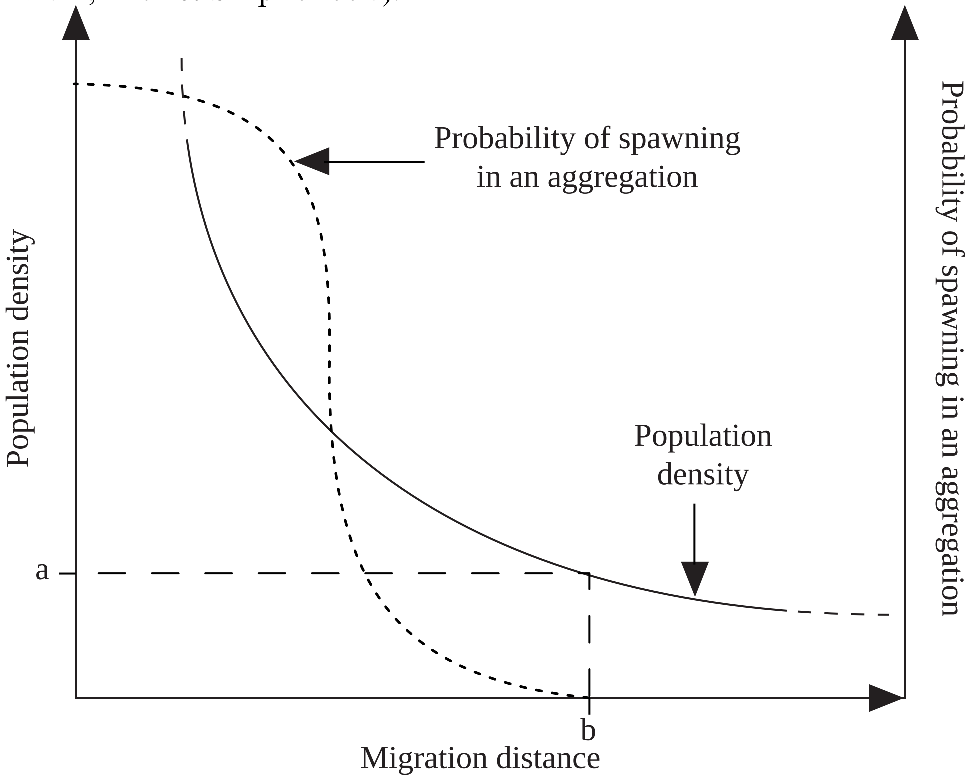

Figure 2.4. The hypothetical interrelationship between population density (full line), migration distance, and the probability that a population will form spawning aggregations (dotted line). When the population density becomes too low (a) the migration distance becomes prohibitively high (b) and spawning aggregations will not be formed.

Whilst population density and ability to migrate further distances under reduced predation pressure may be important in determining whether species spawn aggregatively, both these factors may be related to body size and subsequently phylogeny. Smaller species tend to live at higher densities (Munday & Jones 1998), and larger species are considered, not unequivocally, to be more capable of overcoming the costs of migration (Domeier & Colin 1997, but see Figure 2.3). This may explain why many of the larger predatory species typically found at low densities are also known to form spawning aggregations (see Table 2.1) Unfortunately, the phylogenetic relationships within families of coral reef fish are not presently well described. Until such a time as they are, it will not be possible to assess the relative importance of the interrelated factors of phylogeny, body size, spawning mode and population density in determining whether species form spawning aggregations.

2.4 Where are spawning aggregations formed?

Known spawning aggregations are spatially predictable, being found at the same location over successive spawning seasons (see Domeier & Colin 1997). It is commonly asserted that spawning aggregations are always found at sites on reefs in association with particular physical characteristics, especially promontories, channels and off-reef currents. However, this misconception was highlighted by Domeier et al. (2002), and of the few spawning aggregations with adequately described physical characteristics, only 23% were found on promontories or bommies and only 19% on the down-current margin of reefs, with 54% found on outer reef edges, 47% in channels or passages, and 7% on seaward projections or peninsulas (see Table 2.2). Larger species appear to form spawning aggregations at greater depths than smaller one (15 to <40m compared with <15m, see Table 2.2). Apart from *Epinephelus polyphekadion* which is recorded as forming spawning aggregations exclusively in channels or passages, the physical characteristics of spawning aggregations are not consistent within families or for species where data on multiple sites exist (see Table 2.2 and Domeier et al. 2002). However, it is difficult to make a critical assessment because of the subjective nature of descriptions and the general absence of detailed descriptions of spawning aggregation sites in much of the literature.

The common assertion that spawning aggregations are found in association with particular reef features may derive from the fact that any site is likely to fall into one of very few broad categories. Four reef structures encompass almost all possible reef structures: (1) channels and passages, (2) walls, (3) promontories, and (4) reef slopes. All of the terminology is subjective and greatly dependent on scale. For example, by what distance do two reefs have to be separated before the space between them is no longer considered a channel or a passage? How steep does the incline of a reef have to be in order that it be termed a wall rather than a reef slope? Additionally, the term promontory can be used to encompass a whole range of reef features: projections from the sea floor, sea-mounts, bommies, horizontal projections or penisulars of reef, and submerged plateaus.

Table 2.2. Reef features documented where spawning aggregations are formed.

		Reef Feature						
Species	**Depth (m)**	**Outer Reef Edge**	**Channel/ Passage**	**Promontory/ Bommie**	**Down-Current Margin**	**Seaward Projection**	**Other**	**Reference**
ACANTHURIDAE								
Acanthurus guttatus	/		√		√			1
Acanthurus guttatus	4-7	√	√					2
Acanthurus lineatus	3-7	√			√			3
Acanthurus lineatus	3-7	√				√		3
Acanthurus lineatus	3-5	√	√		√			2
Acanthurus lineatus	/	√		√				1
Acanthurus mata	/						Reef Flat	1
Acanthurus nigrofuscus	9	√		√		√		4
Acanthurus nigrofuscus	2-5	√	√		√			3
Acanthurus nigrofuscus	2-5	√						3
Acanthurus nigrofuscus	<8	√			√			3
Acanthurus triostegus	7		√					5
Acanthurus triostegus	5-7	√	√		√			3
Acanthurus triostegus	/	√	√					1
Acanthurus triostegus	<1-6		√		√			2
Ctenochaetus striatus	9	√		√		√		4
Ctenochaetus striatus	/	√	√		√			3
Ctenochaetus striatus	/	√			√			3
Ctenochaetus striatus	2-7		√		√			6
Naso brevirostris	/		√					1
Naso hexacanthus	/		√					1
Naso unicornis	/	√						1
Paracanthus hepatus	7-8	√			√			3
Zebrasoma scopas	3-6		√	√				5

Table 2.2 continued

		Reef Feature						
Species	**Depth (m)**	**Outer Reef Edge**	**Channel/ Passage**	**Promontory/ Bommie**	**Down-Current Margin**	**Seaward Projection**	**Other**	**Reference**
ALBULIDAE								
Albula vulpes	/	√						1
HEMIRAMPHIDAE								
Rhynchoramphus goergii	/	√						1
CARANGIDAE								
Caranx ignoblis	/	√						1
Selar boops	/	√						1
CAESIONIDAE								
Caesio teres	<2		√	√				7
GERREIDAE								
Gerres abbreviatus	/	√	√					1
Gerres oblongus	/	√	√					1
LABRIDAE								
Cheilinus undulatus	/	√					Reef Walls	8
Choeredon anchorago	/	√						1
Pseudocoris yamashiroi	1-3		√	√				9
Thalassoma amblycephalum	5-7		√	√				9
Thalassoma bifasciatum	7	√				√		10
Thalassoma bifasciatum	<2			√				11
Thalassoma hardwicke	1		√		√			2
Thalassoma lutescens	4-6		√	√				9
Thalassoma quinquenittatum	/		√	√				9
Thalassoma quinquenittatum	1		√		√			2

Table 2.2 continued

		Reef Feature						
Species	**Depth (m)**	**Outer Reef Edge**	**Channel/ Passage**	**Promontory/ Bommie**	**Down-Current Margin**	**Seaward Projection**	**Other**	**Reference**
LETHRINIDAE								
Lethrinus harak	/						Outer lagoon of fringing reef	1
Lethrinus miniatus	/	√					Outer and inner edges of barrier reef	1
Monotaxis grandoculis	/	√					Bottom of reef slopes	1
LUTJANIDAE								
Lutjanus argentimaculatus	/	√					Deep water in lagoon	1
Lutjanus bohar	/	√						1
Lutjanus cyanopterus	2-10			√				12
Lutjanus gibbus	/	√						1
Lutjanus jocu	2-10			√				12
Symphoricthys spilurus	/	√						1
Symphorus nematophorus	/	√						1
SCARIDAE								
Bolbometopon muricatum	/		√					1
Chlororus gibbus	/	√		√				1
Hipposcarus harid	/	√		√				1
Scarus iseri	20	√		√				11
Epinephelus striatus	/			√				13
Sparisoma rubripinne	20	√		√				11

Table 2.2 continued

		Reef Feature						
Species	**Depth (m)**	**Outer Reef Edge**	**Channel/ Passage**	**Promontory/ Bommie**	**Down-Current Margin**	**Seaward Projection**	**Other**	**Reference**
SERRANIDAE								
Epinephelus fuscogutattus	/	√	√					14
Epinephelus polyphekadion	12-35		√					14
Epinephelus polyphekadion	12->35		√					14
Epinephelus polyphekadion	7-42		√					14
Epinephelus polyphekadion	/		√					15
Epinephelus polyphekadion	25->60		√				Reef Wall	16
Epinephelus polyphekadion	/		√					17
Epinephelus polyphekadion	/		√					18
Epinephelus polyphekadion	/		√					19
Epinephelus polyphekadion	/		√					20
Epinephelus striatus	25-30	√			√	√		21
Epinephelus striatus	27-30	√				√		22
Epinephelus striatus	/	√						23
Epinephelus striatus	/	√						24
Epinephelus striatus	29-38		√				Spurs and Grooves	25
Epinephelus striatus	18-21			√			Inshore from reef within <500m from shore	22
Plectropomus areolatus	/		√					8
Plectropomus laevis	/	√		√				8
Plectropomus laevis	/	√						26
Plectropomus leopardus	20-25		√					27
Plectropomus leopardus	15-20	√			√			28

Table 2.2 continued

Species	Depth (m)	Reef Feature Outer Reef Edge	Channel/ Passage	Promontory/ Bommie	Down-Current Margin	Seaward Projection	Other	Reference
SIGANIDAE								
Siganus canaliculatus	/		√					29
Siganus canaliculatus	/	√						1
Siganus lineatus	20	√	√					1
SUMMARY: Number of Times Reef Feature Documented	/	**47**(46%)	**39**(38%)	**19**(17%)	**15**(15%)	**6**(6%)		

Decreasingly Documented Reef Feature

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[1]Johannes 1981; [2]Craig 1998; [3]Robertson 1983; [4]Myrgerg et al. 1988; [5]Randall 1961b; [6] Randall 1961a; [7] Bell & Colin 1986; [8] Johannes & Squire 1988; [9] Colin & Bell 1991; [10] Warner 1995; [11] Randall & Randall 1963; [12] Heyman et al. 2001; [13] Colin 1978; [14] Johannes et al. 1994; [15] D. Wase, personal communication in Rhodes 2002; [16] Rhodes & Sadovy 2002; [17] Johannes & Lam 1999; [18] Passfield 1996; [19]Kulbiciki personal communication in Rhodes 2002; [20]Loubens 1980; [21]Colin et al. 1987; [22]Colin 1992; [23]Burnett-Herkes 1975; [24]Smith 1972; [25]Sala et al. 2001; [26]Carlos & Samoilys 1993; [27]Samoilys 1997; [28]Zeller 1998; [29]Hasse et al. 1977.

The spatial predictability of known spawning aggregations may assign unwarranted importance to the physical features of the sites where these aggregations are found. The flawed argument is that if a site is consistently used, then the characteristics of that site must enhance the fitness of the spawners in some fashion. However, whilst the general location of a spawning aggregation may be predictable, its precise location within that area may not be (Shapiro et al. 1988, Shapiro et al. 1993, Sadovy et al. 1994b). This can be explained in three ways:

(1) Preferable reef features, enhancing the fitness of spawners, may be absent in areas where the precise location of spawning aggregations is more variable. Therefore, there is no selective advantage to spawning consistently in any single precise location. The smaller the catchment area of a spawning aggregation, the less likely the area is to encompass preferable reef features from which to spawn. Therefore, one would expect the precise location of spawning aggregations to be more variable the shorter the migration distance. However, from the limited data available, the opposite appears to be the case (Shapiro et al. 1988, Shapiro et al. 1993, Sadovy et al. 1994b).

(2) Reef features at different locations may enhance the fitness of the spawners only in a limited or specific set of environmental conditions. When these environmental requirements are not met at one precise location, the aggregation is formed at another where the physical characteristics of the reef do enhance fitness in these environmental conditions. Thus the spawning aggregation fine-tunes its precise location to match environmental conditions. The only environmental conditions likely to vary are hydrodynamic, but no studies have examined the hydrodynamic regime in spawning areas on a scale fine enough to investigate this.

(3) The fitness of aggregative spawners is not enhanced by the presence or absence of physical features at their sites of spawning, and thus preferable features *per se* do

> not exist. However, the idea that spawning sites are selected arbitrarily appears to be contradicted by the numerous reports of many species forming spawning aggregations at the same site (Randall & Randall 1963, Thresher 1984, Thresher & Brothers 1985, Bell & Colin 1986, Colin & Bell 1991, Colin 1996, Johannes et al. 1999, Sancho et al. 2000b).

Whilst known spawning aggregations are spatially predictable, the above data suggest that undiscovered spawning aggregations cannot be predictably located from the physical structures of reefs. However, a GIS approach has proved useful in locating previously unknown spawning aggregations of Lutjanids in Belize (W. Heymen, unpubl.), and operators in the live reef food fish trade have employed fishermen to locate likely sites of spawning aggregations from spotter planes (Johannes 1997). The former used bathymetric charts to identify areas with probable current convergence. The latter relied on fishermen being able to locate spawning aggregations from the visible physical characteristics of reefs. How successful these fishermen were in locating spawning aggregations, and the criteria they used are unknown.

The Society for the Conservation of Reef Fish Aggregations (SCRFA) is compiling a database (SCRFA 2004) which is likely to reveal any patterns that exist in the physical characteristics of spawning aggregation sites. However, SCRFA is unlikely to make any such patterns public knowledge for fear that this will lead to further exploitation of previously undiscovered spawning aggregations.

2.5 When are spawning aggregations formed?

Spawning aggregation formation can also be predictable in time. There are four levels to the periodicity of spawning aggregations: seasonal, lunar, diel and tidal. Assigning periodicity to the occurrence of spawning aggregations requires lengthy and systematic sampling, and for this reason knowledge beyond the level of the season is unknown for many species. Many of the spawning aggregations of the Serranidae are formed in association with states of the moon (especially the full and new moons) during limited seasons, but whether spawning occurs at a particular state of the tide or time of day is largely unknown (see Table 2.3). Spawning in association with states of the moon is also displayed by the Acanthuridae, Scaridae and Labridae (see Table 2.3). However, spawning aggregations of these families display a range of periodicities, including being formed daily, on the ebb tide, at certain times of the day, during limited spawning seasons or year-round, and differences within species are common between locations (see Table 2.3). The seasonal and lunar periodicity of spawning aggregation formation of Serranidae also differs within species at different locations and can vary substantially at locations that are relatively close to one another (see Table 2.3). The seasonal differences of *Epinephelus striatus* spawning aggregations at different locations in the Caribbean and western Atlantic are believed to be associated with water temperature (Colin 1992), but no such association has been proposed to account for the different seasons of other tropical serranids throughout the world.

Table 2.3 The periodicity of spawning aggregations of species with data from multiple locations.

Species/Country	Location	Season	Lunar	Tidal	Time of Day	Reference
ACANTHURIDAE						
Acanthurus lineatus						
American Samoa	/	Year round	/	/	Dawn	Craig 1998
Australia	Lizard Island	December	/	Ebb	/	Robertson 1983
Palau	Peleliu	April	New	/	/	Johannes 1981
Palau	Koror Island	February-April	Prior to Full	Ebb	/	Johannes 1981
Acanthurus triostegus						
American Samoa	/	Year round	/	/	Dusk	Craig 1998
Hawaii	/	December-July	12-2 Days before Full	/	/	Randall 1961a
Palau	/	May-August	After New	/	/	Randall 1961b
Seychelles	Aldabra Atoll	November-December	/	Ebb	/	Robertson 1983
Acanthurus nigrofuscus						
Red sea	/	June-September	Daily	/	/	Myberg et al 1988
Seychelles	Aldabra Atoll	November-December	Before New/Full	Ebb	/	Robertson 1983
Australia	Lizard Island	February-April	/	Ebb	/	Robertson 1983
Palau	/	January-April	5-7days before new/full	Ebb	/	Robertson 1983
Ctenochaetus striatus						
Red Sea	/	June-September	/	/	/	Myberg et al 1988
Seychelles	Aldabra Atoll	August-December	4-7days before full/new	Ebb	/	Robertson 1983
Palau	/	January-April	4-7days before full/new	Ebb	/	Robertson 1983
Society Islands	/	February	Not after new/full	/	/	Randall 1961b
SCARIDAE						
Scarus iseri						
Puerto Rico	South West	August-March[1]	/	/	Afternoon	Colin & Clavijo 1988
Jamaica	/	March-August[1]	/	/	/	Colin 1978b

Table 2.3 continued

Species/Country	Location	Season	Lunar	Tidal	Time of Day	Reference
SERRANIDAE						
Epinephelus fuscoguttatus						
Marshall Islands	/	November-December	/	/	/	Johannes 1981
Palau	/	May-June	New-Full	/	/	Johannes 1981
Solomon Islands	Roviana Lagoon	October-January	/	/	/	Johannes & Lam 1999
Solomon Islands	Marovo Lagoon	February-June	/	/	/	Johannes & Lam 1999
Solomon Islands	Ontong Java	2 spawning seasons yr^{-1}	/	/	/	Johannes & Lam 1999
Epinephelus polyphekadion						
Solomon Islands	Roviana Lagoon	October-January	/	/	/	Johannes & Lam 1999
Solomon Islands	Marovo Lagoon	February-June	/	/	/	Johannes & Lam 1999
Solomon Islands	Ontong Java	2 spawning seasons yr^{-1}	/	/	/	Johannes & Lam 1999
Micronesia	Pohnpei	February-April	1-2 Days prior to Full	/	Dusk-Dawn	Rhodes & Sadovy 2002
Palau	States of Koror & Ngarchelong	January-August	New Moon	/	/	Johannes et al. 1999
Cook Islands		April-June	/	/	/	Passfield 1996
New Caledonia	/	October-February	/	/	/	Loubens 1980
New Caledonia	/	November-January	Full Moon	/	/	Kulbicki, pers. comm. in Rhodes 2002
Epinephelus striatus						
Bahamas	/	December-January	Full Moon	/	Sunset	Colin 1992
Belize	/	December-January	Full Moon	/	/	Carter 1989
Bermuda	/	May-July	Full Moon	/	/	Bardach et al. 1958
Bermuda	/	May-August	/	/	/	Smith 1971
Jamaica	South	March	Full Moon	/	/	Thompson & Munro 1983
Virgin Islands	/	January-February	Full Moon	/	/	Olsen & LaPlace 1978
Bonaire	/	March	/	/	/	E. Newton, pers. comm. in Colin 1992

Table 2.3 continued

Species/Country	Location	Season	Lunar	Tidal	Time of Day	Reference
SERRANIDAE continued						
Plectropomus areolatus						
Palau	/	May-June	Full-New	/	/	Johannes 1981
Solomon Islands	Roviana Lagoon	October-January	/	/	/	Johannes & Lam 1999
Solomon Islands	Marovo Lagoon	February-June	Last Lunar Quarter[2]	/	/	Johannes & Lam 1999
Solomon Islands	Ontong Java	2 spawning seasons yr^{-1}	/	/	/	Johannes & Lam 1999
Solomon Islands	/	March-May	7 days before New	/	/	Johannes & Squire 1988
Plectropomus laevis						
Australia	Northern GBR	September-January	/	/	/	Johannes & Squire 1988
Australia	Northern GBR	November-December	/	/	/	Carlos & Samoilys 1993
Plectropomus leopardus						
Australia	Lizard Island	/	New Moon	/	/	Zeller 1998
Australia	Northern GBR	October-November	Full-New	Ebb	Dusk	Samoilys & Squire 1994
Australia	Northern GBR	November-December	/	/	/	Johannes & Squire 1988
Australia	Southern GBR	November-January	/	/	/	Brown et al. 1994
LABRIDAE						
Thalassoma bifasciatum						
Puerto Rico	/	Year round	/	/	Afternoon[4]	Alvey 1990
Barbados	/	Year round	/	Ebb[3]	/	Hunt von Herbing & Hunte 1991

Key: / Data unavailable; [1] Spawning year round but most intense during dates mentioned; [2] (Johannes 1988); [3] Greater spawning activity during spring tides; [4] Exact time differs from reef to reef.

2.6 Hypotheses

Many of the hypotheses explaining where and when spawning aggregations of reef fish are formed are not specific to aggregative spawners, but may apply to pelagically spawning reef fish in general (e.g. Robertson & Hoffman 1977, Johannes 1978, Shapiro et al. 1988). Although focussing on aggregative spawners, where appropriate, data from non-aggregatively spawning reef fish will be included in critical assessment of the pertinent hypotheses. Shapiro et al. (1988) outlined the lack of quantitative research addressing these hypotheses for pelagically spawning coral reef fish, and over a decade later, the situation has not improved. These hypotheses can be divided into two categories, those that explain the phenomenon of aggregative spawning itself, and those that explain where and when spawning aggregations are formed.

2.6.1 Hypotheses explaining the phenomenon of aggregative spawning:

Predator satiation (saturation) hypothesis (Johannes 1978)

The basis of the predator satiation hypothesis is that, at spawning aggregations, predators are presented with more potential food (eggs or spawning adults) than they can eat (Johannes 1978, and see Figure 2.5a). The act of pelagic spawning not only exposes the released eggs to predators, but also the spawners themselves. The spawning rush typical of pelagic spawners takes individuals away from the relative safety of the reef. Predation on many reef fish has been observed almost exclusively during spawning activities activities (Tribble 1982, Thresher 1984, Moyer 1987, Sancho 2000, Sancho et al. 2000a). The selective advantage is not in when and where the spawning occurs, but in the synchrony of the spawning. Such reproductive synchrony is widespread amongst animal taxa, with evidence of predator satiation documented for cicadas (Williams et al. 1993) and for olive ridley turtles (Eckrich & Owens 1995). However, no studies have been undertaken to test this hypothesis specifically for spawning aggregations of fish. Satiation is a reportedly uncommon phenomenon in piscivorous fish (Essington et al. 2000). It would also seem unlikely for planktivores, a functional group that spends the majority of its daily activity feeding, to become satiated even when feeding on a possibly more nutritious and abundant food source of spawned eggs. Predation rates have been measured at spawning aggregation sites, but usually in the absence of control measurements: the predation rates on adults and on eggs spawned outside of spawning aggregations have not been compared to that found within spawning aggregations. From what little information there is, the reported role of predation (piscivory and egg predation) at spawning aggregation sites ranges from being substantial (Thresher 1984, Moyer 1987) to insignificant (Johannes et al. 1999).

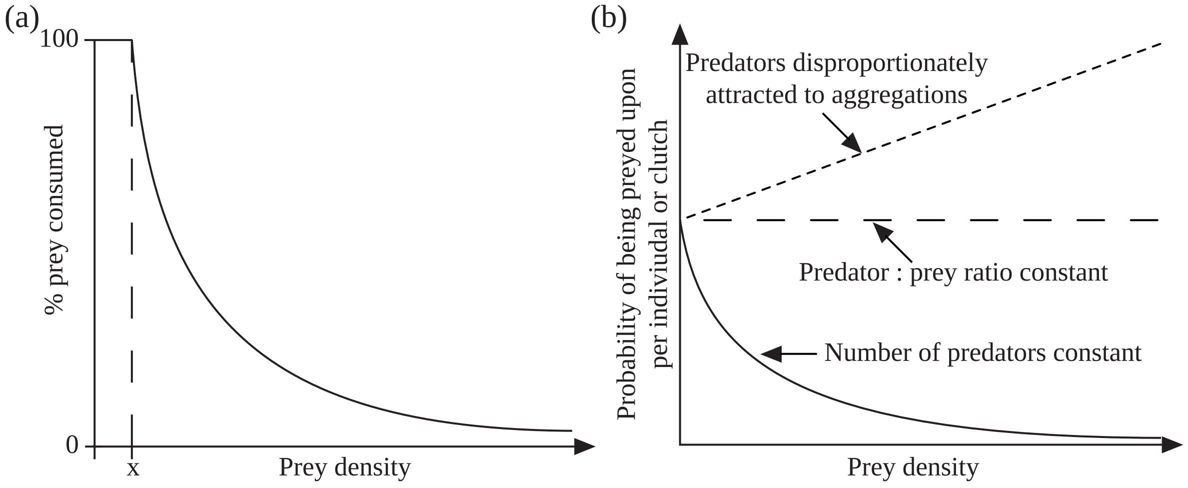

Figure 2.5. (a) The predator satiation hypothesis: the relationship between prey density and the percentage of the prey population that will be consumed. Predators become satiated having consumed x prey. (b) The probability of prey (spawning fish or pelagically released egg) being preyed upon, with increasing prey density for three different predatory scenarios: number of predators constant (full line), predator:prey ratio constant (dashed line), and predators disproportionately attracted to spawning aggregations (dotted line). For all scenarios predators never become satiated.

Whether predators become satiated or not, synchronised spawning can still reduce predation pressure. With a finite number of predators, the greater the number of eggs the less impacted any one clutch is, and the greater the number of spawning adults the less probability there is of any one adult being preyed upon (Johannes 1978). The predation rate of a piscivorous or planktivorous predator will be limited by its handling time (*sensu* Holling 1959), and follow a type II functional response. Predation rate will asymptote causing an increase in potential prey to reduce the probability of any one prey item being preyed upon (see Figure 2.5b). Any degree of satiation will serve to reduce this probability of being preyed upon even further. However, this is a simplistic view that does not account for the fact that the aggregative phenomenon may attract more predators per individual prey than if spawning were to occur in smaller groups or discrete pairs (Randall & Randall 1963, Robertson 1983, Moyer 1987, and see Figure 2.5b).

The synchrony of spawning aggregations can be striking. Fish often spend lengthy periods in aggregations prior to spawning. Once the first spawn occurs, this acts as a trigger for the rest of the aggregation and a rapid sequence of spawning may ensue. The intensity of spawning within a tight time frame reduces the ability of predators to exploit their prey (eggs and spawning fish) even further.

Population structure and social interaction

Aggregative spawning may be important to the social structure of the fish population in question in a number of ways. Firstly, fish living in usually disperse populations, such as commercially important piscivores (e.g. *Epinephelus striatus*) may find locating a mate difficult in the absence of a spawning aggregation. Secondly, the formation of spawning aggregations gives individuals a greater degree of mate selectivity than would be afforded to them if aggregations were not formed. Thirdly, aggregative spawning in disperse populations gives individuals an opportunity to assess the sex ratio of a population. This aggregative social interaction may determine whether individuals change sex accordingly (Shapiro et al. 1993). Without such aggregations, decisions concerning sex change may be made inappropriately. However, it is not known whether disperse populations of aggregative and non-aggregative spawners differ due to the latter's lack of social interaction. Comparisons such as this have not been conducted.

2.6.2 Hypotheses explaining the location and timing of spawning aggregations:

Predator evasion hypothesis (Shapiro et al. 1988)

The predator evasion hypothesis predicts that spawning sites and times afford the spawning adults better protection from predators (Shapiro et al. 1988). Predators are likely to be attracted to spawning aggregations for two reasons: firstly, spawning aggregations represent high concentrations of prey fish, and secondly, the spawning rush associated with many pelagic spawners takes the prey fish up into the water column and away from the relative safety of the reef, leaving them more exposed to predators. The spawning rush up into the water column is also accompanied by an equally or more rapid rush back to the shelter of the reef immediately following gamete release (Robertson & Hoffman 1977). Because pelagic spawning increases exposure to predators, one would expect to find spawning aggregations at sites where predators are absent, and where the reef affords spawners greater protection from predators. There is some evidence that the more weary the species, the greater the potential shelter of the habitat over which it spawns (Beets & Friedlander 1992, Johannes et al. 1999). However, there is no evidence that predation is less efficient at spawning aggregation sites, nor that these sites have lower densities of predators. Although no studies have explicitly investigated this, predation appears to be enhanced at spawning aggregation sites rather than reduced (Robertson 1983, Sancho 2000, Sancho et al. 2000a).

Whilst Domeier and Colin (1997) state that spawners are keenly aware of their surroundings, it is clear that some species are not weary at all, and it is widely reported that these aggregative spawners go into spawning “stupor” (Johannes 1981). In this state, spawning fish are less likely to flee from predators (and from spear guns), and thus the potential shelter from predation afforded by the benthos may never be used by some species. Sharks have been observed feeding freely on a spawning aggregation of acanthurids without disturbing the spawners from their “stupor” (Robertson 1983).

Predator evasion may also be a key factor in dictating what time of day fish spawn. Theoretically, fish should spawn at optimum times when the balance between piscivory and egg predation pressure is least detrimental to fitness, because piscivory is greatest at lower light levels (Hobson 1974, 1975, Danilowicz & Sale 1999), and egg predation is greatest at higher light levels (Hobson & Chess 1978). Optimal spawning time is mediated by the size of the species in question, because the smaller the species the higher the predation pressure. Smaller fish are more likely to spawn at times when predators are least active, and thus at times of higher light levels (Hobson 1974, 1975, Danilowicz & Sale 1999). However, potential egg predators (planktivorous fish) are most active at higher light levels. With the risk of predation being inversely proportional to size, only larger species are able to avoid high egg predation by spawning at times of lower light levels with higher predatory activity. These factors should lead to a negative correlation between size of fish and light intensity at time of spawning. This correlation has been observed at some, but not all locations (Kuwamura 1981). However, the degree of iteroparity of the species in question may also mediate this relationship. The more times an individual reproduces during its lifetime, the less likely it is to jeopardise future reproductive success by reproducing when the risk of predation is high (Mertz 1971, Schaffer 1974, Stearns 1976, 1992, Warner 1998).

Egg predation hypothesis (Johannes 1978, Lobel 1978)

The egg predation hypothesis predicts that adults aggregate to spawn at sites and times that reduce the loss of eggs to predators. This includes sites at down-current areas where eggs are rapidly transported off the reef into deeper water and thus out of the reach of reef associated fishes and invertebrates (Robertson & Hoffman 1977, Johannes 1978, Lobel 1978). This model predicts that the location and timing of spawning aggregation sites coincide with currents that best sweep eggs off the reef. Evidence for this is not equivocal (Shapiro et al. 1988). It is widely perceived that spawning aggregations are found on promontories, and in association with off-reef currents. However, for the most part, this perception is unsubstantiated (see Table 2.2 and Domeier et al. 2002) and the efficacy of egg transport away from reefs is largely anecdotal (Robertson 1983, Thresher & Brothers 1985, Bell & Colin 1986, Moyer 1989, Colin & Bell 1991), and relatively few spawning aggregations are recorded as forming on the down-current margins of reefs (see Table 2.2). In order to investigate this systematically, the rate of egg transport has to be measured at spawning and non-spawning sites at times of spawning activity and of no such activity. This approach would enable valid conclusions as to whether the spawning location and timing actually represents the optimum as far as current driven egg removal is concerned.

Additionally, the dynamics of egg predation are poorly understood, and there is no evidence that egg predation is less at theoretically optimal sites (e.g. reef promontories with an off-reef current). Most studies assume that all planktivores are potential egg predators, but this may not apply to smaller species, and there are at least three different forms of egg predation. Firstly, eggs will be consumed by all planktivores that come into contact with them during their normal planktivorous activity. Although many of these species may be in close proximity and within sight of spawning events, their behaviour is largely unchanged by spawning, and do not actively seek out recently spawned eggs (pers. obs.). Secondly, there are species that specifically target the apex of a spawning rush, anticipating the release of gametes and feeding intensively in the short period before the gamete cloud has dispersed and eggs are no longer efficiently located (e.g. *Melichthys vidua*, Sancho et al. 2000a). Finally, there are species such as the Indian mackerel (*Rastrelliger kanagurta*), the manta ray (*Manta birostris*) and the whale shark (*Rhinchodon typus*) that also target gamete clouds, but are able to feed more efficiently on the gametes due to their filter-feeding habit, swimming in tight circles with their mouths wide open (Colin 1976, Debelius 2000, Heyman et al. 2001). They are able to feed in this fashion for longer periods than the other target egg predators because visual location of individual eggs is not a prerequisite to feeding. Although filter-feeding individuals have the potential to consume the most eggs, the relative loss of eggs to each mode of predation is unknown, and would be hard to quantify.

One would expect pelagic spawning to occur at sites and times of reduced planktivorous activity. This is assumed to be at times of lower light levels when visual procurement of food becomes poor, and when the risk of predation on the planktivores is high. Significantly greater rates of predation on planktonic fish eggs have been reported during the daytime despite these eggs being more abundant at night (Hobson & Chess 1978). Some of the large serranids forming spawning aggregations are known to spawn between dusk and dawn (Colin 1992, Samoilys & Squire 1994, Rhodes & Sadovy 2002), and thus at times of reduced egg predation. The increased risk of predation accompanying lower light levels (Hobson 1974, 1975) may prevent smaller species from also spawning at these times.

The egg dispersal hypothesis (Barlow 1981) versus the larval retention hypothesis (Johannes 1978, Lobel 1978, Lobel & Robinson 1988)

According to the egg dispersal hypothesis, spawning sites and times are expected to be synchronised with currents that disperse eggs and larvae further distances. This long distance dispersal is believed to increase the probability of survival as, once hatched, the larvae are more likely to find a reef upon which to settle (Barlow 1981). This is directly opposed to the larval retention hypothesis which argues that eggs are released at sites and times of favourable currents so that resultant larvae are more likely to return to their natal reefs (Johannes 1978, Lobel 1978, Lobel & Robinson 1988b). Studies that support the egg dispersal hypothesis have measured current patterns on a very broad scale (e.g. Roberts 1997). This approach is likely to be flawed. When eggs are released at a spawning site, these eggs become passively transported plankton in the local currents of that reef. The eggs will not be affected by the oceanic currents until they drift into them, which may never happen. Long distance transport of eggs and larvae may occur but this dispersal will not necessarily increase offspring survival.

Although only one study has directly demonstrated self-recruitment of reef fish (Jones et al. 1999), there is a large body of indirect support for the existence of self-recruiting populations of fish. Jones et al. (1999) listed five such lines of evidence: (1) genetic subdivision of some marine species (Bell et al. 1982, Planes 1993); (2) the persistence of endemic species with pelagic larvae on small isolated islands which must, by definition, be self-recruiting populations (Hourigan & Reese 1987); (3) the persistence of new populations established from marine introductions (Baltz 1991); (4) the persistence of populations with no upcurrent source (Schultz & Cowen 1994), and (5) the behaviour of larvae in the vicinity of reefs (Stobutzki & Bellwood 1994, Doherty & Carleton 1997, Leis & Carsonewart 1997, Stobutzki 1997, Stobutzki & Bellwood 1997, Stobutzki 1998, Stobutzki & Bellwood 1998).

The fact that larvae may return to their natal reefs is not conclusive support for the larval retention hypothesis. A greater percentage of surviving larvae may have returned to the reef if they had been spawned from a “superior” location or time. However, there is considerable circumstantial evidence. Albeit not well documented in the literature, it is often asserted that spawning aggregations are found on the lee of reefs. This is usually accompanied by some form of eddy or gyre off the leeward margin of the reef. Such areas are believed to be favoured as reef fish spawning locations (Hattori 1970). Theoretically, these gyres have the potential to retain planktonic eggs close to the reef, yet away from reef dwelling predators. However, the ability of these gyres to retain planktonic eggs is largely anecdotal. The most convincing of these anecdotes is a report that blood from injured Second World War troops remained undispersed for days off the leeward tip of Pelelieu, Palau (Johannes 1978). This becomes even more compelling in the context of egg and larvae retention because local fishermen report that a well established spawning aggregation site exists upcurrent to where the blood was retained (Emery 1972, Johannes 1978). Retention of drogues within Exuma Sound, Bahamas, illustrated the potential of local egg retention (Colin 1995), but did not illustrate that there were superior sites when or times where eggs should be released.

A wide range of animals migrate up-current to spawn which is believed to be an adaptation that offsets the current driven dispersal of eggs and larvae away from adult habitat and therefore helps to close these animals’ life cycles (Sinclair 1988). However, up-current migration is not a well documented phenomenon for aggregatively spawning coral reef fish, with the opposite, down-current migration, well known for *Thalassoma bifasciatum* (Warner 1995), and acanthurids in general (Randall 1961b, Johannes 1981, Robertson 1983, Craig 1998), with both up-current and down-current migration to spawning aggregations reported for *Epinephelus striatus* (Colin 1992).

With increasing research into the swimming capabilities of different stages of larvae, it is becoming evident that currents will have the greatest effect on dispersal during the egg and early larval stages of the fish (Stobutzki & Bellwood 1994, Leis & Carsonewart

1997, Stobutzki 1997, Stobutzki & Bellwood 1997, Stobutzki 1998, Stobutzki & Bellwood 1998). Thus currents may only play a significant role in dispersal or retention during a relatively small temporal window.

Pelagic survival hypothesis (Doherty et al. 1985)

Doherty et al. (1985) argued that dispersal increases the chances of larvae finding resources, food or otherwise, in a patchy environment. This hypothesis has been adapted to explain the location and timing of spawning aggregations (Shapiro et al. 1988, Appeldoorn et al. 1994, Sadovy 1996, Domeier & Colin 1997). From a computer simulation, Doherty et al. (1985) concluded that dispersal by passively drifting enhanced larval survival. In a patchy environment, movement will increase an organism's chances of finding needed resources, but for reef fish larvae, where these resources are planktonic, passive movement by drifting in the plankton will not increase an organism's chances of finding these resources, regardless of the strength of the current. Albeit an oversimplification of the pelagic larval environment, in this context, passive drifting is equivalent to a terrestrial animal remaining stationary. Active larval swimming will enhance their encounter rate with needed resources. The direction of this movement is irrelevant, and could represent larval retention to rather than dispersal from the natal reef, if swimming is against the current. The site and time of spawning will have no effect on a larva's ability to encounter resources because the selective advantage lies in larval swimming, and not in current driven movement.

In order to maximise the chances that some offspring will encounter suitable larval habitat, one would expect pelagic spawners to spread the release of eggs over as broad a temporal window as possible. Some reef fish spawn daily in aggregations (e.g. *Thalassoma bifasciatum* and *Ctenochaetus striatus*, see Domeier & Colin 1997), which may enhance larval survival in this fashion, but within the day spawning occurs over a short time window. Many other reef fish spawn in with lunar periodicity during a limited season (e.g. *Plectropomus leopardus* and *Epinephelus striatus*), and this limited periodicity does not appear to enhance larval survival in the manner described above.

However, the seasonal periodicity of some fish spawning has been linked with seasonally more abundant larval food, and thus may be important in enhancing larval survival (Jones 1980).

Periodicity and location of spawning aggregations - cues for synchrony

Many studies attempt to reveal the selective advantage of the periodicity of some spawning aggregations. Periodicity has been associated with tidal, lunar, and diel patterns (see Table 2.3). Attempts have been made to explain this periodicity in terms of the currents to which eggs are subjected, the presence/absence of predators, feeding patterns of the adults, and indeed to fit all of the above hypotheses. However, few are convincing. It is entirely possible that the precise timing of spawning, whether it be associated with the moon, tides or sun is a mechanism for synchronising reproduction and has no selective advantage beyond its clarity as a synchronising cue (Lobel 1978, Colin & Clavijo 1988, Colin & Bell 1991). The location of spawning aggregations could also be explained in this fashion. Typical structures associated with spawning aggregations such as promontories, bommies, and channels may serve as easily recognisable features upon which to focus spawning aggregations, rather than affording better survival to adults or eggs and larvae (Moyer & Zaiser 1981). This is supported by the fact that physical features of spawning aggregation sites are not consistent for aggregative spawners in general, within their families or at the level of the species (see Table 2.2, and Domeier et al. 2002). This is further supported by work on spawning aggregations of *Thalassoma bifasciatum* in the Caribbean which illustrated that tradition can play a role in the selection of spawning aggregation sites rather than assessment of the quality of the site itself (Warner 1988b).

The most convincing support for this hypothesis is that the periodicity of spawning aggregation formation differs between and within species. For species that form aggregations monthly during a limited spawning season, aggregations typically form either around the new moon or the full moon (see Table 2.3). Both are equally clear cues, and this may explain why the same species may spawn around the new moon at one location and the full at another. For species that form spawning aggregations daily, there is a trend of forming spawning aggregations in association with a clear tidal cue in areas of high tidal amplitude, whereas in areas of low tidal amplitude, and thus with no clear tidal cue, aggregations are formed in association with a time of day (Domeier & Colin 1997). However, the periodicity of daily spawning aggregations has usually been explained, albeit unconvincingly, by the currents associated with the tide or time of day in question.

Spawning aggregation formation by default, not design:

Spawning aggregations may form regardless of whether there is any selective advantage associated with the aggregative phenomenon itself. As discussed, the selective advantage may lie in the location and timing of pelagic spawning as explained by the predator evasion, egg predation, egg dispersal, larval retention, and pelagic survival hypotheses. According to these hypotheses, individuals will spawn at sites and times that best increase their fitness. Because these sites and times will be the same for all conspecifics within a certain area, a spawning aggregation will result by default. The dimensions of the area over which this would occur would be dictated by the trade off between the costs of migration and the advantages associated with spawning at these locations and times. Because some of the hypotheses make overlapping predictions, and many are complementary, it would be difficult to discern which selective forces are responsible for the phenomenon, location and timing of spawning

2.7 Interpreting behavioural traits of open populations, a caveat

There is much debate as to the degree of connectivity and self-recruitment of reef fish populations (see Jones et al. 1999, Shima 1999, Swearer et al. 1999, Sponaugle et al. 2002, Swearer et al. 2002) and thus to the extent of gene flow between populations. However, even very limited gene flow may prevent populations adapting to local conditions (Warner 1991). Therefore, reef fish species are likely to display behaviours that are adaptive for the population at whatever scale the population becomes closed. Despite the uniqueness of all reefs, local adaptation is not likely to be important for much of a species' life history, because many reef structures, environments and habitats are predictable across reefs. However, reproductive success from pelagic spawning is likely to be affected greatly by local environmental conditions because hydrodynamic regimes are highly variable between reefs. Spawning in association with cues such as tidal state may enhance fitness at some locations, but may be inappropriate at others. The behavioural trait will persist at all locations provided connectivity remains. This phenomenon is well recognised (Lott 1991, Shapiro 1991, Warner 1995), and is an important consideration when interpreting observations of reef fish behaviour, and especially when attempting to assign adaptive significance to behaviours displayed by aggregative spawners.

2.8 Conclusion

Globally, 243 species of coral reef fish from 29 families have been identified forming spawning aggregations. This number is likely to rise as more commercially unimportant species are documented forming spawning aggregations. Aggregatively spawning species are all larger than 10cm maximum T.L., most spawn pelagically, and individuals from larger populations with higher densities are more likely to form spawning aggregations. However, the relative importance of body size, spawning mode, population size, population density, and phylogeny in determining whether species form spawning aggregations is hard to assess because these factors are all interrelated. Individual spawning aggregations can be relocated at known sites at predictable times. However, spawning aggregations form over a number of reef structures, with a range of seasonal, lunar, diel and tidal associations that can vary between species and between aggregations of the same species separated by relatively small distances.

Spawning aggregations of reef fish are not well understood. The phenomenon, location and timing of spawning aggregations of reef fish may enhance the survival of pelagic eggs and larvae, increase larvae's chances of recruiting to reefs, natal or otherwise, reduce the risk of predation on adults, and help to regulate the sex ratio of some populations. However, relatively little research has been conducted on spawning aggregations, especially in the Indo-Pacific, and even less research has attempted to answer these questions systematically.

CHAPTER 3: SPAWNING AGGREGATIONS: SPECIES, LOCATION AND TIMING

3.1 Introduction

The ability of marine animals to synchronise behaviours with diel, tidal, lunar and seasonal cycles is well established (Palmer 1932, DeCoursey 1976). Temporal synchrony of reproductive activities is displayed by a multiphyletic array of marine animals. Examples of these include: mass spawning corals on the Great Barrier Reef (Willis et al. 1985), epitoke release by palolo worms in the Pacific (Itano & Buckley 1988), giant cuttlefish spawning aggregations in Australia (Hall & Hanlon 2002), Christmas Island red crab larvae release (Adamczewska & Morris 2001), and egg laying *arribadas* of olive ridley turtles in Mexico (Eckrich & Owens 1995). Whilst corals and other sessile invertebrates are only able to synchronise these activities in time, mobile species are also able to synchronise reproductive activities spatially. This spatial and temporal synchrony of reproductive activities leads to the formation of conspecific breeding aggregations. The most impressive, easily recognisable and well documented of these breeding aggregations involve large species migrating over 100’s of km (e.g. gray whales, Jones et al. 1984), and those that aggregate with 1000’s of conspecifics (e.g. anadromous salmonids, Groot & Margolis 1991, Klemesten et al. 2003). However, identical processes are involved in the formation of breeding aggregations occurring over much more modest scales, with smaller species migrating over shorter distances (e.g. many species of coral reef fishes, Domeier & Colin 1997, Claydon 2004), involving as few as 3 individuals.

In coral reef environments, the reproductive synchrony of fish is manifested best by the 243 species from 29 families that are presently known to form spawning aggregations throughout the world’s coral reefs (see Chapter 2). Many of these form spawning aggregations at predictable sites and times (see Domeier & Colin 1997) and can involve over 100,000 individuals spawning at the same site (*Epinephelus striatus*, Smith 1972). Despite spawning aggregation formation being a well-known phenomenon in coral reef fish, it is not well understood and substantial gaps in knowledge exist. With notable exceptions (e.g. Sancho et al. 2000b), most studies focus on a single species and/or a single site. The species studied are typically large and commercially important, migrating between reefs to form spawning aggregations at specific times of the lunar month over a limited spawning season. Such spawning aggregations are referred to as *transient* and contrast with the *resident* aggregations formed often daily by species that do not migrate between reefs (Domeier & Colin 1997). The distinction between *transient* and *resident* spawning aggregations is merely a matter of scale (see Claydon 2004) and reinforces a misperception that the spawning aggregations formed by large fish are fundamentally different to those formed by smaller ones.

For the purposes of this study, a spawning aggregation is defined *as any temporary aggregation of fish that have migrated for the specific purpose of spawning* (as per Claydon 2004). Whilst the size of spawning aggregations ranges considerably, consisting of as many as 100,000 individuals for *Epinephelus striatus* (Smith 1972), and as few as 30 for *Plectropomus leopardus* (Samoilys & Squire 2002), in order to be described as a spawning aggregation 3 or more individuals have to be aggregated for the specific purpose of spawning. A lower limit higher than 3 individuals would be entirely arbitrary and thus meaningless. Two individuals cannot be regarded as forming a spawning aggregation, despite the fact that the individuals concerned may migrate in a manner identical to those forming spawning aggregations with large numbers of conspecifics.

Spawning aggregations are believed to occur for two primary and complementary reasons: firstly, reproducing within an aggregation is intrinsically beneficial perhaps for social, reproductive or anti-predatory reasons, and secondly, the site and time of spawning are intrinsically beneficial, enhancing the survival of spawning adults and their young (see Claydon 2004). If the benefits from the latter are derived from environmental variables such as spawning pelagically at sites and times coinciding with currents that best sweep eggs away from reef based predators (Robertson & Hoffman 1977, Johannes 1978, Lobel 1978), then all species should go to the same site and spawn at the same time. However, if the time of spawning is dictated by a species-specific trade-off between the threat posed to eggs by planktivorous fish and the threat posed to adults by piscivores, then different species would be expected to spawn at characteristically different times

(Sancho et al. 2000b, Claydon 2004). With planktivory being more intense at high light levels (Hobson & Chess 1978), piscivory being most intense at low light levels (Hobson 1974, 1975, Danilowicz & Sale 1999), and the size of the fish being inversely proportional to its risk of predation, larger fish are expected to spawn at lower light levels and smaller fish at higher light levels. This pattern has been observed at some but not all locations (Kuwamura 1981).

To date, the species of coral reef fish identified as forming spawning aggregations share two characteristics: the overwhelming majority spawn pelagically, and none are smaller than 10cm T.L. (see Chapter 2 and Claydon 2004). Smaller-bodied fish are believed to be prevented from migrating to spawning aggregations because of the prohibitively high threat from predators. It is also believed that a species is more likely to form a spawning aggregations when it is found in large local populations at high densities rather than in small or low density populations (see Chapter 2 and Claydon 2004).

3.1.1 Aims

This study tests the predictions that spawning aggregations are more likely to be formed by larger, pelagically spawning species found in larger, more dense populations. It will also test whether the diel timing of spawning aggregation formation fits a pattern dictated by synchrony with environmental variables or by a species-specific trade-off between piscivory and planktivory.

Specifically, this study aims to:

(1) establish where spawning aggregations are formed, the species forming them and the number of individuals involved;

(2) establish whether there are any temporal rhythms associated with the formation of spawning aggregations; and

(3) identify any unifying characteristics between the species forming spawning aggregations.

Figure 3.1. Study area. Kimbe Bay, West New Britain Province, Papua New Guinea 5°30’S 150°6’E.

Figure 3.2. Study reefs close to the Mahonia na Dari Research and Conservation Centre (MND). See Figures 4 to 7 for more details on location of sites within Kume, Hanging Gardens, Maya's, and Limuka.

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Figure 3.3. Kume reef and sites studied

Figure 3.4. Hanging Gardens reef and sites studied.

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Figure 3.5. Maya's reef and sites studied.

Figure 3.6. Limuka reef and sites studied.

3.2 Methods

3.2.1 Locating spawning aggregations

Spawning aggregations were located by snorkelling around the inshore reefs of Kimbe Bay (5^{o}30’S 150^{o}6’E), New Britain, Papua New Guinea (see Figures 2.1 to 2.7), and noting the species, the number of individuals aggregating, the location and the time of spawning. Non-aggregative pelagic spawning was also recorded. Spawning aggregations were confirmed only by witnessing the release of gametes and if individuals were deemed to have migrated to form the aggregation. Migrations were confirmed by monitoring the sites where spawning was observed to ensure that aggregations were absent from these sites on all occasions other than when spawning occurred. All confirmed spawning aggregations occurred at sites where between 30 to over 100hrs of such monitoring was conducted at times ranging from dawn to dusk. *Ctenochaetus striatus* spawning aggregations were primarily sought after, with many additional species being opportunistically recorded. Three reefs were studied intensively (Hanging Gardens, Maya’s and Limuka). Spawning aggregations of *C. striatus* were also intensively sought after on Kume but other species were largely ignored. Sightings of spawning aggregations on three other reefs (Gava Gava, Luba Luba, and Madaro) were opportunistic. SCUBA was employed to search for spawning aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* on 12 occasions on days leading to the new moon in 2003 and 2004.

Spawning aggregation sites were named arbitrarily or for convenient reference in subsequent chapters (see Figures 2.1 to 2.7). Details of the locations of probable spawning aggregations of *Plectropomus areolatus, Epinephelus fuscoguttatus,* and *Pseudobalistes flavimarginatus* have not been given, because of the sensitivity of such information to the species’ exploitation (Domeier et al. 2002).

3.2.2 Spawning rhythms: seasonal, lunar, diel and tidal:

Over 2000hrs of observations were made, spanning 190 days between June 2001 to May 2004, ranging from before dawn to after dusk, and covering all days of the lunar month. For species other than *Ctenochaetus striatus*, the seasonal, lunar, diel and tidal data from all spawning aggregation sites were combined separately for each species. This was achieved by concentrating observations on a selection of sites where the greatest numbers of species were known to spawn (Hanging Gardens Sites 1 and 3, and Maya's Sites 1 and 4). Additional observations were made at all spawning aggregation sites of *Ctenochaetus striatus* on Hanging Gardens, Maya's and Limuka in order to establish any possible site-specific spawning patterns.

Tidal data were obtained under license from Seafarer®Tides 2001,2002,2003,2004 (Australian National Tide Tables; license no: 884SL). For logistical and safety reasons, early morning observations were only undertaken during periods of high tide. Therefore, for species seen spawning exclusively around dawn, no conclusion could be drawn from the range of tidal heights over which reproduction occurred.

3.2.3 Species presence, abundance and size

In order to assess whether species that formed spawning aggregations were more abundant on the study reefs than those that did not, the abundance of species on Limuka and Hanging Gardens was established from the monitoring data collected since 1997 by Jones et al. (2004). Data for other reefs were not collected. Where species were not recorded in any of Jones et al.'s surveys, but were observed in the present study, abundance was assumed to be amongst the lowest of species found on that reef.

In order to establish whether the tendency to form spawning aggregations was dependent on body size, the sizes of fish found forming spawning aggregations were compared to those not found spawning aggregatively. The presence of reef fishes in Kimbe Bay was taken from Allen & Munday (1996), and the maximum T.L. of species was established from Froese & Pauly (2000). The sizes of individuals seen spawning were also estimated *in situ*.

3.2.4 Data Analyses

G-tests were performed to establish whether the observed distribution of spawning differed significantly ($p<0.05$) from that predicted by sampling effort. Data were pooled where appropriate and a William's correction was employed (Sokal & Rohlf 1995). Such G-tests were performed for both the distribution of spawning over the lunar month and for the distribution of spawning throughout times of the day for all species where sufficient data permitted. G-tests were also performed to establish whether the distribution of tidal characteristics over which a species spawned differed significantly from the distribution predicted to occur within each species' diel spawning interval on the days observations were made. The tidal characteristics tested were time +/- high tide and tidal height. Separate G-tests were performed on tidal characteristics for each site where *Ctenochaetus striatus* spawned, provided enough observations permitted analyses. Predicted distributions were calculated for each site from the distribution of tidal characteristics during the diel spawning interval of *C. striatus* at the site in question on the days that site was observed.

A two-way nested ANOVA was performed to test whether spawning times of *C. striatus* differed significantly between sites and reefs. In the analysis sites were nested within reefs. A one-way ANOVA was also performed to test whether the tidal amplitude in Kimbe Bay differed significantly between days of the new moon, 1st lunar quarter, full moon and 3rd lunar quarter.

STATISTICA 6 statistics package was used for ANOVA. Zar (1999) χ^2 tables were consulted for p-values of G-tests. α-levels for all analyses were 0.05.

3.3 Results

3.3.1 Species identified forming spawning aggregations

Spawning aggregations were confirmed for 37 species of coral reef fish from 6 families, with spawning aggregations of another 5 species from 3 additional families being unconfirmed (see Tables 3.1 & 3.2). 12 of these species have not previously been described as forming spawning aggregations (8 wrasses, *Bodianus mesothorax, Cheilinus trilobatus, Gomphosus varius, Novaculichthys taeniourus, Thalassoma jansenii, Halichoeres marginatus, Halichoeres melanurus* and *Anampses caeruleopunctatus,* the goatfish, *Parupeneus barberinus*, and 2 parrotfish, *Scarus quoyi* and *Scarus spinus*). No species with maximum T.L. of less than 10cm were found spawning in aggregations, with the majority of species being between 21 and 30cm T.L. (see Figure 3.7). Whilst a number of individuals <10cm T.L. were observed spawning in aggregations, none were <5cm T.L. No pattern was found between a species' density on a reef and whether it forms spawning aggregations. In 4 of the 6 nine families (Acanthuridae, Labridae, Scaridae and Siganidae) the species found spawning in aggregations ranged from the most to least abundant, and in all but one of the families with unconfirmed aggregations (Balistidae and Serranidae) only the least abundant but largest species were observed forming spawning aggregations.

With the exception of the two species of Siganidae and the one species of Balistidae, all species spawned pelagic eggs which, when fertilized, are buoyant and drift passively in currents. The two Siganidae, *Siganus lineatus* and *Siganus spinus*, spawned pelagically but their eggs settle on the substratum (Thresher 1984), whilst the Balistidae, *Pseudobalistes flavimarginatus*, guarded a nest in which it lays eggs (Gladstone 1994). Pelagic spawning occurred within 1m of the sea's surface for all species except *Acanthurus olivaceus* (which released eggs from a range of depths between 2 and 15m), *Acanthurus lineatus* (0-3m), *Pygoplites diacanthus* (1-2m), and the non-aggregatively spawning *Centropyge vroliki* (1-2m). Spawning was never witnessed in *Plectropomus areolatus* or *Epinephelus fuscoguttatus* but spawning aggregations were formed on areas of reef with depths between of 5 to 10m and 15 to 25m respectively. The nests of *Pseudobalistes flavimarginatus* were formed in substratum at depths of 5 to 10m.

Most species spawned in discrete pairs within small aggregations (<15 individuals). *Ctenochaetus striatus*, *Acanthurus lineatus*, *Acanthurus nigrofuscus*, *Acanthurus triostegus*, spawned in groups. *Scarus quoyi*, *Stethojulis trilineata*, *Thalassoma amblycephalum*, *Thalassoma hardwicke*, *Thalassoma lunare* spawned in both groups and pairs. Pair spawning of *Parupeneus bifasciatus*, *Chlorurus bleekeri*, *Epibulis insidiator* and wrasses of the genus *Thalassoma* were occasionally seen to have additional male streakers. Of all the species observed spawning pelagically only 3 species were observed spawning exclusively outside of aggregations, with 11 species seen spawning both within and outside of aggregations (see Table 3.3). The spawning behaviour of these 11 species remained unchanged regardless of whether they spawned aggregatively or not.

Interspecifically, the maximum size of spawning aggregations ranged from 3 to 2000 individuals. Intraspecifically, variation was of a similar magnitude: *Acanthurus triostegus* 3 to 200, *Ctenochaetus striatus* 20 to 2000, *Thalassoma hardwicke* 5 to 1000 (see Table 3.1). The size of spawning aggregations also varied substantially over different days for the same species within the same site (e.g. *C. striatus* ranged from <50 to 2000 individuals at Kume Site 2).

Ctenochaetus striatus were found forming spawning aggregations at 29 different sites on less than 7km of reef edge investigated, averaging >1 per 200m of intensively studied reef edge. Over 200 spawning aggregations of this species were observed during the study period.

Table 3.1. Species found forming spawning aggregations on inshore reefs of Kimbe Bay. Sites were named arbitrarily and follow nomenclature in Figures 3.3 to 3.6. Numbers in species' rows correspond to the maximum number of individuals aggregating at that site.

HANGING GARDENS Species	Number of individuals aggregating							HANGING GARDENS Species	Number of individuals aggregating						
	Site 1	Site 2	Site 3	Site #41	Site 4	Site 5	Site 6		Site 1	Site 2	Site 3	Site #41	Site 4	Site 5	Site 6
ACANTHURIDAE:								MULLIDAE							
Acanthurus lineatus	/	/	200	/	/	/	/	*Parupeneus barberinus*	/	/	4	/	/	/	/
Acanthurus nigrofuscus	6	/	5	/	/	/	/	*Parupeneus bifasciatus*	10	/	10	/	/	/	/
Acanthurus olivaceus	/	/	4	/	/	/	/	*Parupeneus multifasciatus*	/	/	/	/	/	/	6
Acanthurus triostegus	/	/	40	/	/	/	/								
Ctenochaetus striatus	600	/	450	400	/	/	60	OSTRACIIDAE:							
Zebrasoma scopas	5	/	3	/	/	10	/	*Ostracion meleagris*	/	/	3	/	/	/	/
LABRIDAE:								POMACANTHIDAE:							
Bodianus mesothorax	4	/	/	/	/	/	/	*Pygoplites diacanthus*	/	/	4	/	/	/	/
Cheilinus fasciatus	3	/	7	/	/	3	/								
Cheilinus trilobatus	4	/	9	/	/	/	/	SCARIDAE:							
Epibulis insidiator	10	/	25	/	/	/	/	*Chlorurus bleekeri*	7	/	20	/	/	/	7
Gomphosus varius	7	/	4	/	/	/	/	*Scarus dimidiatus*	/	/	100	/	/	/	/
Halichoeres hortulanus	5	8	7	/	/	/	3	*Scarus flavipectoralis*	/	/	/	/	8	/	/
Novaculichthys taeniourus	/	/	/	3	/	/	/	*Scarus microrhinos*	4	/	5	/	/	/	/
Stethojulis trilineata	50	8	12	40	/	/	80	*Scarus niger*	/	/	5	/	/	/	/
Thalassoma amblycephalum	100		300	/	/	/	/	*Scarus psittacus*	/	/	45	/	/	/	/
Thalassoma hardwicke	250	16	200	/	/	/	1000	*Scarus quoyi*	30	/	17	/	/	/	3
Thalassoma jansenii	4	/	/	/	/	/	/	*Scarus schlegeli*	/	/	8	/	/	/	/
Thalassoma lunare	80	/	100	/	/	/	/	*Scarus spinus*	/	/	10	/	/	/	/

Table 3.1. (continued).

MAYA'S	Number of individuals aggregating						LIMUKA	Number of individuals aggregating					
Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
ACANTHURIDAE							ACANTHURIDAE						
Acanthurus lineatus	/	/	/	150	/	/	*Acanthurus lineatus*	/	/	/	150	/	/
Acanthurus nigrofuscus	12	/	/	5	/	/	*Acanthurus nigrofuscus*	/	10	/	7	/	/
Ctenochaetus striatus	400	/	/	300	/	/	*Acanthurus triostegus*	/	/	/	4	/	/
Zebrasoma scopas	/	/	3	5	/	/	*Ctenochaetus striatus*	250	200	500	/	1000	/
							Zebrasoma scopas	3	/	3	/	5	/
LABRIDAE							LABRIDAE	/	/	/	/	/	/
Anampses caeruleopunctatus	/	/	3	/	/	/	*Halichoeres hortulanus*	5	5	/	/	3	/
Cheilinus trilobatus	/	/	3	/	/	/	*Novaculichthys taeniourus*	/	/	/	/	4	/
Coris aygula	/	/	/	3	/	/	*Stethojulis trilineata*	/	/	4	/	/	/
Halichoeres hortulanus	3	3	4	/	/	3	*Thalassoma hardwicke*	/	/	50	/	9	/
Halichoeres marginatus	/	/	/	3	/	/							
Halichoeres melanurus	/	/	/	6	/	/							
Stethojulis trilineata	/	/	3	/	/	/							
Thalassoma amblycephalum	/	/	10	60	/	/							
Thalassoma hardwicke	20	60	10	20	/	5							
SCARIDAE							SCARIDAE						
Chlorurus bleekeri	3	3	3	3	/	/	*Chlorurus bleekeri*	3	/	/	/	3	/
							Scarus quoyi	>3	/	>3	/	>3	/

Table 3.1. (continued).

KUME Species	Number of individuals aggregating															
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15	Site 16
ACANTHURIDAE																
Acanthurus nigrofuscus	/	8	/	/	/	7	/	/	/	30	/	/	10	/	/	/
Acanthurus triostegus	/	/	/	/	200	/	/	/	/	/	/	/	/	/	/	/
Ctenochaetus striatus	100	2000	350	/	600	200	50	30	50	20	50	150	30	250	50	30
LABRIDAE																
Cheilinus trilobatus	/	/	/	/	/	/	/	/	/	4	/	/	/	/	/	/
Halichoeres hortulanus	/	/	6	/	/	/	/	/	/	/	/	/	3	4	4	/
Novaculichthys taeniourus	/	3	/	/	/	/	/	/	/	/	/	/	/	/	/	/
Stethojulis trilineata	/	8	/	10	20	9	/	/	/	/	/	/	10	10	/	5
Thalassoma amblycephalum	/	1000	350	/	/	/	/	/	/	40	/	/	200	100	/	/
Thalassoma jansenii	/	4	/	/	/	/	/	/	/	/	/	/	/	/	/	/
SCARIDAE																
Chlorurus bleekeri	/	/	/	/	/	/	/	/	/	5	/	/	/	/	/	/
Scarus quoyi	/	/	/	/	/	/	/	/	/	/	/	/	30	/	10	/

	Other reefs (opportunistic observations)				
	Gava Gava	Luba Luba Site 1	Luba Luba Site 2	Madaro Site 1	Madaro Site 2
ACANTHURIDAE					
Ctenochaetus striatus	200	300	/	1500	50
LABRIDAE					
Halichoeres hortulanus	/	/	/	12	/
Thalassoma hardwicke	/	/	200	/	/

N.B. Spawning aggregations of *Ctenochaetus striatus* were the most actively sought after. Whilst aggregations of other species were also intensively searched for on Hanging Gardens, Maya's and, to a lesser extent, Limuka, only spawning aggregations of *C. striatus* were specifically sought after on Kume. All observations of spawning aggregations of species other than *C. striatus* on Kume were opportunistic, and all observations of all spawning aggregations on Gava Gava, Luba Luba and Madaro were also opportunistic. Such opportunistic observations are likely to be under-representative of the number of species aggregating to spawn and the number of sites used.

Table 3.2. Probable but unconfirmed spawning aggregations.

Species	Kimbe Bay 1	Kimbe Bay 2	Kimbe Bay 3	Limuka Site 5	Limuka flat near Site 4	Kimbe Bay 5	Kimbe Bay 6	Kimbe Bay 7	Kimbe Bay 8
BALLISTIDAE									
Pseudobalistes flavimarginatus[1]	/	3+	3+	/	/	3+	/	/	/
SERRANIDAE									
Epinephelus fuscoguttatus[2]	/	7	/	/	/	/	/	/	/
Plectropomus areolatus[2]	12	15	/	/	/	/	60	60	20
SIGANIDAE									
Siganus lineatus[3]	/	/	/	200	/	/	/	/	/
Siganus spinus[4]	/	/	/	/	20	/	/	/	/

[1] Spawning never witnessed, as this species lays eggs in a nest. Periodic increases in densities accompanied with aggressive egg defence indicative of spawning aggregation formation as documented in Gladstone (1994). [2] Spawning never witnessed (probably occurs at night). High densities, spawning colouration and territoriality displayed. [3] Spawning possibly witnessed. Sudden appearance of milkiness in water by a greatly larger than usual aggregation. [4] Spawning witnessed, but species never seen before or after. Therefore, it is not known whether a temporary aggregation formed or always found in schools of this size.

Table 3.3. Species seen spawning pelagically in pairs outside of aggregations.

Species	Reef/Site		
ACANTHURIDAE			
*Zebrasoma scopas**	Kume Site 15		
LABRIDAE			
*Anampses caeruleopunctatus**	HG Site 1	*Halichoeres marginatus**	Hg Site 1, Maya's Site 3**, Maya's Site 6
*Bodianus mesothorax**	HG Site 3, HG Site 1**, Maya's Site 1	*Halichoeres melanurus**	HG Site 1
Cheilinus chlorourus	HG Site 1	*Labrichthys unilineatus*	HG Site #41
*Cheilinus fasciatus**	HG Site 1, HG Site 5, Maya's Site 6	*Labroides dimidiatus*	HG Site 1
*Cheilinus trilobatus**	Maya's Site 2	*Novaculichthys taeniourus**	HG Site #41, Limuka Site 5
*Epibulis insidiator**	Limuka Site 3		
OSTRACIIDAE			
*Ostracion meleagris**	HG Site 1, HG Site 3**		
POMACANTHIDAE			
Centropyge vroliki	HG Site 3, HG Site 2, HG Site 3, HG Site 4, HG Site 5, HG Site 6, Maya's Site 1, Maya's Site 6	*Pygoplites diacanthus**	HG Site 2

* Species also observed forming spawning aggregations. ** Species also observed forming spawning aggregation at this site. HG ~ Hanging Gardens

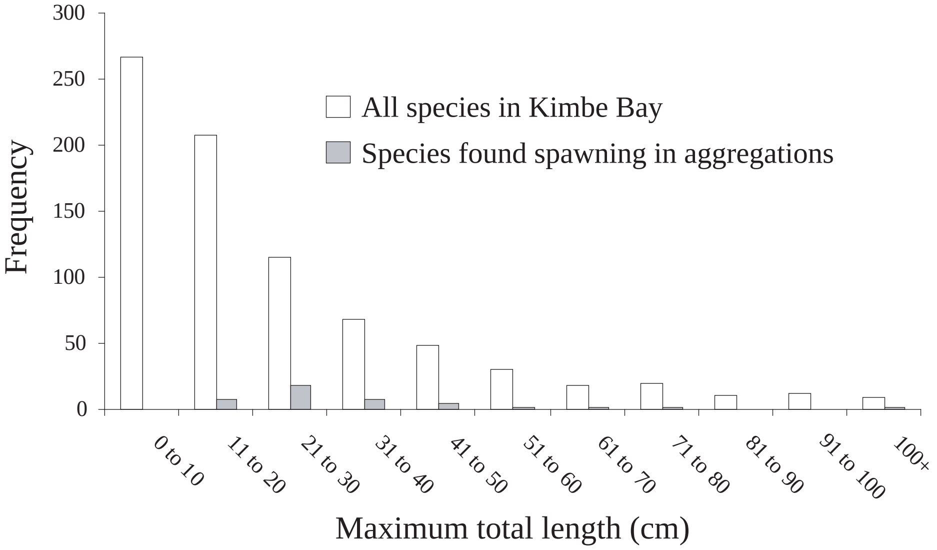

Figure 3.7. Size frequency distribution of all species of reef fish in Kimbe Bay and those found forming spawning aggregations. Sizes from Froese & Pauly (2000), and species presence from Allen & Munday (1996).

3.3.2 Multiple species use of sites

On the more intensively studied reefs (Hanging Gardens, Maya’s and Limuka), most sites where spawning occurred were locations for spawning aggregations of more than one species (see Table 3.1). Of the 29 sites used by *Ctenochaetus striatus*, 20 were also used by other species, with the remaining 9 likely to reflect a lack of observations rather than a lack of additional aggregative spawners at these sites. The most intensively studied sites, Hanging Gardens Site 1 and Site 3, had 18 and 27 species forming spawning aggregations respectively, with all species spawning consistently within an area less than 10m x 10m at Site 3. Spawning at other sites also occurred consistently between days and between species within discrete areas of a similar scale. In total, spawning aggregations of 35 species were found on Hanging Gardens. Of the species not seen forming spawning aggregations on this reef, 31 of them are known to form spawning aggregations in other locations.

3.3.3 Seasonal and lunar periodicity

Only *Plectropomus areolatus* appeared to have a restricted spawning season, with suspected spawning aggregations not seen from August to December (see Figure 3.8). The low frequency of days when spawning was documented for species other than *Ctenochaetus striatus* during April to October is more a reflection of sampling effort focussing on *C. striatus* during this period than a reduction of spawning of other species (see Figure 3.8). Of the 14 species with sufficient numbers of observations for analysis, only 4 displayed patterns of spawning over the lunar month that differed significantly from sampling effort, with 2 wrasses (*Thalassoma amblycephalum* and *Thalassoma hardwicke*) and one parrotfish (*Scarus quoyi*) spawning more often around the new moon, and one wrasse (*Cheilinus trilobatus*) spawning more often over the first lunar quarter (see Figures 3.9 & 3.10 and Table 3.4). Of the remaining species analysed a general but non-significant pattern of spawning more often over the new moon was evident in all but one species which spawned more often over the first lunar quarter. All except one of these 14 species were observed spawning during all four lunar quarters. *P. areolatus* and *Epinephelus fuscoguttatus* were only observed forming suspected spawning aggregations on the few days immediately prior to the full moon, but sampling effort was biased to this period.

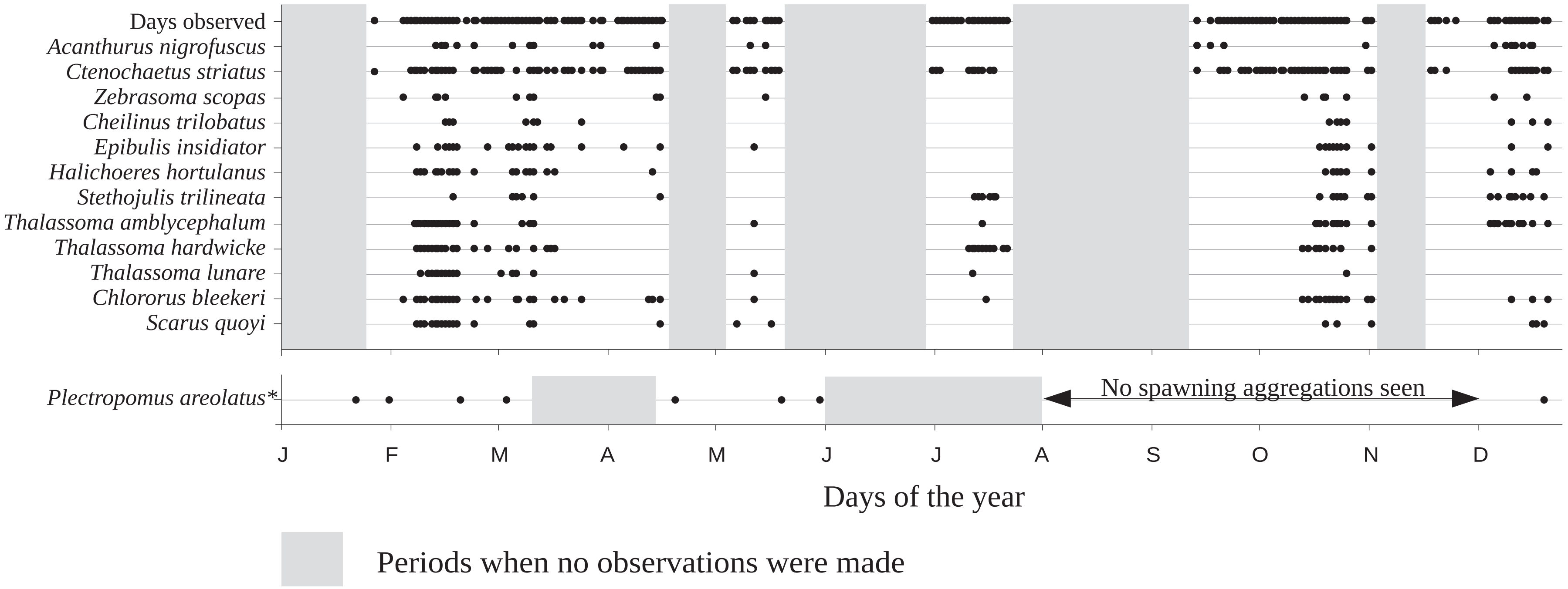

Figure 3.8. Annual patterns of spawning activity in different species of reef fish. Observations were made over 3 years (2001-2004). *~ spawning never witnessed but probable spawning aggregations observed; data for *Plectropomus areolatus* were collected on a limited number of occasions during 2003-2004 on days prior to the new moon.

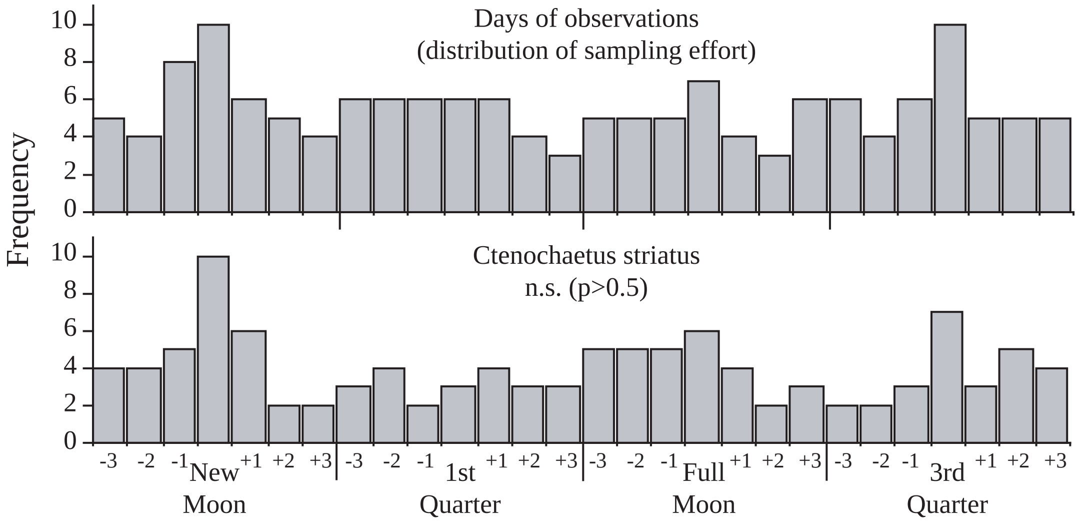

Figure 3.9. Lunar spawning patterns in *Ctenochaetus striatus*. Williams-corrected goodness-of-fit G-tests compared frequency of spawning on days of the lunar month with the frequency with which observations were made. n.s. ~ no significant difference between observed and expected frequency (alpha = 0.05).

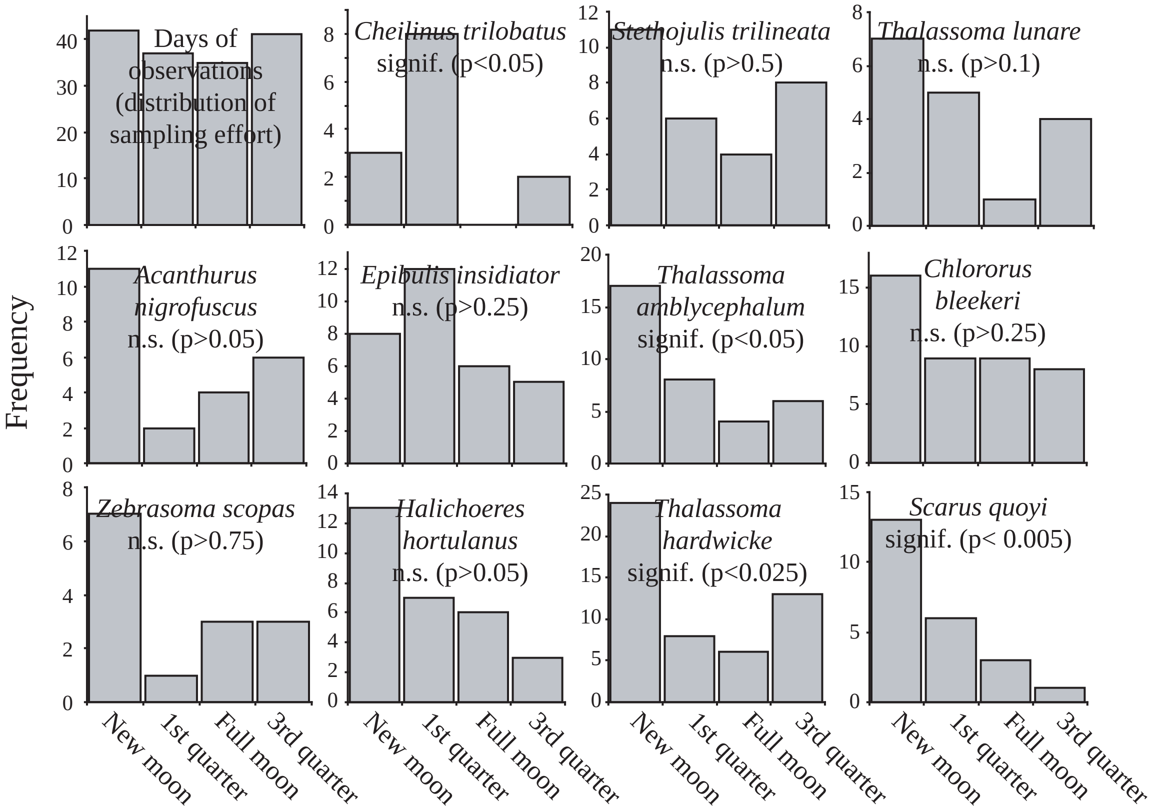

Figure 3.10. Lunar spawning patterns of reef fish species. Williams-corrected goodness-of-fit G-tests compared frequency of spawning during lunar quarters with the frequency with which observations were made. n.s. ~ no significant difference between observed and expected frequency; signif. ~ observed and expected frequencies differ significantly (alpha = 0.05).

Table 3.4. Lunar, diel and tidal patterns to spawning. Summary of the results of William's-corrected G-tests comparing the distribution of spawning compared to that predicted by sampling effort and with that predicted by species' diel range of spawning times (alpha = 0.05).

	Lunar cycle*		Time of day**		Time +/- peak high tide[†]		Tide height[††]	
	Result significant?		Result significant?		Result significant?		Result significant?	
Species	Yes/No	p	Yes/No	P	Yes/No	p	Yes/No	p
ACANTHURIDAE								
Acanthurus nigrofuscus	No	>0.05	Yes	<0.001	No	>0.75	No	>0.25
Acanthurus triostegus	No	>0.975	Yes	<0.005	No	>0.5	Yes	<0.025
Ctenochaetus striatus	No	>0.25	Yes	<0.001	No	>0.25	Yes	<0.005
Zebrasoma scopas	No	>0.75	Yes	<0.001	No	>0.1	No	>0.5
LABRIDAE								
Cheilinus trilobatus	Yes	<0.05	Yes	<0.001	Yes	<0.01	Yes	<0.01
Epibulis insidiator	No	>0.25	Yes	<0.001	Yes	<0.001	Yes	<0.005
Halichoeres hortulanus	No	>0.05	Yes	<0.001	Yes	<0.001	Yes	<0.001
Stethojulis trilineata	No	>0.05	Yes	<0.001	No	>0.5	No	>0.5
Thalassoma amblycephalum	Yes	<0.05	Yes	<0.001	Yes	<0.001	Yes	<0.001
Thalassoma hardwicke	Yes	<0.025	Yes	<0.001	Yes	<0.001	Yes	<0.005
Thalassoma lunare	No	>0.1	Yes	<0.001	Yes	<0.05	Yes	<0.005
SCARIDAE								
Chlorurus bleekeri	No	>0.25	Yes	<0.001	Yes	<0.001	Yes	<0.01
Scarus quoyi	Yes	<0.05	Yes	<0.001	Yes	<0.001	Yes	<0.001

* The frequency with which spawning occurred on different days of the lunar month compared with the frequency with which observations were made on these days of the lunar month ** The frequency with which species spawn during various time intervals compared with the frequency with which observations were made during these time intervals.. [†] The frequency with which spawning was observed at various time intervals +/- peak high tide compared with the frequency that these tidal states occurred within a species' diel range of spawning times on the days that observations were made. [††] The frequency with which spawning occurred at various tidal heights compared with the frequency that these tidal heights occurred within a species' diel range of spawning times on the days that observations were made. *p* ~ the probability that observed and expected distributions are the same (alpha = 0.05).

3.3.4 Time of day of spawning

The time of day that individuals spawned varied considerably between species, ranging from dawn (05:30 to 06:15hrs) to dusk (17:45 to 18:30hrs; see Figure 3.11). Spawning activity appeared to be reduced from 09:00 to 13:00hrs. However, this may be a reflection of under-sampling during this period. The majority of species spawned in the mid to late afternoon. A species' diel spawning interval was restricted and, for all species analysed, the pattern of spawning throughout the day differed significantly from that expected by sampling effort alone (see Table 3.4). Intra-familial patterns in daily spawning intervals were mixed: Mullidae, Ostraciidae and Pomacanthidae spawned exclusively within 1½ hours of dusk; Labridae spawned over the latter half of the day avoiding dusk; Acanthuridae and Scaridae were the only families represented by species that spawned at dawn and in the early morning, but other species of surgeonfish and parrotfish spawned in the afternoon. Dawn/early morning spawners and late afternoon/dusk spawners appear to have more restricted daily spawning intervals than species that spawn at other periods of the day. However, the time of spawning was significantly different between sites (one-way ANOVA, $F_{(7,161)} = 19.77$, $p<0.001$) for *Ctenochaetus striatus*, with the time of spawning at each site being restricted to an interval of less than 2 hours (see Figure 3.12 and Table 3.5). Similar between site analyses for other species were prevented by insufficient data, but for the wrasses and parrotfish with broad daily spawning intervals, these spawning intervals were no more restricted within sites.

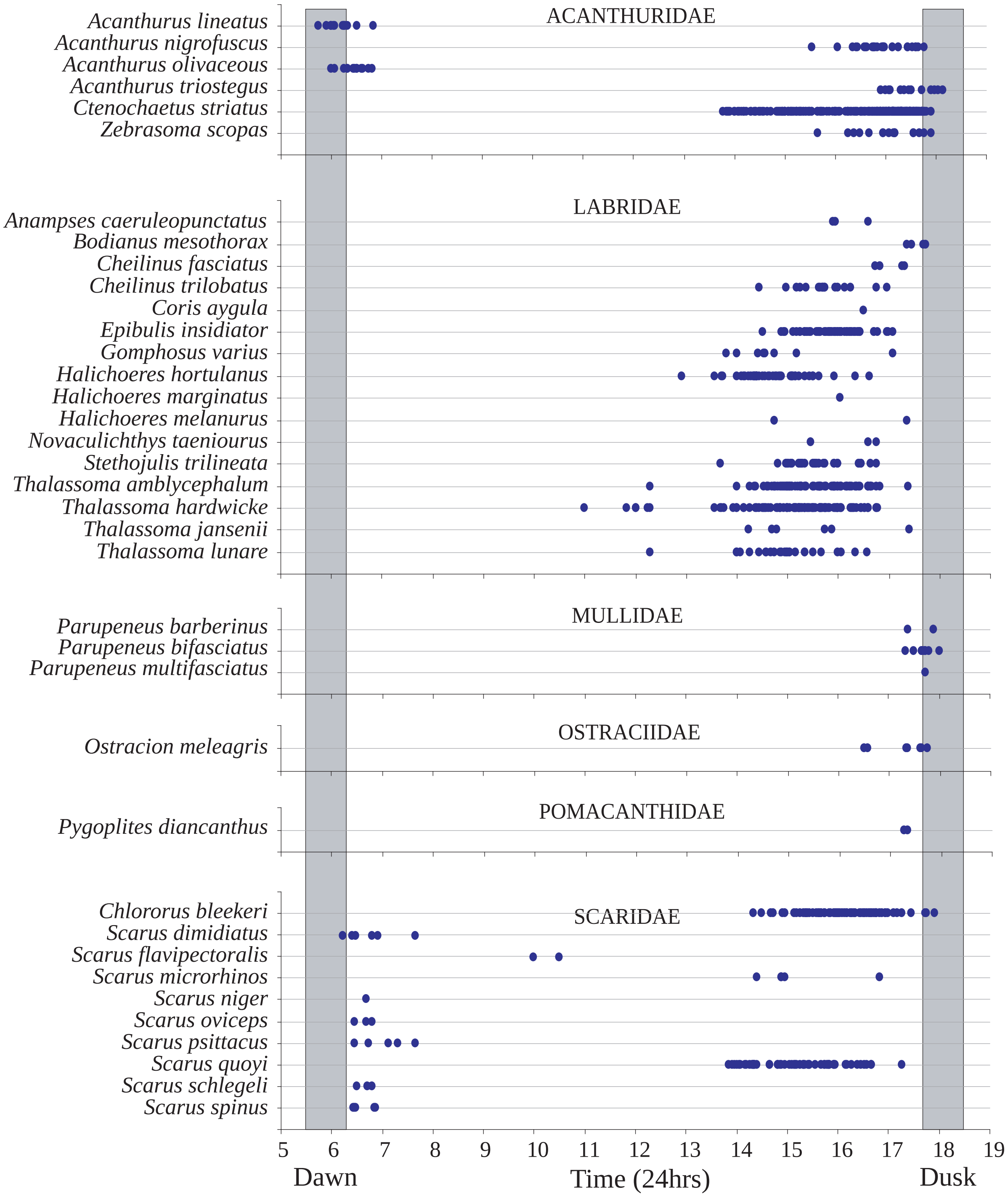

Figure 3.11. Diel patterns of spawning in species of reef fish. Shaded columns represent dawn (05:30 - 06:15) and dusk (17:45 - 18:30).

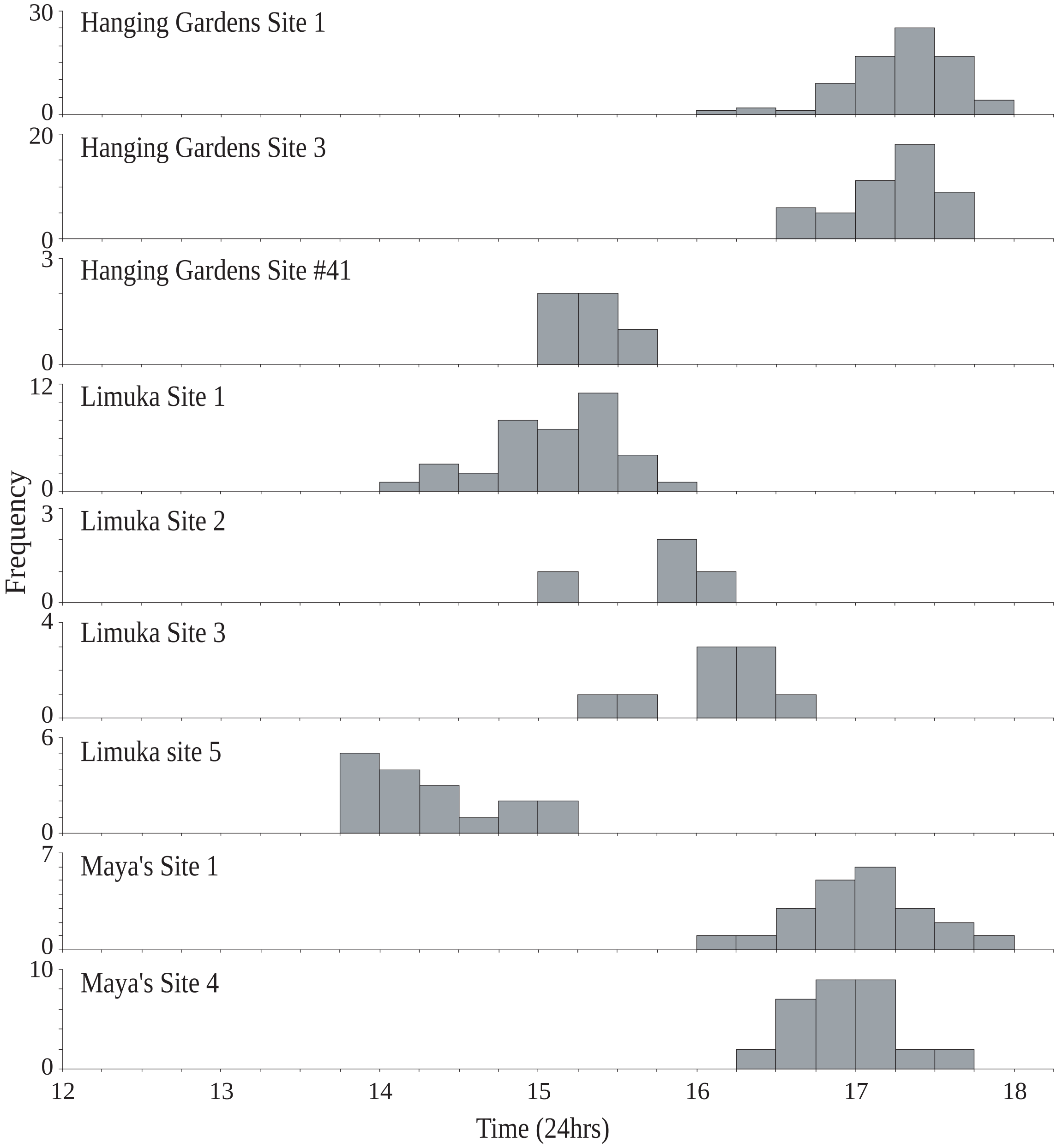

Figure 3.12. Diel patterns of spawning in *Ctenochaetus striatus* at different sites on Hanging Gardens, Limuka, and Maya's. Spawning times differ significantly between sites (one-way ANOVA: F(7,161) = 19.77, p<0.001).

Table 3.5. Diel and tidal spawning patterns of *Ctenochaetus* striatus. Summary of the results of William's-corrected G-tests comparing the distribution of spawning of *C. striatus* at different sites to that predicted by sampling effort and that predicted by *C. striatus*' diel range of spawning times at each site.

Site	Time of day**		Time +/- high tide†		Tide height††	
	Result significant?		Result significant?		Result significant?	
	Yes/No	p	Yes/No	p	Yes/No	p
Hanging Gardens Site 1	Yes	<0.001	Yes	<0.001	No	>0.25
Hanging Gardens Site 3	Yes	<0.001	No	>0.1	No	>0.5
Limuka Site 1	Yes	<0.001	Yes	<0.001	Yes	<0.001
Limuka Site 5	Yes	<0.001	No	>0.05	Yes	<0.05
Maya's Site 1	Yes	<0.001	Yes	<0.01	No	>0.75
Maya's Site 4	Yes	<0.001	No	>0.25	No	>0.5

Key (**, †, and ††) as in Figure 3.4

3.3.5 Spawning in relation to the tide

The range of times that species spawned in relation to the high tide was considerably greater for all species than their daily spawning intervals (see Figure 3.13). G-tests revealed significant differences between the distribution of spawning times before or after high tide and the distribution predicted by species' daily spawning intervals on days observations were taken for both parrotfish and all but one species of wrasse analysed (see Table 3.4). However, none of these species spawn predictably more often on ebb or flood tides. No significant differences were found for any surgeonfish. Within site analyses of *Ctenochaetus striatus* yielded significant results from 3 of the 6 sites with ebb tides favoured at 2 sites and flood tides at one (see Figure 3.14 and Table 3.5).

Although the majority of species spawned at times when tides where high ("high" and "low" tide being in the upper and lower halves of the tidal range respectively), spawning was also witnessed at low tides for 9 species (see Figure 3.15). The distribution of tidal heights over which species spawned differed significantly from the distribution expected within a species' known daily spawning interval for 11 of the 14 species analysed (see Table 3.4). All but one of these 11 species (*Thalassoma hardwicke*) spawned significantly more often at higher tides. Within site analyses for *Ctenochaetus striatus* revealed significantly different distributions from those predicted by site-specific diel spawning intervals for only 2 sites (see Figure 3.16 and Table 3.5). However, only at one of these sites (Limuka Site 1) was this difference attributable to significantly more spawning at higher states of the tide.

A one-way ANOVA on 10 years of tidal data (1994-2004) displayed no significant difference in the tidal amplitude between days of the new moon, 1st lunar quarter, full moon, and new moon ($F_{(3,442)} = 1.279$, $p>0.25$). Therefore, the new and full moons do not represent spring tides, nor do the 1st and 3rd lunar quarters represent neap tides, and thus tidal water movement cannot be inferred from lunar period.

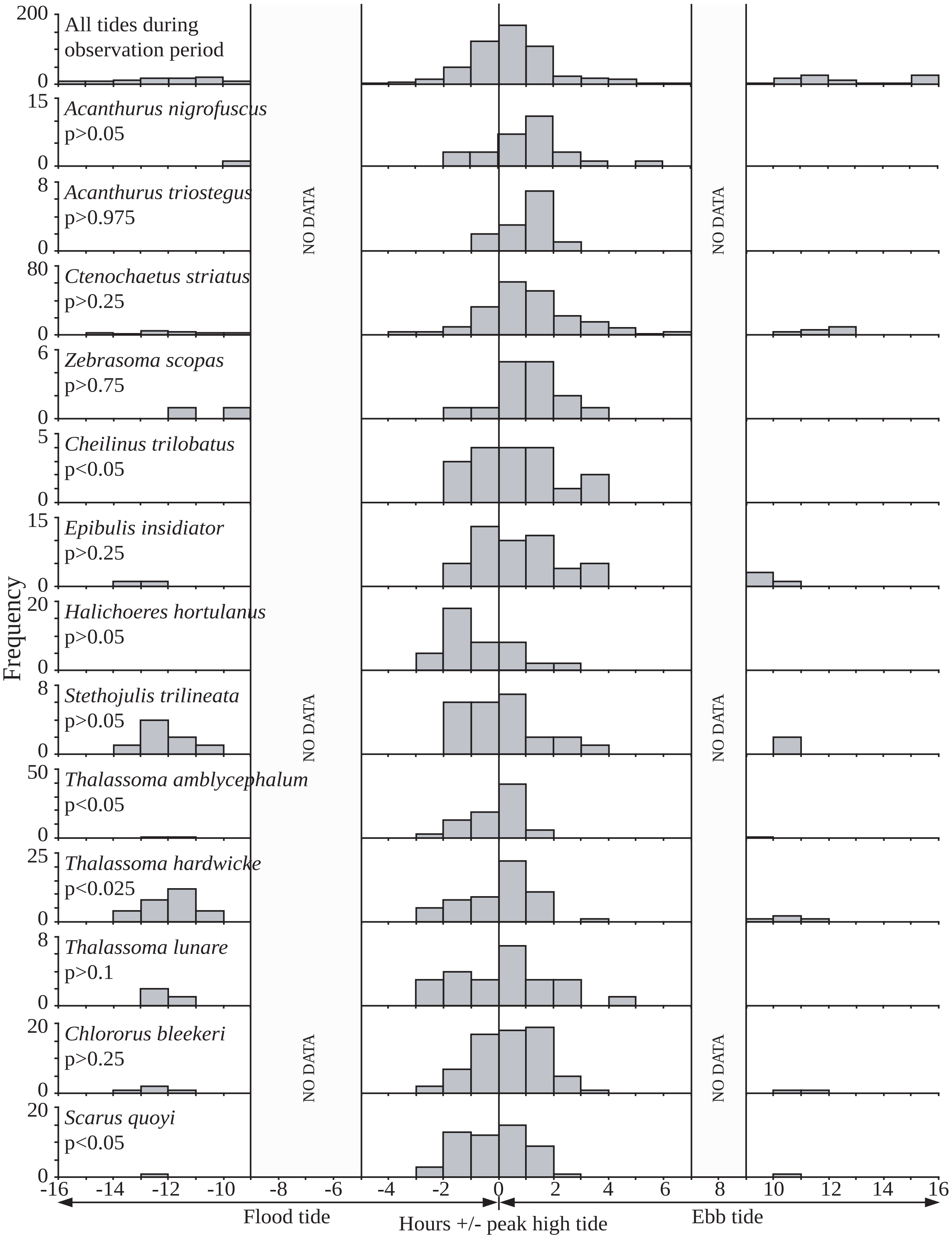

Figure 3.13. Tidal patterns of spawning in species of reef fish. Frequency ~ number of days spawning seen during time interval +/- peak high tide. p ~ resultant probability from Williams corrected goodness-of-fit G-tests that observed distribution differs from that expected from the species' known diel spawning interval and the days observations were made (data pooled where necessary; Sokal & Rohlf 1995).

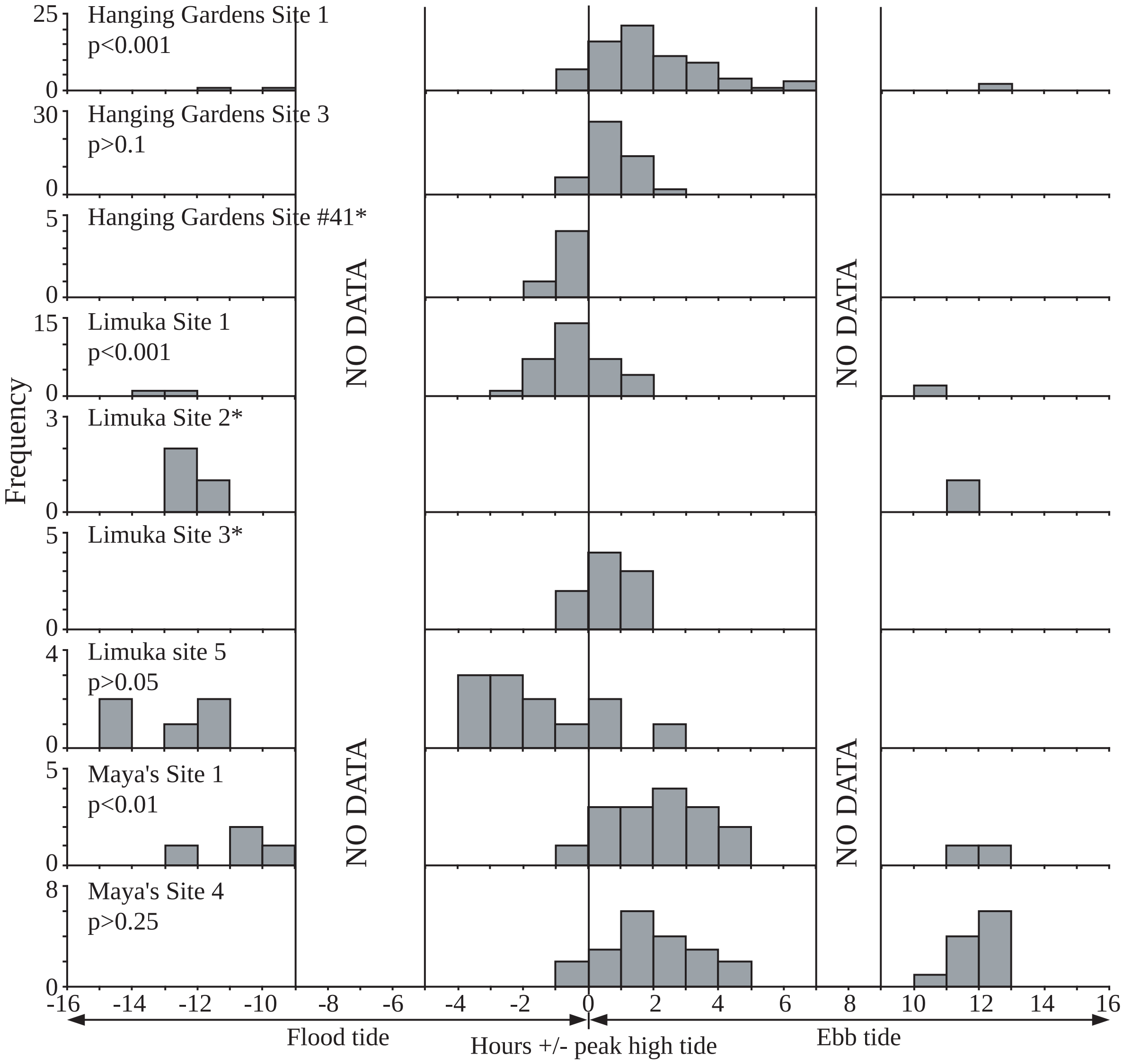

Figure 3.14. Tidal patterns of spawning in *Ctenochaetus striatus* at different sites. Frequency ~ number of days spawning seen during time interval +/- peak high tide. p ~ resultant probability from Williams-corrected goodness-of-fit G-tests that observed distribution differs from that expected from the known diel spawning interval for *C. striatus* at that site on the days observations were made (data pooled where necessary; Sokal & Rohlf 1995). * ~ insufficient data for analysis.

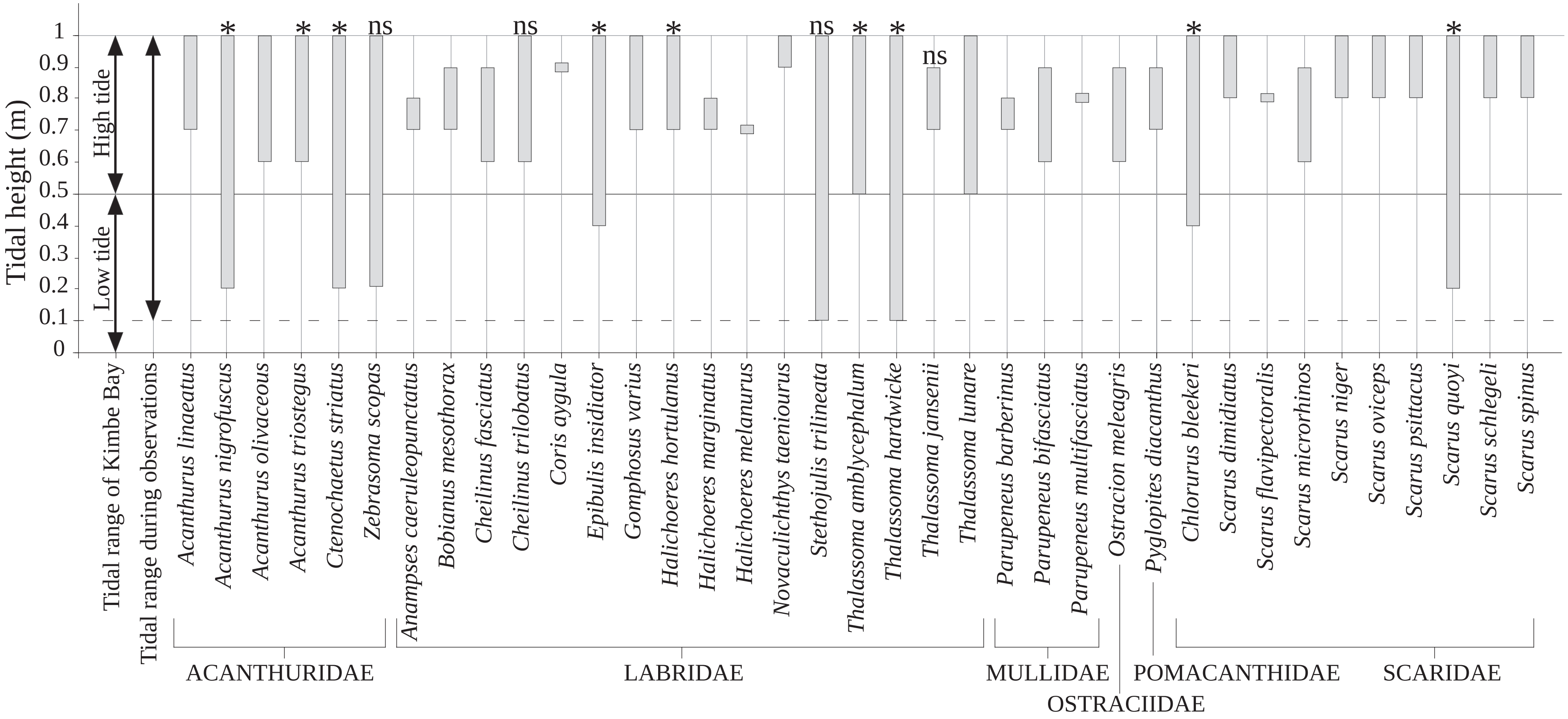

Figure 3.15. Tidal heights over which species of reef fish spawned. Where sufficient data permitted, a Williams-corrected goodness-of-fit G-test was used to compare the distribution of tidal heights over which a species spawned to that predicted by its diel spawing interval on the days observations were made. * ~ observed distribution differs significantly form that expected ($p<0.05$). ns ~ no significant difference between the observed and expected distributions. Absence of annotation indicates insufficient observations for analysis.

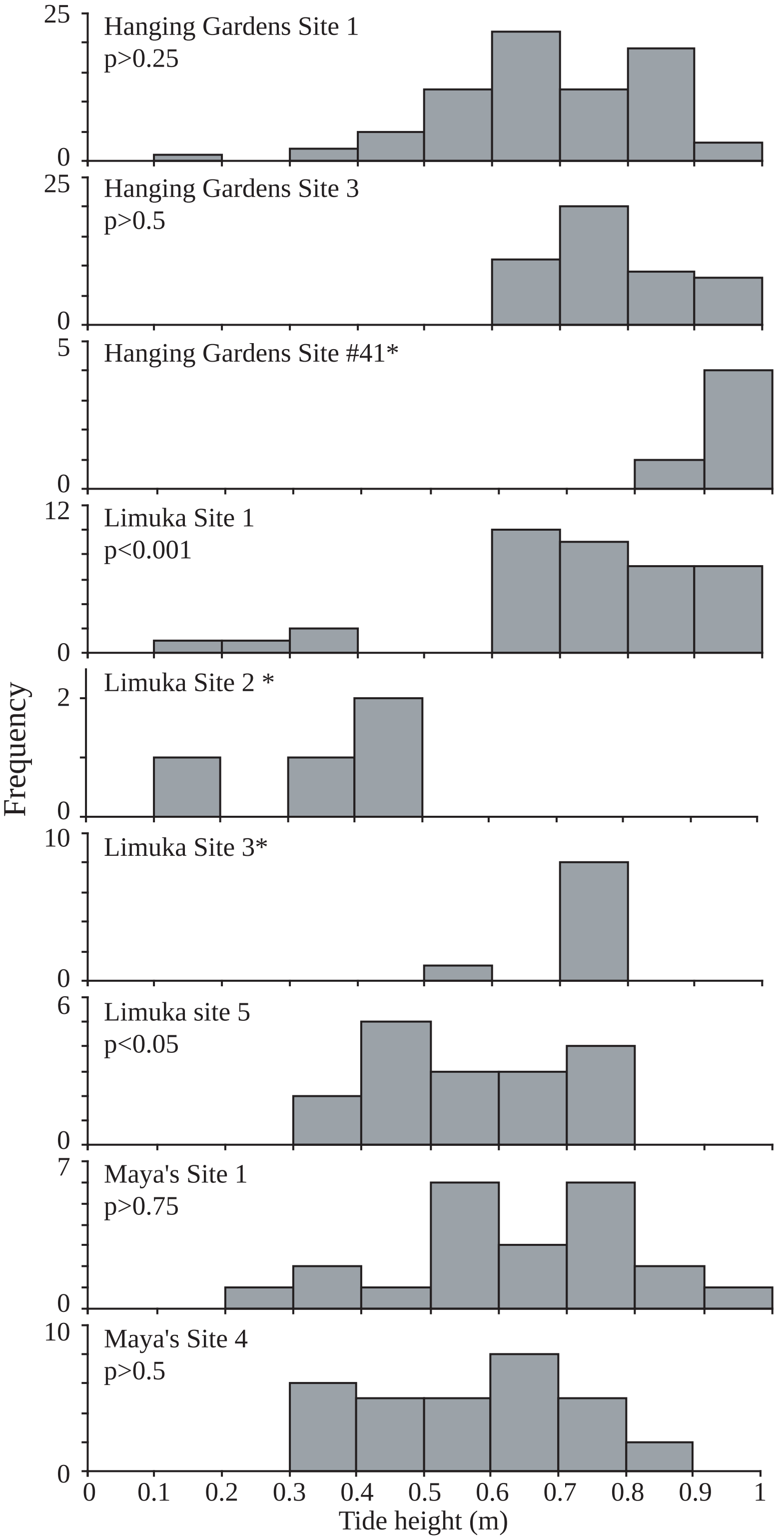

Figure 3.16. Tidal heights over which *Ctenochaetus striatus* spawned at different sites on Hanging Gardens, Limuka and Maya's. Where sufficient observations permitted, Williams-corrected goodness-of-fit G-tests were used to compare the distribution of tidal heights over which spawning occurred to that predicted by the diel spawning interval of *C. striatus* at that site on the days observations were made at the site. p ~ probability that the observed distribution differs from that expected. * ~ insufficient data for analysis.

3.4 Discussion

3.4.1 Characteristics of species found forming spawning aggregations

Spawning aggregation formation was a common phenomenon on the inshore reefs of Kimbe Bay. In total, 37 species from 6 families were confirmed spawning in aggregations spread across 38 sites on the study reefs. At least an additional 31 species known to form spawning aggregations were also observed on the study reefs, but never observed spawning aggregatively or otherwise. Although the methodology employed is likely to under-represent the species that form spawning aggregations in deeper water, those that spawn at night, and those that migrate to areas outside the study reefs to spawn (which may account for many of these 31 species), the characteristics of the species found forming spawning aggregations are largely consistent with those described in Chapter 2 and by Claydon (2004). All species are larger than 10cm maximum total length and all but one spawns pelagically. However, the hypothetical interrelationship between a species' density and its likelihood of forming spawning aggregations (see Chapter 2 and Claydon 2004) is not supported by this study, with aggregatively spawning species ranging from the least to the most abundant, both within their families and on the study reefs in general.

Spawning aggregation formation does not appear to be a density dependent phenomenon with spawning aggregations ranging in size inter-specifically from 3 to 2000 individuals, and from <10 to 2000 intra-specifically. The larger spawning aggregations were typified by group spawning species, whereas smaller ones were dominated by pair spawners. Pair spawning and group spawning may also be explained phylogenetically. However, the characteristics of the spawning aggregations formed by some species may be density dependent in a similar fashion to that described by Warner & Hoffman (1980) in the Caribbean: 1 species of parrotfish and 4 species of wrasse (3 of them congeners of the species described by Warner & Hoffman 1980) formed small pair spawning aggregations as well as large group spawning ones.

Of the four species that were seen spawning exclusively in pairs outside of aggregations, only two, the cleaner wrasse *Labroides dimidiatus* and the angelfish *Centropyge vroliki*, do not appear to migrate prior to spawning. The limited observations of non-migratory pelagic spawning is similar to that found by Moyer (1989). However, rather than being indicative of the general lack of non-migratory pelagic spawners on coral reefs, both studies focused observations on sites known to be used by aggregatively spawning species and thus may have missed spawning by many other species. The focus on specific sites in the present study is also likely to have under-represented non-aggregative spawning species that migrate to other locations, as well as those species that do not migrate at all. The two other species seen spawning outside of aggregations, the wrasses, *Labrichthys unilineatus* and *Cheilinus chlorourus*, migrate to spawn in a similar fashion to those species that form spawning aggregations, with the latter being known to form spawning aggregations at other locations (Squire & Samoilys unpubl. in Russell 2001). The distinction between a species forming spawning aggregations when more than two individuals are aggregated and not forming spawning aggregations when only two have migrated is technically correct but in many cases biologically meaningless. The distinction becomes meaningful if the behaviour involved differs between spawning in and outside of aggregations. This was not the case for any of the 11 such species from 4 families identified in this study, nor is it likely to be the case with other strictly pair spawning species. For these species, aggregative and non-aggregative spawning exist on the same continuum, differing only in the number of individuals involved and described by a single process – migrating to a site to spawn.

Although *Pseudobalistes flavimarginatus* was the only species seen forming spawning aggregations that lays eggs in a nest, egg-laying *per se* is not likely to preclude spawning aggregation formation. Spawning aggregations of egg-laying species of fish are well documented in other aquatic environments (e.g. anadromous salmonids, Groot & Margolis 1991, and the Atlantic silverside, *Menidia menidia*, Conover & Kynard 1984) as well as massive spawning aggregations being formed by the egg-laying giant cuttlefish, *Sepia apama* (Hall & Hanlon 2002). Within coral reef environments, two other egg-laying species are thought to form spawning aggregations, another triggerfish, *Canthidermis sufflamen* (Whaylen et al. 2004), and the damselfish, *Chromis viridis* (Lewis 1997, McCormick pers. comm.), and whilst typically referred to as egg-scattering (Thresher 1984), several species of the egg-laying but pelagically spawning Siganidae are known to form spawning aggregations (present study, and see Claydon 2004, Domeier & Colin 1997). However, many egg laying species may be precluded from migrating to form spawning aggregations not because of their mode of reproduction but because of: (a) their typically smaller sizes (see Munday & Jones 1998) and the higher risks of predation to which smaller species would be exposed during migration and at the spawning aggregation site (see Chapter 2 and Claydon 2004); (b) the tendency of these smaller species to be territorial and thus forfeit loosing resources if they migrate away from territories to spawn, and (c); the increased time spent at the spawning aggregation site due to many egg-laying species' habit of tending and guarding eggs, thus increasing time exposed to predators. The large size of *P. flavimarginatus* and thus the limited threat from predators may enable them to spend time caring for their eggs at spawning aggregation sites, a prohibitively costly behaviour for smaller egg-layers. The aggregatively spawning rabbitfish overcome this by not tending their eggs following spawning. Additionally, suitable spawning habitat may be less limited for many egg-laying species than for their pelagically spawning counterparts, thus migrating to spawn (in aggregations or otherwise) may be less advantageous for egg-laying species. This is supported by the fact that *P. flavimarginatus* is seen forming spawning aggregations only when suitable habitat for nests is not present in their home ranges (Gladstone 1994).

3.4.2 Multiple species use of spawning aggregations sites

This study documents 27 separate locations where spawning aggregations are formed by more than one species at the same site. At one site, 27 different species were observed spawning aggregatively within an area of less than 10x10m. Whilst multi-specific spawning at single sites is well known (Lobel & Neudecker 1985, Moyer 1989, Colin & Bell 1991, Johannes et al. 1999, Sancho et al. 2000b, Heyman et al. 2001, Whaylen et al. 2004), consistent spawning aggregation formation by so many species within such a small area as demonstrated in the present study has not previously been described.

Pelagically spawning reef fish are widely believed to optimise the survival of their offspring by releasing eggs at sites and times that: (a) have limited predator densities (Shapiro et al. 1988); (b) coincide with currents that limit the time these eggs are exposed to these predators (Johannes 1978, Lobel 1978); and (c) enhance the future settlement of larvae onto reefs (Lobel 1978, Barlow 1981, Lobel & Robinson 1988a). If fish optimise their offspring's survival in such a fashion, then, ignoring species-specific limits to migratory distances and diel behaviour, all species would migrate to the same site and spawn at the same time. This does not happen. Whilst many species in the present study formed spawning aggregations within the same limited areas, spawning aggregation formation was less restricted temporarily between species, with characteristically dawn spawning, afternoon spawning and dusk spawning species differentiated. Similar patterns have been observed in other locations (Colin 1982, Moyer 1989, Sancho et al. 2000b). Despite the limited evidence to support the existence of theoretically more suitable sites from which to spawn pelagic eggs (Shapiro et al. 1988, Appeldoorn et al. 1994, Hensley et al. 1994, Claydon 2004), the consistent use of the same site by many species supports the notion that the site in question is intrinsically beneficial. However, the broad range of spawning times between and in some cases within species does not support the argument that these fish are synchronizing egg release temporally with any specific environmental variable that directly enhances their offspring's survival. It is also unlikely that the differences in the precise timing of spawning reflects the species-specific environmental requirements of their pelagically spawned eggs.

3.4.3 Spawning periodicity

Of all the species more frequently observed spawning, none appear to have a spawning season, but spawning was observed in all months observations were made. However, *Plectropomus areolatus* was not seen aggregating on every new moon, and despite never witnessing spawning, this species appears to form spawning aggregations on all months except from around August to December. Discrepancy between *P. areolatus* and other species is surprising. Traditional explanations of seasonal patterns of coral reef fish spawning are based on the inhibitory effect of unfavourable temperatures on egg production. Thus one would expect seasonality in all species or none.

All species observed spawning pelagically in Kimbe Bay appear to restrict this spawning to a species-specific range of times in the day. Such diel spawning patterns are widespread amongst coral reef fish (see Sancho et al. 2000b). The pattern of days upon which spawning occurs within this time range differs between species and for most is not more likely to occur on days when this time interval coincides with a certain lunar period, nor with ebb or flood tides. However, in most species, spawning is more likely to occur on days when a species' spawning interval coincides with high tides. Such synchrony with higher tides is likely to reduce the chances of mortality from both mechanical damage from the substratum and predation by fish and sessile invertebrate planktivores by increasing the distance of eggs from these threats. The threat from mechanical damage is emphasized by the fact that inshore reefs of Kimbe Bay can become exposed at low tides. However, spawning at low tides, albeit uncommon, was witnessed for a number of species.

3.4.4 Trade-off between predatory threats

A species' diel spawning interval is proposed to optimise the trade off between the threat of predation to eggs and that suffered by adults (see Chapter 2, Sancho et al. 2000b, and Claydon 2004). Albeit supported by observations elsewhere (Kuwamura 1981), this appears to be contradicted by some of the observations in this study, with the large bodied *Chlorurus bleekeri*, *Scarus microrhinos* and *Scarus quoyi* spawning at a range of times during the mid to late afternoon and the smaller bodied boxfish, *Ostracion meleagris,* and goatfishes *Parupeneus barberinus*, *Parupeneus bifasciatus* and *Parupeneus multifasciatus* spawning at dusk. The trade-off between predation of adults and eggs was also proposed to be mediated by a species' iteroparity, with the more highly iteroparous species less likely to risk future reproductive success by exposing themselves to piscivores (see Chapter 2 and Claydon 2004). However, whilst a species' degree of iteroparity is inestimable from the data collected in this study, it is unlikely to differ greatly between sites on the same reef. Therefore, differences between spawning times of a single species at different sites, such as those displayed by *Ctenochaetus striatus*, suggest that the time of spawning is not determined a trade-off between predatory threats on eggs and spawning adults.

3.4.5 Crepuscular vs. day spawning

Species of coral reef fish that spawn around dusk are consistently reported as spawning within narrow, highly predictable time frames (Moyer & Zaiser 1981, Moyer et al. 1983, Sancho et al. 2000b), with proximity to sunset dictating the shortness of this time range (Colin 1982). The dusk spawning species in the present study also fit this pattern. Sancho et al. (2000b) suggest that this is because the egg-predators that hinder and delay spawning at other times of the day are limited at dusk. The species identified in this study as spawning around dawn also have restricted ranges of spawning times similar to their dusk counterparts. Thus narrowing of the spawning window is likely to be a crepuscular phenomenon rather than strictly dusk-related. Variation in predatory threats on eggs and consequentially delayed spawning does not adequately explain this phenomenon, because no species of surgeonfish was observed modifying its spawning behaviour in response to egg-predators, but continued spawning regardless of the loss of eggs. It is more likely that dusk and dawn are much more easily distinguished than other times of the day or night. Thus precise synchronization of behaviours and endogenous processes such as egg hydration may be increasingly difficult at times increasingly further away from dawn or dusk, and thus in the absence of such clear cues.

3.4.6 Intraspecific variation in spawning times between and within reefs

Ctenochaetus striatus spawned during time intervals that differed between adjacent reefs in a similar fashion to that displayed by *Thalassoma bifasciatum* on reefs in Puerto Rico (Alvey 1990). However, the exact time of spawning at different sites within reefs also differs significantly. Such a phenomenon has not previously been documented for species spawning within the same habitat, and poses interesting questions as to how this can arise. If species are synchronizing spawning in response to environmental cues, then the precise timing of spawning is likely to differ between reefs as the response to the cue remains constant but the environmental variable itself differs between reefs. The different times of day over which *C. striatus* spawns on different reefs in Kimbe Bay can be explained in such a fashion, as can that for *T. bifasciatum* in Puerto Rico (Alvey 1990). However, the difference in spawning times at different sites within reefs requires a different explanation. Whilst the sites themselves may be exposed to different environmental regimes, the individuals that migrate to these sites may not. There will be areas on reefs where the home ranges of individuals migrating to adjacent spawning aggregation sites overlap. These individuals are unlikely to be exposed to vastly different environmental variables, but do respond differently. The same response to the same environmental cue is therefore not likely to explain *C. striatus* spawning patterns, and neither is local adaptation on such a fine scale. One explanation is that the spawning time of *C. striatus* at each site is maintained traditionally. This timing may itself be adaptive, enhancing the survival of offspring spawned from that site, or it may be arbitrary, serving only to synchronize spawning as suggested for other temporal cues (Lobel 1978, Colin & Clavijo 1988, Colin & Bell 1991, Claydon 2004). Tradition has been suggested to play a role in the location of spawning aggregation formation in *T. bifasciatum* (Warner 1988b, 1990b), but it is equally applicable to the timing of spawning.

3.4.7 Unwarranted assumptions concerning tidal and lunar cycles

A number of species of aggregatively spawning reef fish, especially serranids, display strong lunar patterns of spawning (see reviews in Domeier & Colin 1997, and Claydon 2004). The periodicity of pelagic spawning is often assumed to be dictated by the currents into which eggs are spawned (see Shapiro et al. 1988 for critical assessment of such assumptions). The state of the tide and moon are often misrepresented as reflecting these currents (Warner 1997), and thus tenuous explanations and unwarranted emphasis on the adaptive significance of such lunar and tidal patterns can arise. This problem is compounded by the fact that some taxa show remarkable synchrony to lunar, tidal and diel cycles in order to utilise currents (e.g. intertidal crabs, Forward 1987, Morgan 1987, Morgan & Christy 1994, Morgan 1996, Kellmeyer & Salmon 2001, Stillman & Barnwell

2004) and thus it is assumed that coral reef fish may also possess the ability to do so (Shapiro et al. 1997, Sancho et al. 2000b), despite limited evidence to support this and limited evidence to suggest that such synchrony would be adaptive in coral reef fish. Lunar and tidal patterns are assumed to exist and, if found, patterns are assumed to be hydrologically adaptive when this is not necessarily the case (Conover & Kynard 1984). Spawning in association with currents is addressed in detail in Chapter 4.

In Kimbe Bay, tidal amplitude is not consistently higher during any lunar quarter, and thus any lunar periodicity found cannot be explained by tidal movements. Nonetheless, most species analysed spawn more frequently around the new moon, however this is only statistically significant for three of them and another species spawns significantly more often around the first lunar quarter. For all but this last species, spawning occurred during all lunar quarters. The absence of clear lunar associations to spawning patterns of most species studied may reflect the lack of a predictable lunar-tidal relationship. However, the persistence of *Plectropomus areolatus* (and probably *Epinephelus fuscoguttatus*) forming what appear to be spawning aggregations (spawning was never witnessed) in association with the new moon in Kimbe Bay suggests that tidal movement is not the reason such lunar periodicity exists in other, larger species. Such a conclusion ignores the geographical scale of these species' reproductive populations which may extend beyond Kimbe Bay and into areas where predictable lunar-tidal relationships do exist. However, additional observations question whether spawning with lunar periodicity is hydrologically adaptive: in the Caribbean, *Epinephelus striatus* spawns in aggregations around the full moon (Bardach et al. 1958, Thompson & Munro 1983, Carter 1989, Colin 1992) despite weak tidal movements in this region (Colin 1982); and rabbitfish spawn with well-documented lunar periodicity (Hasse et al. 1977, Rahman et al. 2003) despite increased tidal movements being of no benefit to a species that spawns demersal eggs. The contention that certain stages of the lunar cycle are not adaptive beyond their clarity as cues to which spawning can be synchronized is more convincing (Claydon 2004) and supported by the observations in this study. In smaller species that are capable of spawning on a near-daily basis, such synchrony to lunar patterns would only serve to limit reproductive output.

3.5 Conclusion

The species found forming spawning aggregations on the inshore reefs of Kimbe Bay, share certain characteristics, such as being larger than 10cm maximum T.L. and predominantly spawning pelagically. However, the characteristics of these species, the populations in which they are found and the size and nature of their spawning aggregations vary widely. Fish restrict spawning to limited species-specific time ranges, which, for a single species can differ between reefs and between sites within the same reef. In general, the wide range of spawning times between closely related species suggests that rather than reflecting a trade-off between the predatory threats of adults and eggs, or synchronizing spawning with favourable environmental variables, the time of day that species spawn is not adaptive, but merely facilitates synchronized spawning. Albeit spawning was never witnessed, the lunar pattern of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* aggregation formation in the absence of increased tidal movements is also explained in this fashion. However, the days upon which some species spawned take advantage of higher tides with the probable effect of enhancing egg survival by reducing the mortality caused by predators and attrition.

The results of this study indicate that there may be something intrinsically advantageous about the sites from which pelagic eggs are spawned. This conclusion is derived from the fact that many species migrate to the same small areas on reefs to spawn. Further investigation into the characteristics of these sites is warranted in order to assess whether they do serve as better platforms from which to spawn pelagic eggs than other sites on reefs, and what the physical and biotic characteristics of such sites may be.

CHAPTER 4: SPAWNING AGGREGATION SITES: PHYSICAL AND BIOTIC CHARACTERISTICS

4.1. Introduction

A large number of marine species migrate prior to breeding. For many of these species, such migrations are necessary because suitable habitat in which to breed is not found in the species' feeding areas. These species include, turtles which feed in the sea but need to lay eggs on sandy beaches (Hendrickson 1980), anadromous fishes which must return from the sea to lay eggs in freshwater streams (Klemesten et al. 2003), and the Christmas Island red crab which migrates across land to release eggs in the sea (Adamczewska & Morris 2001). Such migrations are essential for their offspring's survival. However, for other species, breeding migrations are less easily explained in terms of the spatial separation of breeding and feeding habitat. Spawning aggregations are known to be formed by a number of coral reef fish, most of which spawn pelagically (see Claydon 2004). Water into which eggs are spawned is not limited, yet some individuals have been documented migrating over 100km to spawn in aggregations at certain locations and times (Colin 1992, Carter et al. 1994, Bolden 2000). It seems unlikely that effective reproduction necessitates such migrations, because a host of pelagically spawning coral reef animals, both vertebrate and invertebrate, do not and/or cannot migrate prior to spawning (e.g. some species of reef fish, Donaldson 1989; Popper & Fishelson 1973; sponges, Fell 1974; and corals, Willis et al. 1985).

It is often suggested that the sites where pelagic spawning occurs have characteristics that are intrinsically beneficial to the individuals spawning (e.g. Thresher 1984, Donaldson 1990, Shapiro et al. 1993, Whaylen et al. 2004). Such assertions are unsurprising, particularly in the context of spawning aggregation formation: the site represents a choice made from a sometimes very large area of reef (e.g. *Epinephelus striatus*, Colin 1992, Carter et al. 1994, Bolden 2000); this choice seldom appears to be arbitrary because such sites are typically perceived to have distinctive characteristics (not necessarily correctly, see Domeier et al. 2002, Claydon 2004), and the same choice can be made by very large numbers of conspecifics (over 100,000, Smith 1972) as well as by several other species, forming spawning aggregations at the same site (Moyer 1989, Colin & Bell 1991, Carter et al. 1994, Johannes et al. 1999, Sancho et al. 2000b, Domeier et al. 2002, Whaylen et al. 2004). The more conspecifics and the greater number of species that choose the same site, the more convincing this assertion becomes. Despite being rarely documented, more than 10 species spawning aggregatively at the same site is likely to be common for both relatively small species (Sancho et al. 2000b), and larger predatory species (Whaylen et al. 2004). As many as 60 species of both types of reef fish have been documented spawning at the same site (Johannes et al. 1999). Whilst this observation may include a misleadingly elevated number of smaller species because of the inappropriately large spatial scale over which it was made, 27 species have been observed forming spawning aggregations at a site less than 10 x 10m on a reef in Papua New Guinea (see Chapter 2).

The physical characteristics of these sites are proposed to enhance the survival of spawning adults and their eggs by means of a number of mechanisms: (1) the geomorphology and topography of the sites limit the foraging efficiency of piscivores and offer abundant refuge to prey (Shapiro et al. 1988, Hugie & Dill 1994), (2) the geomorphology of sites facilitates the rapid removal of eggs away from the reef into deeper less planktivore-rich waters (Johannes 1978), and (3) the currents found at these sites enhance this off-reef egg transport (Robertson & Hoffman 1977, Johannes 1978) and may facilitate the future recruitment of larvae back onto reefs (Lobel 1978, Barlow 1981). These sites are also proposed to have characteristically lower abundances of potential predators of both spawning adults and their planktonic eggs (Johannes 1978). There are two reef features that may facilitate the more rapid removal of eggs away from planktivores: horizontal seaward projections and steep slopes. In a random current regime, the further a point on a reef projects out to sea the more likely currents at that point flow directly away from the reef. The steeper the reef slope the less time it takes for eggs to be swept into deeper less planktivore-rich waters. Therefore, eggs spawned from sites with these two features will be less exposed to reef-associated planktivores than those spawned from straighter margins of reef with shallow inclining reef slopes.

The physical characteristics of spawning aggregation sites are seldom described in less than ambiguous terms. This ambiguity reinforces the perception that spawning aggregations form at sites with distinctive characteristics. However, when all reef formations are likely to be characterized by only a few categories (e.g. slope, wall, promontory, channel, seaward projection), the distinctiveness of such characteristics is questionable (see Claydon 2004). Even if sites were adequately described, it is necessary to describe many such sites and compare these to sites where spawning aggregations are not formed. Almost without exception, spawning aggregations are documented without detailed reference to surrounding areas of reef. Therefore, it is usually impossible to ascertain the range from which a choice of sites was made, and there is little quantitative support that the choice of sites for spawning aggregation formation enhances the survival of adults or their offspring.

4.1.1 Aims:

The aims of this study are to investigate whether spawning aggregations of coral reef fish are formed at characteristic locations and with regard to physical and biological parameters. Specifically, this study will test the prediction that spawning aggregations are formed at locations and times where the physical and biological characteristics serve to reduce predation on eggs and adults. The physical characteristics investigated are both the broad-scale measurements of reef slope and the degree to which the reef margin projects seawards, as well as measurements taken on a finer scale: potential refuge from predators as indicated by topographic complexity and the number of holes in the substratum. Currents are treated comprehensively in a separate study (see Chapter 5). The biological characteristics of interest are the abundance and activities of piscivorous and planktivorous predators.

Figure 4.1. The inshore study reefs of Hanging Gardens, Kume, Maya's, and Limuka in Kimbe Bay, West New Britain, Papua New Guinea. All study reefs were accessed from the Mahonia na Dari Research and Conservation Centre (MND). All sites shown on Kume (Sites 1 to 3 & 5 to 16) and all sites marked with asterisks on Hanging Gardens, Maya's and Limuka are spawning aggregation sites of *Ctenochaetus striatus*. Site names correspond to those given in Chapter 2.

4.2 Materials and Methods:

4.2.1 Study species:

The “lined bristletooth” surgeonfish, *Ctenochaetus striatus* (max S.L. 16cm), was observed forming spawning aggregations with up to 2000 individuals on the inshore study reefs of Kimbe Bay. Study of aggregative spawning in this species was facilitated by the fact that: (1) spawning aggregations were consistently formed at specific sites on reefs, (2) many reefs had a number of such spawning sites, and (3) spawning occurred within a 2hour site-specific time window.

4.2.2 Study area and study sites:

Fieldwork was conducted from the Mahonia na Dari Research and Conservation Centre, Kimbe Bay, West New Britain Province, Papua New Guinea. The study focused on 4 inshore reefs in Kimbe Bay: Hanging Gardens, Kume, Limuka and Maya’s (see Figure 4.1). These reefs are characterised by shallow reef flats (1m at high tide) that are exposed at extreme low tides, and all margins of reef descend rapidly to over 20m down steep reef slopes or vertical walls. Reefs are separated by depths of over 50m.

The broad-scale physical characteristics (the degree to which the reef projected seawards and the incline of the reef slope) were calculated from aerial photographs of the 4 reefs taken in 2004. The biotic and fine-scale physical characteristics were measured at 6 sites each on Hanging Gardens, Maya’s and Limuka (see Figure 4.1). At least 2 sites on each reef were known to be locations where *Ctenochaetus striatus* formed spawning aggregations (Hanging Gardens Sites 1,3 & 6, Maya’s Sites 1 & 4, Limuka Sites 1,2,3 & 5), and at least 2 sites were known to be locations where no such aggregations were formed (Hanging Gardens Sites 2, 4, & 5, Maya’s Sites 2,3,5 & 6, and Limuka Sites 4 & 6). The latter sites cannot be regarded as random because they were preferentially chosen from margins of reef with prominent seaward projections (a feature shown in this study to be characteristic of *C. striatus* spawning aggregation sites; see results). If no such areas of reef were available, then sites were chosen randomly from the remainder of the reef.

4.2.3 Broad-scale physical characteristics:

The degree to which the reef projected in a seaward direction was calculated from aerial photographs of the reefs. Sections 20m long were taken across the 1m depth contour so that each end of the section lay on the contour. The scale of the sections was set at 20m because smaller sections also failed to identify seaward projections, and larger sections were not appropriate to the spatial scale of spawning aggregation formation. The 1m depth contour was used because this was the depth at which *Ctenochaetus striatus* formed spawning aggregations. The distance of the 1m contour perpendicular to this section was calculated at 2m intervals (excluding the 2 end points of the section). This distance was negative if the 1m contour bent back towards the reef in a concave manner, and positive if projecting seawards. The maximum distance for each site was obtained from these 9 measurements (see Figure 4.2). The maximum seaward projection was calculated at all known *C. striatus* spawning aggregation sites on Hanging Gardens, Kume, Limuka and Maya’s reefs. The remainder of each reef was divided up into 20m sections along the 1m depth contour and maximum seaward projection was calculated perpendicular to all of these additional sections. Measurements were not taken on the back reef area of Kume (the south-western margin from Site 1 to Site 16; see Figure 4.1) because searches for spawning aggregations of *C. striatus* were not performed on this section of reef. For each section, the maximum seaward projection was the measure chosen rather than the mean of the 9 measurements because the latter failed to identify many seaward projections.

The reef slope was measured on 2 scales: the slope from 1m to 5m, and 1m to 10m. Measurements were taken from the 1m, 5m and 10m depth contours estimated from aerial photographs of Hanging Gardens, Kume, Limuka, and Maya’s reefs, and the slope was calculated by means of trigonometry. The maximum slope (closest to vertical) was calculated at the two end points of each 20m section used for the maximum seaward projection measurements and at 9 additional points along the 1m contour within the section. In this way the mean slope was calculated both at 1 to 5m and 1 to 10m at all *Ctenochaetus striatus* spawning aggregation sites and at all other margins of all 4 reefs (except the back reef of Kume; see above).

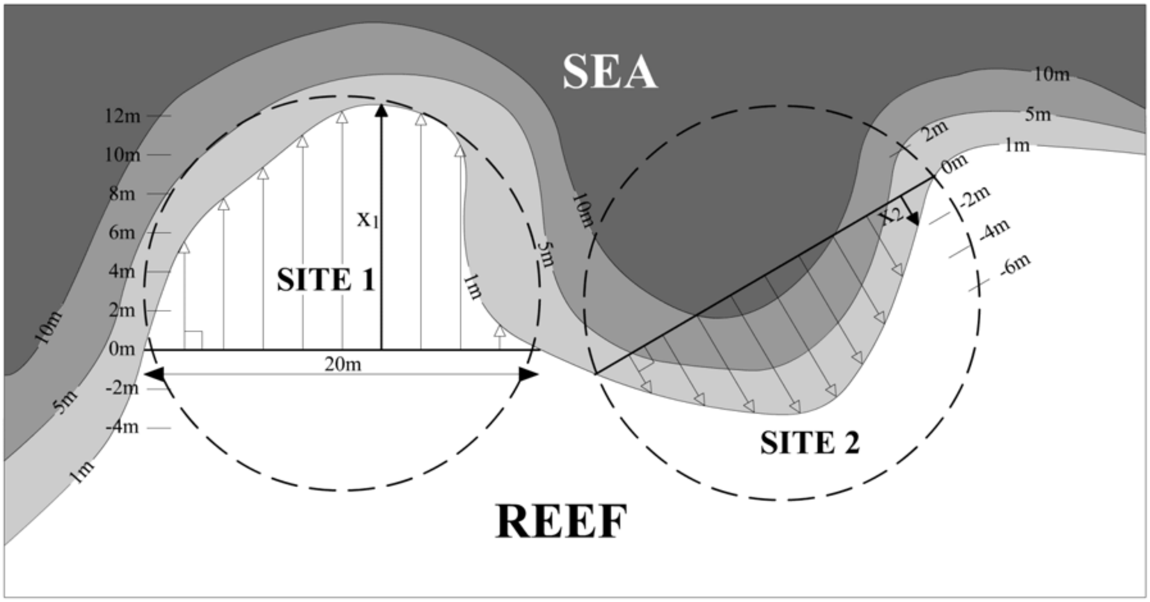

Figure 4.2. Measurement of maximum seaward projection at convex (Site 1) and concave (Site 2) areas of reef. x_1 = maximum seaward projection at Site 1; x_2 = maximum seaward projection at Site 2.

4.2.4 Fine-scale physical and biotic characteristics:

At each of the 6 sites on Hanging Gardens, Limuka and Maya's, the potential refuge from pisicvorous predators afforded to *Ctenochaetus striatus* by the substratum was measured along 4 randomly placed 10 m long transects. 10m long transects were chosen because this was the maximum length that could be used whilst still exclusively representing the site in question. Potential refuge from predation was measured directly by counting the number of holes lying under each transect line. Holes were counted only if they were of a size that could be used by *C. striatus* as shelter whilst also being too small for piscivores to enter (holes of a maximum diameter between 6 to 20cm). Potential refuge was also estimated indirectly from a measure of topographic complexity. Topographic complexity was measured using the contoured vs. linear length ("chain and tape") method (Risk 1972).

4.2.5 Piscivorous and planktivorous fishes:

The abundance of piscivorous and planktivorous fishes was measured at sites in order to investigate whether the densities of predatory fishes (both of spawning adults and eggs) were reduced at sites and times where and when *Ctenochaetus striatus* formed spawning aggregations. This was achieved by recording all fishes found within a radius of 5m from a fixed point in each site during a 2 minute interval, categorising fish seen as: spawners, piscivores, planktivores, and egg predators. Piscivores of interest were those deemed capable of preying upon *C. striatus* (carangids, carcharhinids, lutjanids, scombrids, and serranids >30cm S.L.). Because of the low densities of piscivores, their presence was further established by means of a timed (3 minute) swim around each site recording piscivores up to a depth of 7.5m. Planktivorous fishes were further categorised as those that consumed eggs within seconds of being spawned whilst the gamete cloud was still visible by targeting the apex of spawning rushes, hereafter referred to as *target egg predators*, and those that did not. On any given day, data were collected at a single reef, moving round the reef from one site to the next from early afternoon until sunset. In this fashion a record of the assemblage of planktivorous and piscivorous fishes was established for each site at varying times in the afternoon. This was necessary because the abundance and activity of piscivores and planktivores is known to vary throughout the day (Hobson 1974, 1975, Hobson & Chess 1978, Danilowicz & Sale 1999). For sites where *C. striatus* formed spawning aggregations, the assemblage of fishes within sites was established at both times of aggregative spawning and at times of no such spawning. The wet weight biomass of planktivores was estimated by length-weight relationships in Froese and Pauly (2000). The estimate of wet weight biomass gave a measure of planktivory that could be compared between sites and times. Data were collected over 27 days at Hanging Gardens, 19 days at Limuka and 31 days at Maya’s, and represent over 300hrs of observations spread over days in March, April, May, October and November in 2003.

4.2.6 Data analyses:

Seaward projection and slope- Data from each reef were treated separately. Student’s t-tests were used to compare means from spawning aggregation sites with means from non spawning aggregation sites within a reef for maximum seaward projection and for incline of reef slope data (both 1 to 5m and 1 to 10m). Williams corrected goodness of fit G-tests were used to test whether spawning aggregations were formed at sites on Kume with greater seaward projection at a significantly higher frequency than that predicted by a random distribution of sites. Such G-tests could not be performed on data from other reefs because there were too few spawning aggregation sites for analyses (expected frequencies were too low; Sokal & Rohlf 1995).

Fine-scale physical, piscivore and planktivore data- For each reef, separate 2-factor one-way ANOVA's were used to compare topographic index, number of holes, planktivore biomass, target egg predator biomass, and piscivore abundance. Factors were (1) spawning aggregation site vs. site where no aggregation formed, and (2) site. Student's t-tests were used to compare planktivore biomass, target egg predator biomass, and piscivore abundance at times of spawning aggregation formation and at other times within spawning aggregation sites.

STATISTICA 6 statistics package was used for ANOVA and t-test analyses. Zar (1999) χ^2 tables were consulted for p-values of G-tests. α-levels for all analyses were 0.05.

4.3 Results:

4.3.1 Seaward projection of reef margin:

All sites where *Ctenochaetus striatus* formed spawning aggregations were found on areas of reef that projected seawards (i.e. all sites were on convex margins of reef). On all reefs spawning aggregations were formed at sites where the reef margin projected further seawards than other areas of reef (see Figure 4.3). However, this relationship was only significant at two of the four reefs, with Maya's having insufficient data for analysis (see Figure 4.3 and Table 4.1). Not all prominent seaward projections were used as spawning aggregation sites: areas of reef where spawning aggregations were not formed included sites where the reef margin projected further seawards than at some of the spawning aggregation sites. However, on Kume spawning aggregations were formed at sites with greater seaward projection at a significantly higher frequency than that predicted by a random distribution of sites (Williams corrected goodness of fit G-test: G_{adj} = 17.26, df =

1, $p < 0.001$). Such G-tests could not be performed on data from other reefs because there were too few spawning aggregation sites for analyses (expected frequencies were too low; Sokal & Rohlf 1995).

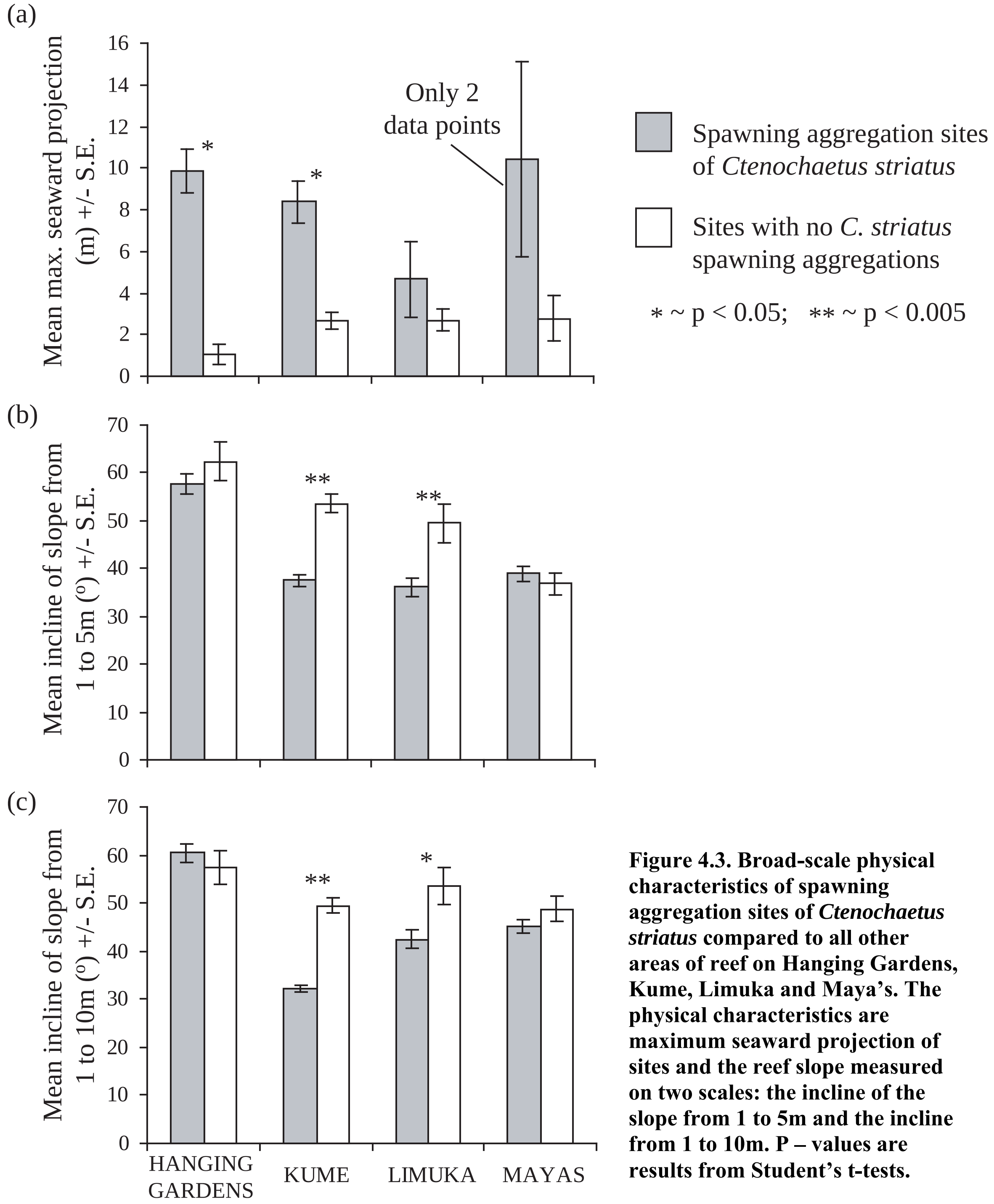

Figure 4.3. Broad-scale physical characteristics of spawning aggregation sites of *Ctenochaetus striatus* compared to all other areas of reef on Hanging Gardens, Kume, Limuka and Maya's. The physical characteristics are maximum seaward projection of sites and the reef slope measured on two scales: the incline of the slope from 1 to 5m and the incline from 1 to 10m. P – values are results from Student's t-tests.

4.3.2 Reef slope:

The incline of the reef slope ranged from 3 to 90^o and 5 to 90^o (shallow incline to vertical drop) at scales of 1 to 5m and 1 to 10m respectively. However, despite a hypothetical enhancement to the survival of eggs spawned from areas of reef with steeper reef slopes, spawning aggregations were not formed exclusively at such locations: at Kume and Limuka spawning aggregation sites were found on margins of reef with significantly less steep slopes than the other areas of reef, whilst on Hanging Gardens and Maya's there were no significant differences (see Figure 4.3 and Table 4.1).

Table 4.1. Broad-scale physical data: results of Student's t-tests between spawning aggregation sites and all other sites on reefs for maximum seaward projection of sites, incline of reef slope from 1 to 5m, and incline of reef slope from 1 to 10m. *~ p < 0.05; **~ p < 0.005.

		t-value	df	P
Max. seaward projection	Hanging Gardens	7.199	27	0.000**
	Kume	6.753	59	0.000**
	Limuka	1.156	20	0.261
	Maya's	Insufficient data	/	/
Incline of reef slope 1 to 5m	Hanging Gardens	0.844	317	0.399
	Kume	6.233	935	0.000**
	Limuka	2.914	240	0.004**
	Maya's	0.493	185	0.623
Incline of reef slope 1 to 10m	Hanging Gardens	0.545	317	0.586
	Kume	10.575	935	0.0000**
	Limuka	2.578	240	0.011*
	Maya's	1.010	185	0.314

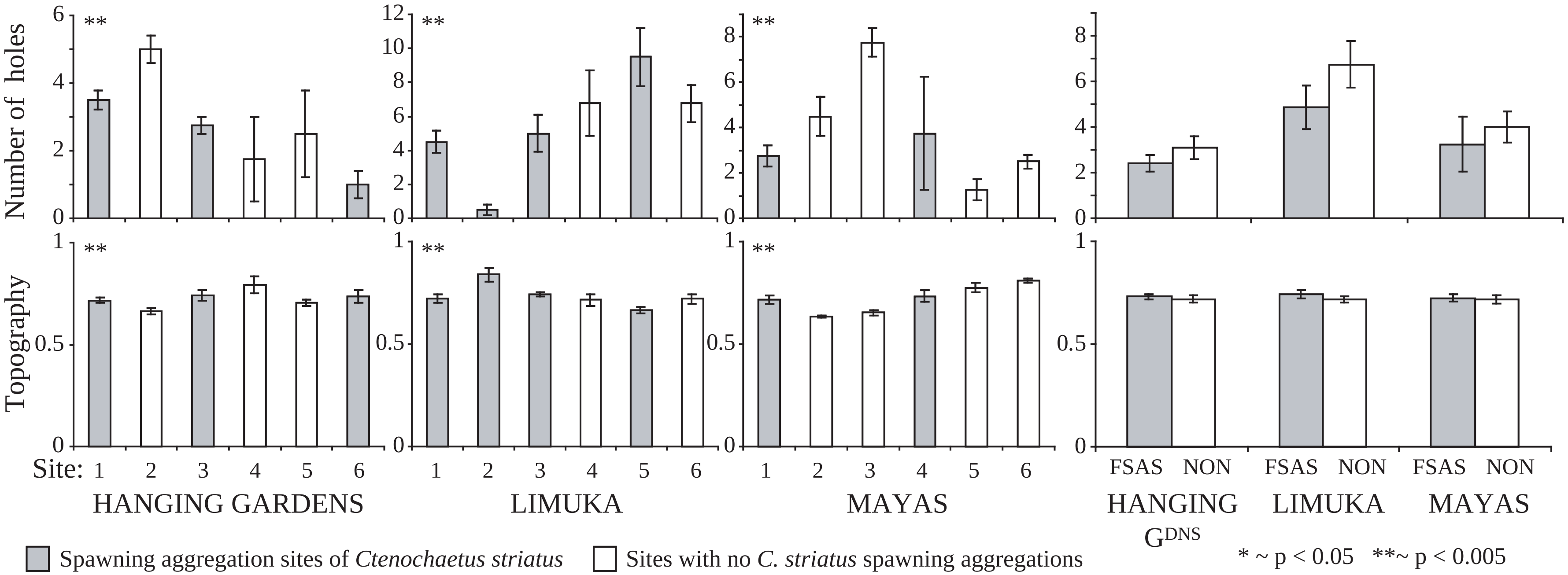

Figure 4.4. The mean number of holes in the substratum (between 6 and 20 cm maximum aperture), and topographic complexity (Topography; 1 = flat, <1 =topographically complex) +/- S.E. at all 6 sites on Hanging Gardens, Limuka and Maya's. The means for all spawning aggregation sites (FSAS) vs. sites where spawning aggregations are not formed (NON) are also shown. P - values are the resultant probabilities from one-way ANOVA's.

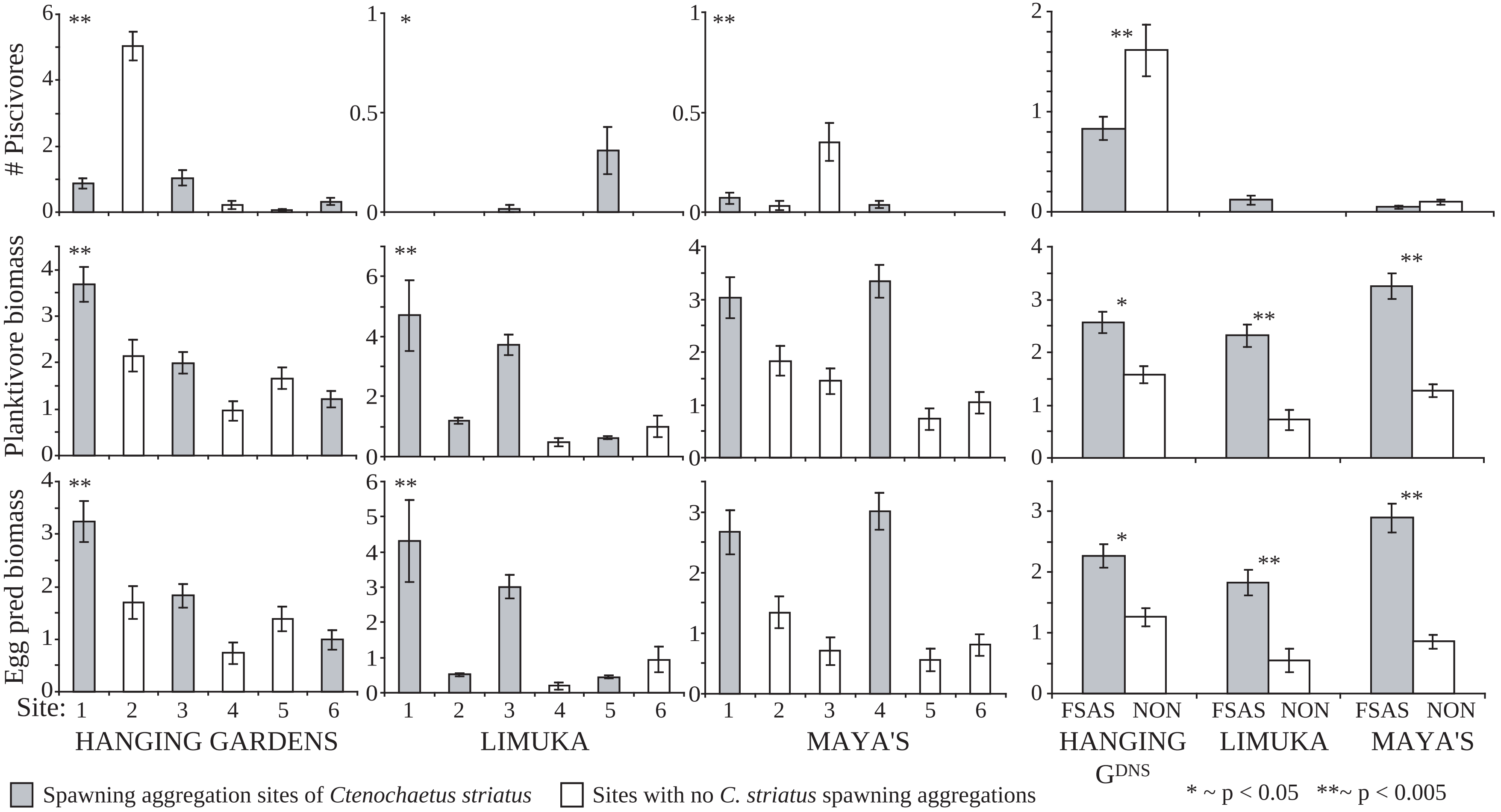

Figure 4.5. The piscivore presence (number of individuals) and planktivore biomass (kg) at study sites: the abundance of piscivores (>30cm S.L.), the estimated biomass of all planktivores, and the estimated biomass of target egg predators (Egg pred) at all sites on Hanging Gardens, Limuka and Maya's, and the means for all spawning aggregation sites (FSAS) vs. sites where spawning aggregations are not formed (NON) are also shown. All values are means +/- S.E. P - values are the resultant probabilities from one-way ANOVA's.

Table 4.2. Results of one-way ANOVA's comparing number of holes, topographic complexity, number of piscivores (>30cm S.L.), total planktivore biomass, and target egg predator biomass between spawning aggregation sites and other sites (*spawning sites vs. non*) within reefs, and between all 6 sites on the reef (*among sites*). * ~ p < 0.05; ** ~ p < 0.005.

Source of variation:		Spawning sites vs. non		Among sites	
		$F_{(1,18)}$	P	$F_{(4,18)}$	p
# Holes	Hanging G$^{\underline{dns}}$	3.097	0.095	9.083	0.0001**
	Limuka	2.948	0.103	6.396	0.0022**
	Maya's	5.684	0.461	4.666	0.0093**
Topographic complexity	Hanging G$^{\underline{dns}}$	0.454	0.509	5.153	0.006**
	Limuka	1.546	0.230	7.343	0.0011**
	Maya's	0.144	0.708	16.980	0.00001**
		F	P	F	p
# Piscivores (>30cm S.L.)	Hanging G$^{\underline{dns}}$	$F_{(1,317)}$ =24.692	0.000001**	$F_{(4,317)}$ =51.325	0.000001**
	Limuka	$F_{(1,172)}$ =0.731	0.394	$F_{(4,172)}$ =3.346	0.011*
	Maya's	$F_{(1,461)}$ =1.931	0.165	$F_{(4,461)}$ =13.040	0.000001**
Total planktivore biomass	Hanging G$^{\underline{dns}}$	$F_{(1,317)}$ =5.811	0.016*	$F_{(4,317)}$ =10.162	0.000001**
	Limuka	$F_{(1,172)}$ =21.026	0.00001**	$F_{(4,172)}$ =24.113	0.000001**
	Maya's	$F_{(1,461)}$ =47.114	0.000001**	$F_{(4,461)}$ =1.343	0.253
Target egg predator biomass	Hanging G$^{\underline{dns}}$	$F_{(1,317)}$ =6.441	0.012*	$F_{(4,317)}$ =7.849	0.000005**
	Limuka	$F_{(1,172)}$ =15.063	0.0001**	$F_{(4,172)}$ =21.059	0.00001**
	Maya's	$F_{(1,461)}$ =53.158	0.000001**	$F_{(4,461)}$ =0.846	0.497

4.3.3 Refuge from predation:

The potential refuge from predation afforded to *Ctenochaetus striatus* by the substratum at sites, as estimated by number of size-specific holes and topographic complexity, varied significantly between sites within reefs (see Figure 4.4 and Table 4.2). However, the choice of spawning aggregation sites did not appear to take advantage of refuge from piscivores: on all three reefs, there was no significant difference between the number of holes in the reef nor the topographic complexity between sites where spawning aggregations were formed and those not home to such aggregations (see Figure 4.4 and Table 4.2).

4.3.4 Piscivores:

The piscivores >30 cm S.L. observed included species of Carcharinidae, Carangidae, Lethrinidae, Lutjanidae, and Serranidae. The abundance of these piscivores was generally low, with 6 out of 18 sites having a complete absence of piscivores >30cm S.L. (see Figure 4.5). It is unlikely that piscivores are maintained at an artificially low level by fishing pressure: although artisanal fishing occurs, this is at very low intensities, and fishing is prohibited altogether on Limuka. However, due to the nature of cryptic piscivores, it is likely their presence was underestimated especially at crepuscular times. Not one predatory attack on *Ctenochaetus striatus* was witnessed during observations that spanned over 1000hrs and include over 10,000 separate spawns of *C. striatus*. The only successful predatory attacks on any species occurred when two lutjanids attacked a bait ball (high-density school of several 1000 baitfish). Piscivores swam through sites on only 21 occasions. These predators were exclusively carangids (90.5%) and scombrids (9.5%), and on all but 2 occasions they swam through and disrupted spawning aggregations of *C. striatus*. On the 2 remaining occasions the spawning activities of labrids (*Cheilinus trilobata*, *Epibulis insidiator*) and a scarid (*Chlororus bleekeri*) were interrupted. Although potential prey sought refuge within the reef or advanced closer to it, the piscivores swam through sites at speeds well below that which would be considered a predatory attack. Such behaviour occurred significantly more often during spawning aggregations of *C. striatus* than predicted by sampling effort alone (Williams corrected G-test: $G_{adj} = 41.6$, df = 1, $p < 0.001$). However, the mean abundance of piscivores at spawning aggregation sites was only significantly greater than the mean at other sites on one reef, Hanging Gardens (see Figure 4.5 and Table 4.2). Furthermore, there were no significant differences between the abundance of piscivores at times of spawning aggregation formation than at other times at any of the spawning aggregation sites on any of the 3 reefs (see Table 4.3 and see Figure 4.6).

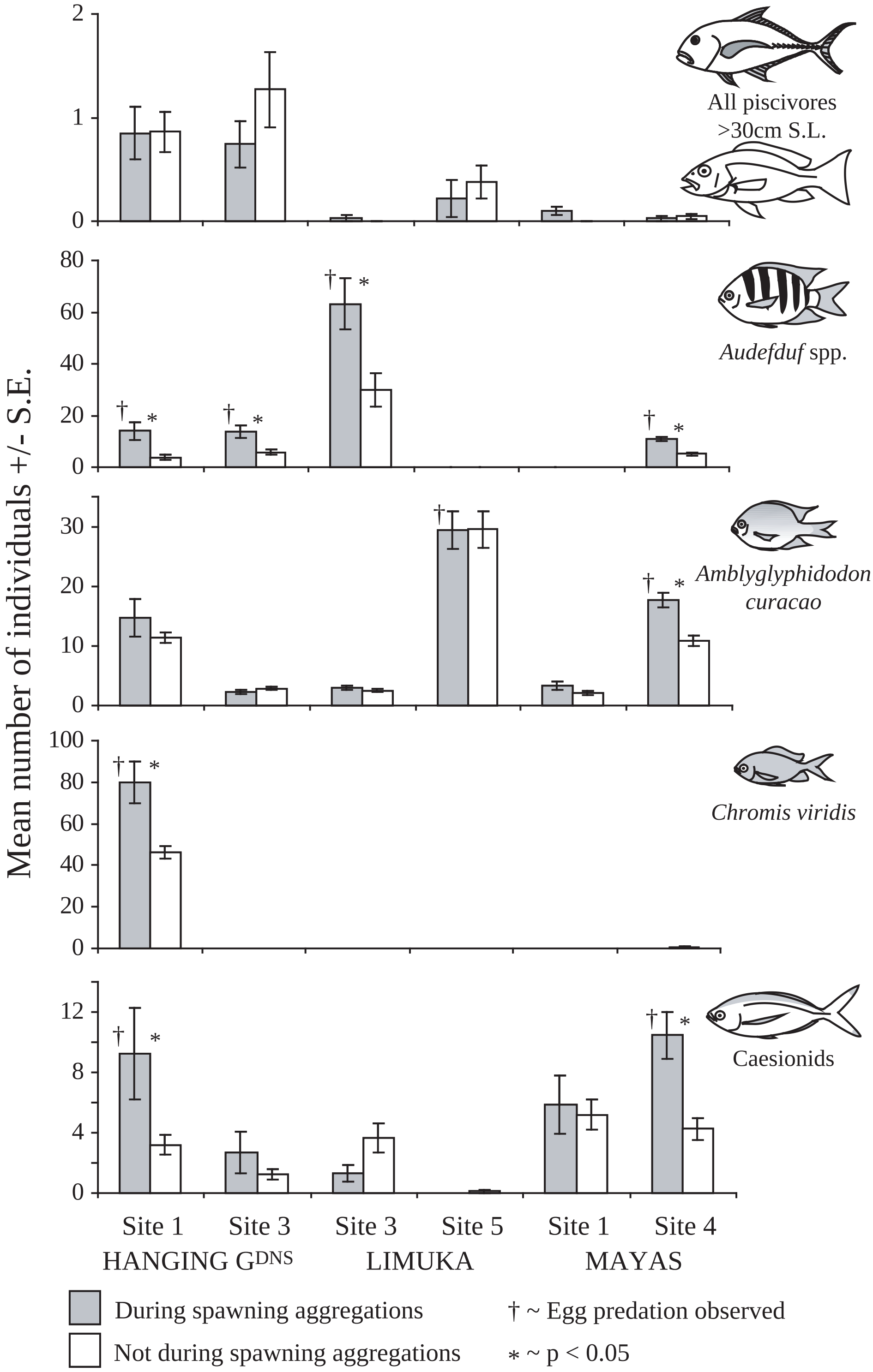

Figure 4.6. The abundance of piscivores and target egg predators at spawning aggregation sites at times when spawning aggregations are formed and at times when they are not. Only piscivores >30cm S.L. were included. Target egg predators illustrated are *Abudefduf* spp., *Amblyglyphidodon curacao*, *Chromis viridis*, and caesionids. Only sites with sufficient observations during spawning aggregations were included. P-values are the results of Student's t-tests between the abundance at times of spawning aggregation formation and abundance at other times.

Table 4.3. The response of piscivores (>30 cm S.L.) to spawning aggregation formation. t-values and p-values are results of Student's t-tests between mean abundance piscivores during spawning aggregations and at other times within the site. Only spawning aggregation sites with sufficient data were included.

		Significantly greater abundance of piscivores during spawning aggregations?			
		√/X	t-value	df	p
Abundance of piscivores (>30 cm S.L.)	Hanging G$^{\underline{dns}}$ Site 1	X	1.41	90	>0.15
	Hanging G$^{\underline{dns}}$ Site 3	X	0.34	81	>0.7
	Limuka Site 3	X	1.18	55	>0.2
	Limuka Site 5	X	0.64	50	>0.5
	Maya's Site 1	X	0.69	70	>0.4
	Maya's Site 4	X	0.90	159	>0.35

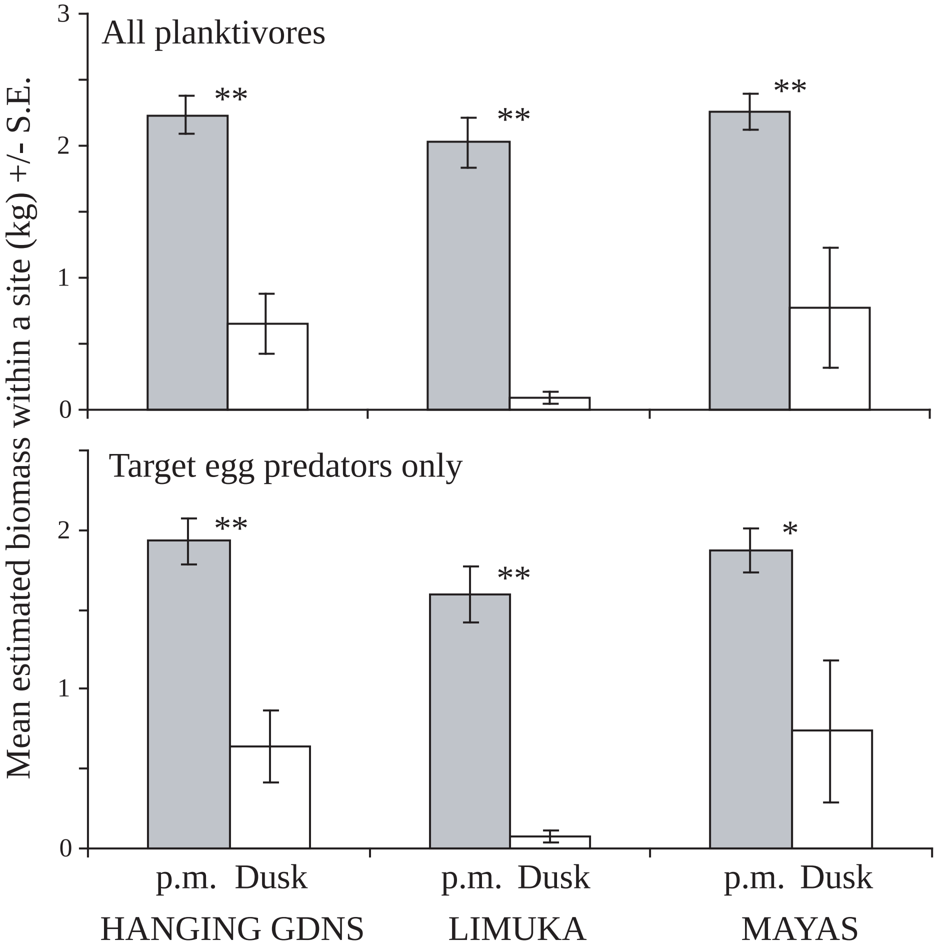

Figure 4.7. Mean estimated biomass of all planktivores and target egg predators only at times in the afternoon (p.m.) and at dusk (17:45 – 18:20 hrs). Means derived from data from all sites within reefs. * ~ $p < 0.05$; **~ $p < 0.005$. p – values are results of Student's t-tests between mean biomass in the afternoon and mean at dusk.

4.3.5 Planktivores:

Several species of planktivore were observed consumed eggs within seconds of being spawned by targeting the apex of *Ctenochaetus striatus* spawning rushes whilst gamete clouds were still visible (see Table 4.4 for list of target egg predators). The relative number of spawns attacked by these target egg predators was too difficult to quantify because of the rapid succession of spawns (>10 sec^{-1}) within a small area and often large numbers of fishes feeding on eggs. However, target egg predation was observed during every spawning aggregation of *C. striatus*. Unlike pelagic spawning reef fish from other families which were observed delaying spawning in the presence of target egg predators or chasing them away, *C. striatus* continued spawning despite heavy losses of eggs. In this way *C. striatus* released eggs within cms of awaiting target egg predators.

The estimated biomass of planktivores and target egg predators was significantly higher on all reefs at times in the afternoon compared to dusk (between 17:45 and 18:20hrs; see Figure 4.7 and Table 4.5). However, aggregative spawning of *Ctenochaetus striatus* was only witnessed once during this period, with all other spawning occurring during the more planktivore-rich times in the afternoon.

The potential threat to eggs posed by planktivores appears to be greater at spawning aggregation sites than at alternative sites on reefs: on all three reefs the estimated biomass of planktivores in general and the biomass of species known to be target egg predators were significantly greater at spawning aggregation sites (see Figure 4.4 and Table 4.2). Additionally, some species of target egg predator appear to be attracted to spawning aggregations of *Ctenochaetus striatus*, moving from locations outside the sampling area to feed on spawned eggs: with the exception of sites where *Abudefduf* spp. were never seen, the mean abundances of *Abudefduf* spp. were significantly higher at times when spawning aggregations were formed than at other times within all spawning aggregation sites for which sufficient data were available for analyses (see Figure 4.6 and Table 4.6). Whenever *C. striatus* spawned, all *Abudefduf* spp. within the sampling area fed exclusively above the aggregation of surgeonfish. No other species of target egg predator displayed such a strong behavioural response to *C. striatus* spawning: despite being present at sites during aggregative spawning, *Chromis viridis*, *Amblyglyphidodon curacao*, and species of caesionid were not always observed feeding on spawned eggs. Furthermore, these egg predators were not observed feeding on spawned eggs in all *C. striatus* spawning aggregation sites in which they were found (see Figure 4.6 and Table 4.6). However, with only one exception, these egg predators were found in significantly higher numbers during *C. striatus* spawning aggregations at all sites in which they were observed feeding on *C. striatus* eggs (see Figure 4.6 and Table 4.6). The only exception to this was *A. curacao* at Limuka Site 5. Nonetheless, *A. curacao* also appeared to be attracted to this spawning aggregation. The data do not reflect this because the spawning aggregation was so large (over 1000 individuals) that most of it lay outside of the sampling area and individuals attracted to the aggregation were also found outside the sampling area.

Table 4.4. Species observed feeding on eggs spawned by *Ctenochaetus striatus* on the inshore reefs of Kimbe Bay.

Family	**Genus**	**Species**
Balistidae	*Melichthys*	*vidua*
Caesionidae	Unidentified spp.	(>10cm S.L.)
Labridae	*Thalassoma*	*hardwicke*
	Thalassoma	*lunare*
Lutjanidae	*Macolor*	*niger* (juvenile)
Pomacentridae	*Abudefduf*	unidentified spp.
	Acanthochromis	*polyacanthus*
	Amblyglyphidodon	*curacao*
	Amblyglyphidodon	*leucogaster*
	Chromis	*viridis*
Scombridae	*Rastrelliger*	*kanagurta*

Table 4.5. The results of Student's t-tests between the mean biomass of planktivores and target egg predators at times in the afternoon and at dusk (17:45 – 18:20hrs).

		Is biomass in afternoon significantly greater than at dusk?			
		√/X	t-value	df	p
Mean planktivore biomass	Hanging G$^{\underline{dns}}$	√	3.720	360	<0.0005
	Limuka	√	3.549	197	<0.0005
	Maya's	√	3.316	518	<0.001
Mean target egg predator biomass	Hanging G$^{\underline{dns}}$	√	3.088	360	<0.005
	Limuka	√	2.954	197	<0.005
	Maya's	√	2.594	518	<0.01

Table 4.6. Feeding responses of target egg predators, *Abudefduf* spp., *Amblyglyphidodon curacao*, *Chromis viridis* and species of caesionid, to spawning aggregations of *Ctenochaetus striatus*. Only sites where egg predators were present are included. Egg pred$^{\underline{n}}$ ~ feeding on spawns of *C. striatus* observed at site; t-value and p-values are results of Student's t-tests between mean abundance of egg predators during spawning aggregations and at other times within the site. Only spawning aggregation sites with sufficient data were included. † ~ significantly less egg predators during spawning aggregations.

		Egg pred$^{\underline{n}}$?	Significantly greater abundance of egg predators during spawning aggregations?			
		√/X	√/X	t-value	df	p
Abudefduf spp.	Hanging G$^{\underline{dns}}$ Site 1	√	√	3.78	90	<0.0005
	Hanging G$^{\underline{dns}}$ Site 3	√	√	3.34	81	<0.002
	Limuka Site 3	√	√	2.77	55	<0.01
	Maya's Site 4	√	√	5.11	159	<0.0001
Amblyglyphidodon curacao	Hanging G$^{\underline{dns}}$ Site 1	X	X	1.35	90	>0.15
	Hanging G$^{\underline{dns}}$ Site 3	X	X	1.37	81	>0.15
	Limuka Site 3	X	X	1.08	55	>0.25
	Limuka Site 5	√	X	0.04	50	>0.95
	Maya's Site 1	X	X	1.73	70	>0.05
	Maya's Site 4	√	√	17.73	159	<0.0001
Chromis viridis	Hanging G$^{\underline{dns}}$ Site 1	√	√	4.12	90	<0.0001
	Maya's Site 4	X	X	1.93	159	>0.05
Caesionids	Hanging G$^{\underline{dns}}$ Site 1	√	√	2.91	90	<0.005
	Hanging G$^{\underline{dns}}$ Site 3	X	X	1.36	81	>0.15
	Limuka Site 3	X	X†	2.01	55	<0.05
	Limuka Site 5	X	X	0.63	50	>0.5
	Maya's Site 1	X	X	0.27	70	>0.75
	Maya's Site 4	√	√	4.10	159	<0.0001

4.4 Discussion:

4.4.1 Seaward projections and reef slope:

Spawning aggregations of *Ctenochaetus striatus* were formed at areas of reef projecting seawards rather than straighter margins of reef, but there was no consistent pattern to the incline of the reef slope at spawning aggregation sites. Hypothetically, eggs spawned from sites projecting further seawards are more likely to be swept away from reefs and are therefore less likely to be consumed by reef-associated planktivores. However, some of the most prominent points on the study reefs were not used by *C. striatus* as spawning sites, and in a separate study, the currents at spawning aggregation sites did not sweep eggs more rapidly or more frequently away from reefs (see Chapter 5). Therefore, convex margins of reef may be favoured for reasons other than egg survival. One explanation is that the spatial synchrony of spawning aggregation formation is facilitated by forming at sites with more readily distinguishable features (Colin & Clavijo 1988). Outside of spawning aggregation formation, the activities of most individuals would be spatially separated from the site in which they spawn. They would therefore have limited familiarity with the site in question and may rely on distinctive broad-scale features in order to recognise it. The further a species migrates to spawn, the more compelling this case becomes because individuals have to distinguish a spawning aggregation site from a greater area of unfamiliar reef. Whilst spawning aggregations are known to be formed at a range of reef features both within and between species (see Chapter 2, Domeier et al. 2002, and Claydon 2004), on the study reefs, seaward projections are one of the few distinguishing features available to *C. striatus* at this species' scale of spawning aggregation formation.

4.4.2 Refuge from predation:

A wealth of anecdotal evidence suggests that pelagically spawning reef fish are preyed upon at higher rates during reproductive activities (Robertson 1983, Thresher 1984, Moyer 1987, Colin & Bell 1991, Johannes et al. 1999), a notion with limited empirical support (but see Sancho et al. 2000a). Accordingly, it is unsurprising that aggregative spawning has been observed occurring over habitat that is more topographically complex or has greater numbers of holes in which spawners can evade predatory attacks (Beets & Friedlander 1998, Johannes et al. 1999, Sancho et al. 2000a). However, these observations pertain to differences between the habitat within spawning sites rather than between a range of potential sites. In the present study, *Ctenochaetus striatus* did not spawn in aggregations at sites with greater potential refuge from predation. The immeasurably low levels of piscivory in the study area may be too weak to drive such selection, but even under higher predation pressures it remains unlikely that greater refuge from predation will be a characteristic feature of the substratum over which spawning aggregations are formed. Firstly, shallow coral reefs are dynamic environments where dramatic changes in the benthos are evident between successive years (see Connell et al. 1997). As the benthos and substratum within a site change due to various biotic and physical disturbances so does the relative shelter from predators that they represent, yet spawning aggregations form at the same site for decades (Johannes 1981, Aguilar-Perera 1994, Colin 1996) and even centuries (Johannes & Riepen 1995). Thus, the persistence of aggregative spawning at the same site over such prolonged timescales is unlikely to be attributable to comparative assessments of the potential refuge from predators. However, the broader-scale physical characteristics of shallow reefs will persist over time periods longer than or comparable to spawning aggregation longevity. Thus, in the present study, it is unsurprising that the only feature of the substratum distinguishing spawning aggregation sites from alternative areas (the degree of convexity/concavity of the reef margin) fell within this more geological scale. Secondly, during reproductive activities, certain species in some locations display “spawning stupor”, a lack of wariness to predators (Johannes 1981). In such cases, the potential refuge from predators afforded by the substratum is irrelevant because spawning adults do not seek shelter from predatory attacks (Johannes 1981, Robertson 1983).

4.4.3 Piscivores and planktivores:

In the present study, piscivory was inestimably low whereas egg predation was intense. The lack of predatory attacks on adult *Ctenochaetus striatus* does not appear to be facilitated by the location and timing of spawning, but rather due to the generally low threat from piscivores on this surgeonfish on the inshore reefs of Kimbe Bay. The location and timing of aggregative spawning did not reduce the heavy loss of eggs to planktivores: there were greater biomasses of planktivores and target egg predators at spawning aggregation sites, and spawning occurred in the afternoon rather than at the less planktivore-rich period around dusk. Additionally, target egg predators were attracted to spawning aggregations. Thus, predation did not appear to play an important role in the timing or location of spawning aggregation formation in *C. striatus*.

Apart from *Abudefduf* spp., the feeding response of target egg predators was variable between sites within species, with pelagically spawned eggs being an important component of the diet of *Amblyglyphidodon curacao*, *Chromis viridis* and species of caesionid at one site, even attracting individuals to the aggregation, whereas conspecifics found at other sites did not prey on eggs at all. Quite why this is the case is unclear: egg predation in some species may have some form of density dependency, both in terms of the numbers of spawners and the numbers of planktivores; it may be a behaviour that has not been learned at all sites, or preying recently spawned eggs may expose planktivores to unacceptably high risks of predation at some sites rather than others. However, this study presents no empirical support for such speculation.

Some similar studies also reveal low rates of predation on aggregatively spawning acanthurids (Colin & Clavijo 1988, Craig 1998). However, high predation rates are more frequently documented (Johannes 1981, Robertson 1983, Johannes et al. 1999, Sancho et al. 2000a). Amongst all species of aggregatively spawning reef fish, egg predation also varies from being intense (Colin 1976, Meyer 1977, Craig 1998, Heyman et al. 2001) to negligible (Colin & Bell 1991, Colin 1992) between locations. Irrespective of the geographic variability in the intensity of predation, spawning aggregations represent predictable, high-density, readily exploitable sources of food to which certain piscivorous and planktivorous predators are attracted. Spawning aggregations are predictably exploited not only by individuals resident to the reef in question, such as the species of pomacentrid and caesionid egg predators in the present study, but also by larger less site-restricted fish such as the whale shark, *Rhincodon typus*, which aggregates to feed on eggs at a spawning aggregation of lutjanids in Belize (Heyman et al. 2001). The relative importance of these trophic links, both at the level of the individual predators and the populations from which they come, is hard to estimate from presently available data, but would be a valuable area of research to explore, with intriguing implications on fecundity and larval quality of offspring between conspecifics that target eggs and those that do not (see McCormick 2003).

4.4.4 Continued spawning despite predation of eggs:

It is curious that *Ctenochaetus striatus* continued to spawn regardless of the loss of its eggs to target egg predators. This is analogous to spawning stupor, the uninterrupted spawning behaviour despite predatory attacks on adults that has been documented at some spawning aggregations (Johannes 1981, Robertson 1983). This is especially curious because such disregard to egg predators appeared to be unique to acanthurids. Having sustained the unwarranted attention of planktivores during reproductive activities, all pelagically spawning fish from other families were observed attempting to limit the loss of their eggs to these predators. These smaller aggregations or discrete pairs typically elicited interest of solitary target egg predators. Many delayed spawning. Some chased target egg predators away, and others were even observed to forgo spawning altogether. It is therefore important to ask why *C. striatus* does not also display such behavioural responses.

With large groups of spawning fish such as the aggregations of up to 1000 individuals in the present study, it may be inevitable that large numbers of planktivorous fish are attracted to feed on the eggs. Attempting to chase away such large numbers of egg predators may be a relentlessly futile activity, being energetically expensive and serving only to jeopardise the spawning opportunities of those individuals engaged in the pursuit. Attempting to out-wait planktivores by delaying spawning may be equally futile in large aggregations: planktivores are rewarded for their wait by the guarantee of a plentiful and rich source of food. Thus, in the context of large spawning aggregations, there may be no advantage in behaving like fish from other families. However, disregard to egg predation may be phylogenetic: none of the 6 species of surgeonfish observed spawning in Kimbe Bay (see Chapter 3) ever chased awaiting egg predators away. Only two of these species, *Acanthurus lineatus* and *Acanthurus triostegus*, were also known to form spawning aggregations of more than 100 individuals, and all species including *Ctenochaetus striatus* had been observed spawning on occasions in aggregations of less than 10 individuals.

Ctenochaetus striatus may not respond to egg predators in the same fashion as species from other families, but it does appear to employ an alternative strategy to limit the loss of its eggs to planktivores. The synchrony with which spawning occurred within *C. striatus* aggregations was impressive. The first spawn triggered a succession of spawns from other groups at a rate of often more than 10 per second. In this fashion, all spawns from aggregations of up to 1000 fish were completed in only a few minutes. This resulted in a large number of eggs from many females being released into the water column almost simultaneously and within close proximity of one another. With an upper rate of consumption limited by handling time (sensu Holling 1959), a spatially and temporally restricted pulse of eggs may be less efficiently preyed upon than a more prolonged pulse. Thus, loss of eggs to planktivores is likely to be reduced by predator satiation/saturation (Johannes 1978, Claydon 2004, and see Chapter 2). Predator satiation/saturation may be a particularly effective strategy when egg predators restrict feeding to a limited period following gamete release, a feeding characteristic observed in this study and elsewhere (Colin & Bell 1991, Sancho et al. 2000a).

4.5 Conclusion

Breeding migrations are traditionally explained by the spatial separation of suitable breeding and feeding habitat. However, within the context of predation, there is little evidence that spawning aggregation sites of *Ctenochaetus striatus* in Kimbe Bay are any more suitable as locations from which to spawn pelagic eggs than alternative areas of reef. Sites with distinctive broad-scale characteristics persisting over time, such as seaward projecting margins of reef, may be selected as landmarks in order to facilitate the spatial synchrony of spawning aggregation formation. Several aspects of the spawning aggregation formation in *C. striatus* appeared to enhance the loss of eggs to predators: higher planktivore biomass at spawning aggregation sites, the attraction of egg predators to spawning aggregations, and spawning at times of the day whilst planktivore presence was high. However, loss of eggs to predators may be limited by the spatial and temporal synchrony of spawning within aggregations, overwhelming predators with potential prey. Thus, any selective advantage derived from spawning aggregation formation appears to lie in the aggregative phenomenon itself rather than in its location or timing.

CHAPTER 5: SPAWNING AGGREGATIONS AND CURRENTS

5.1 Introduction

Pelagic spawning is a reproductive strategy employed by many marine animals ranging from sessile invertebrates, such as sponges (Fell 1974) and corals (Willis et al. 1985), to mobile animals, such as echinoderms (Holland 1974) and fish (Potts & Wootton 1984). Unlike eggs laid in nests, once released, pelagically spawned eggs can be afforded little protection by their parents, and those that are not distasteful or toxic are easy prey for planktivorous predators (Colin 1976, Meyer 1977, Nemtzov & Clark 1994, Craig 1998, Heyman et al. 2001, Pratchett et al. 2001). Whilst these planktonic eggs remain at risk from predators, the magnitude of this risk depends on the nature of the marine environment into which they drift. In tropical seas, high densities of planktivorous fish are a characteristic feature of coral reef environments, whereas the pelagic waters surrounding reefs are typified by a general absence of such planktivores. Despite the potentially high risks to their offspring, many coral reef fish spawn pelagically (Thresher 1984) releasing eggs into predator-rich waters. These high predatory threats are expected to drive selection, giving rise to behavioural adaptations in pelagically spawning coral reef fishes that minimise the loss of eggs to predators. Such adaptations are proposed to include: (1) overwhelming predators with eggs by synchronising the spawning of a number of individuals in time and space (Johannes 1978); (2) spawning at sites and times of limited planktivorous activity or reduced planktivorous efficacy (Shapiro et al. 1988); and (3) spawning at sites and times where and when currents most readily carry eggs off the reef and thus away from planktivores (Johannes 1978, hereafter referred to as "the egg predation hypothesis").

The patterns of pelagic spawning amongst coral reef fishes display widely varying responses to the predatory threats faced by their eggs. A number of species are known to synchronise spawning both spatially and temporally, forming spawning aggregations (Johannes 1978, Domeier & Colin 1997, Claydon 2004). Despite these spawning aggregations being formed almost exclusively by pelagic spawners (see Chapter 2 and Claydon 2004), and the theoretically higher survival rates of their eggs (Johannes 1978), aggregative spawning is not widespread amongst species of pelagically spawning coral reef fishes (see Claydon 2004). Aggregative pelagic spawning often occurs at predictable sites and times (Johannes 1978, Domeier & Colin 1997, Claydon 2004), but spawning does not occur exclusively at sites or times of lower predatory threats to eggs, and predation on eggs is commonly observed (Colin 1976, Thresher 1982, Colin & Bell 1991, Craig 1998, Heyman et al. 2001). However, the location and timing of pelagic spawning in reef fishes, both in aggregations and otherwise, is frequently interpreted as facilitating the transport of eggs away from reefs into deeper, safer waters and thus support for the egg predation hypothesis appears to be widespread (see references in Hensley et al. 1994 and Shapiro et al. 1988).

Tautologically, in order for a behaviour to be adaptive it must enhance an individual's fitness. The fact that pelagically spawned eggs are removed from reefs does not mean the site and time of spawning are adaptive. Provided eggs are not eaten or washed onto areas of reef exposed at low tide, it is more than likely that eggs will eventually end up in deeper, safer off-reef waters regardless of when or where they are spawned. However, if the site and time of spawning leads to the more rapid removal of eggs from reef than would occur at alternative sites and times, then this behaviour can be thought of as adaptive (Shapiro et al. 1988). Viewed in this context, definitive support for the egg predation hypothesis is almost entirely lacking (Shapiro et al. 1988, Hensley et al. 1994). Studies seldom compare currents at sites and times of spawning with those occurring where and when spawning does not. With a few notable exceptions (see Appeldoorn et al. 1994, Hensley et al. 1994, Sancho et al. 2000b), currents are rarely measured directly, but more often assumed to carry eggs off-reef quickly because of the state of the tide at the time of spawning. Additionally, spawning has frequently been observed at locations and times that do not appear to favour transport of eggs off-reef (see reviews in Hensley et al. 1994, & Shapiro et al. 1988).

Despite limited evidence that sites and times of pelagic spawning actually enhance the movement of eggs away from reefs compared to alternative sites and times, and with an equally convincing body of evidence suggesting that they do not, the patterns of spawning documented are almost invariably moulded to fit the egg predation hypothesis (see Shapiro et al. 1988). It is unsurprising, therefore, that this hypothesis has become a “virtual paradigm” (Hensley et al. 1994), and as such is somewhat self-perpetuating: whilst the location and time of spawning are explained by currents, the nature of these currents is often inferred by the fact that spawning is occurring. Evidently, valid conclusions cannot be drawn with such circular logic. Challenging this paradigm is central to a better understanding of the reproductive ecology of many species of coral reef fish.

Whilst planktivory is often regarded as a constant in coral reef environments, the rate at which pelagically spawned eggs are consumed is likely to differ enormously during its time over a reef. The greatest threat to an egg’s survival occurs immediately following spawning: many planktivorous fishes target the apex of the spawning rush feeding intensively during the brief period that eggs remain at high densities (Colin 1976, Colin & Bell 1991, Sancho et al. 2000a, Claydon 2004). Thereafter, the gamete cloud disperses, no longer remaining visible and no longer representing an easily exploitable high density food source. The rate of this dispersion is likely to be proportional to the current speeds into which eggs are spawned, but inversely proportional to the amount of eggs that can be consumed by a target egg predator from a single spawn. Thus it is expected that spawning will occur at higher current speeds (regardless of the direction of flow) because they reduce the feeding efficiency of target egg predators. This novel hypothesis is hereafter referred to as the “prey dispersal hypothesis”.

A number of pelagically spawning species do not appear to migrate to spawn (see Popper & Fishelson 1973, Thresher 1984). Such species would be inappropriate models upon which to test either the egg predation or prey dispersal hypotheses. Whilst these species may select the time of spawning in order to coincide with more favourable currents, they cannot possibly be choosing more preferable sites from which to spawn (unless this was assessed at the time of settlement onto the reef). However, determining whether species of reef fish migrate to spawn may in itself be difficult and ambiguous. These problems are overcome by concentrating studies on species of fish that form spawning aggregations: such species are migratory by definition (see Chapter 2 and Claydon 2004) and thus good models upon which to base such research.

5.1.1 Aims

The aims of this study are to investigate whether the patterns of pelagic spawning in coral reef fishes that form spawning aggregations follow the predictions of the egg predation and prey dispersal hypotheses. Specifically, the following predictions will be tested: (1) spawning aggregations are formed at sites where the general pattern of currents flows faster, flows more rapidly in an off-reef direction, and flows more frequently off-reef than at other sites; (2) more species form spawning aggregations at such sites than others; and (3) within sites aggregative spawning will occur at times when currents are faster, and flow more rapidly and more frequently off-reef than at other times.

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Figure 5.1. Inshore study reefs of Hanging Gardens, Limuka and Maya's in Kimbe Bay, New Britain. Reefs were accessed from the Mahonia na Dari Research and Conservation Centre (MND). Sites 1-6 on the 3 study reefs indicate where current measuring devices were deployed. Site names correspond to those given in Chapter 3.

5.2 Materials and Methods:

5.2.1 Study species:

The primary study species was the surgeonfish *Ctenochaetus striatus*. However, the aggregative spawning of all species observed within study sites was recorded.

5.2.2 Study area:

Field work was conducted from the Mahonia na Dari Research and Conservation Centre, Kimbe Bay, West New Britain Province, Papua New Guinea. The study focussed on 3 inshore reefs in Kimbe Bay: Hanging Gardens, Limuka and Maya's (see Figure 5.1). These reefs are characterised by shallow reef flats (1m at high tide) that are exposed at extreme low tides, and all margins of reef descend rapidly to over 20m down steep reef slopes or vertical walls. Reefs are separated by depths of over 50m.

5.2.3 Current Measuring Device:

Due to the prohibitive expense of digital current measuring devices a low-tech alternative was employed (see Figure 5.2). This device was designed to measure currents on a scale appropriate to address both the egg predation and prey dispersal hypotheses on the inshore reefs in Kimbe Bay. The device consisted of a steel hoop of 80cm radius mounted horizontally on a steel pole. The steel pole was cemented into a hole bored into the reef and attached to the pole by means of a bracket that allowed the height of the hoop in the water to be adjusted according to the tide so that each hoop remained at 10-20cm below the surface of the water (the depth at which most species were observed releasing eggs). The centre of the hoops were marked by 10mm steel pipe. The current was measured by releasing a wooden bead up through the 10mm pipe and timing how long it took to drift over the edge of the hoop. The current speed in msec^{-1} was calculated as the distance travelled (the radius of the hoop, 0.8m) divided by the time taken:

$$\text{Current speed (msec}^{-1}\text{)} \quad = \quad \frac{0.8}{\text{Time}}$$

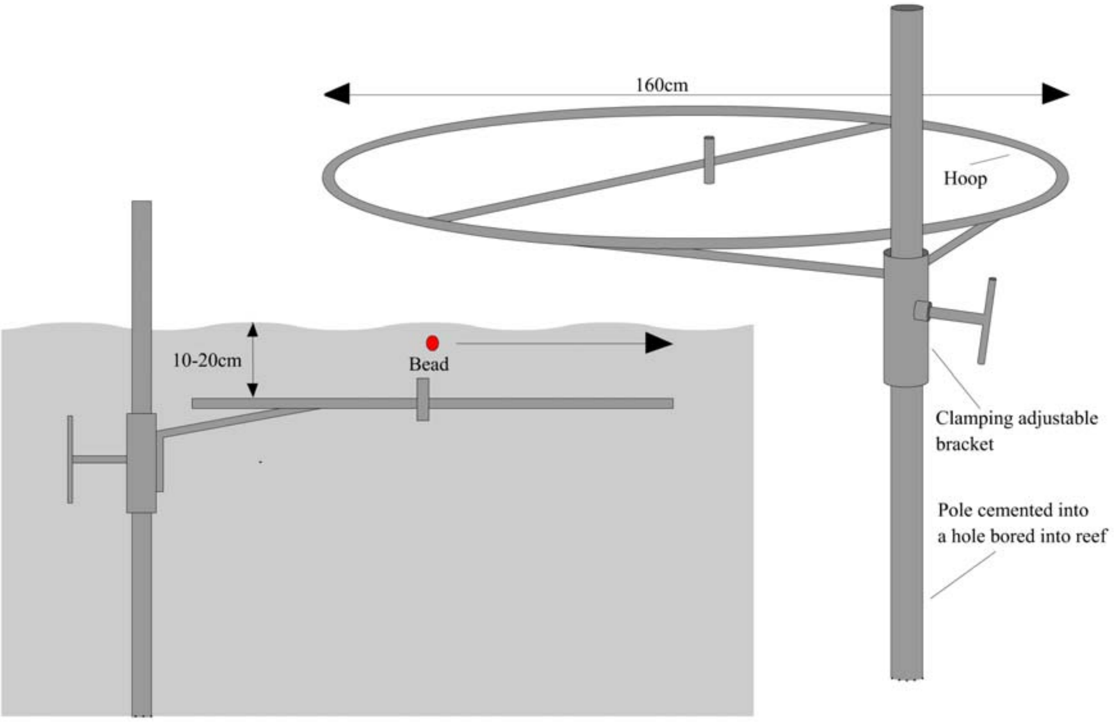


Figure 5.2. Current measuring device

The direction of the current was measured by lining up the point where the bead crossed the edge of the hoop with the hoop's centre and measuring this bearing with a compass. This bearing was then adjusted by 180^{o} in order to establish the bearing the bead was heading and thus establishing the current direction.

It was important to reduce the effect of winds on the movement of the beads. This was achieved by leaving beads to soak in salt-water for up to 24 hours prior to use. This procedure reduced their buoyancy, minimising the area of bead exposed above water to such an extent that the influence of winds was rendered negligible.

5.2.4 Off-reef current speed:

At each site, the range of directions that constitute movement directly away from the reef was determined (off-reef) *in situ* with a hand-held compass. This range of directions included any direction from the point of spawning in which eggs could travel into progressively deeper water. Any direction that maintained eggs in water of the same depth (parallel to the reef) or into shallower water (back over the reef) was determined to be on-reef.

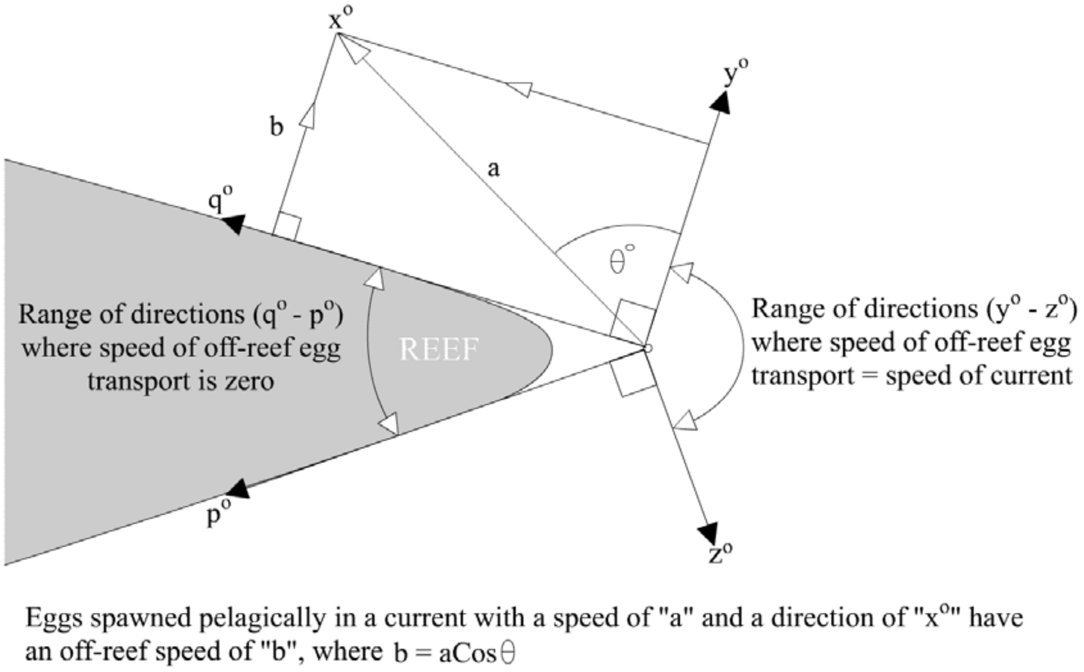


Figure 5.3. Calculation of off-reef current speeds.

From these on/off-reef boundaries, a range of directions was determined for each site whereby the path of eggs off-reef would be fastest at any given speed. The limits of this optimal range were perpendicular to the on/off-reef boundaries (see Figure 5.3). The speed of any current within this range was equal to its speed off-reef. Any currents travelling on-reef had an off-reef speed of zero. The off-reef speed of any currents that had bearings falling outside the optimum off-reef range whilst not being on-reef, was determined by trigonometry (see Figure 5.3).

5.2.5 Study Sites:

In total, 18 current measuring devices were deployed, one at each of 6 sites on 3 different reefs, *Hanging Gardens*, *Maya's* and *Limuka* (see Figure 5.1). Current measuring devices were placed at sites where *Ctenochaetus striatus* were known to form spawning aggregations (Hanging Gardens 1,3 & 6, Maya's 1 & 4, Limuka 1,2,3 & 5) and at sites where no such aggregations were known to form (Hanging Gardens 2, 4, & 5, Maya's 2,3,5 & 6, and Limuka 4 & 6). Thus each reef had at least two spawning aggregation sites of *C. striatus* and at least two sites where *C. striatus* was not known to form spawning aggregations. The latter sites cannot be regarded as random because the sites tended to be chosen at margins of reef with prominent seaward projections, a feature hypothesised to be favoured for the release of pelagic eggs. If no such sites existed, then sites were chosen randomly from areas of reef with substratum hard enough for a hole to be bored and into which a post could be cemented.

5.2.6 Data Collection:

The speed and direction of currents were measured at each site in conjunction with a record of any species spawning in aggregations within a 5m radius of the post holding the current measuring device. On any given day, data was collected at a single reef, moving round the reef from one site to the next from early afternoon until sunset. In this fashion a record of currents for each site was established over a period of days. These currents could be distinguished as those occurring at times when *Ctenochaetus striatus* spawned in aggregations, those when other species spawned aggregatively, and those currents at times of no spawning activity. Data was collected over 27 days at Hanging Gardens, 19 days at Limuka and 31 days at Maya's, and represent over 300hrs of observations spread over days in March, April, May, October and November in 2003.

5.2.7 Data analyses:

One factor ANOVAs were used to assess whether the mean current speeds and off-reef current speeds differed significantly between sites within reefs. Repeated measures G-tests for homogeneity were used to test whether the frequencies with which currents flowed on and off-reef differed significantly between sites within reefs. T-tests were used to compare the mean current speeds (both off-reef and non-directional) at each site between sites within reefs in order to establish whether the currents into which *C. striatus* spawned differed significantly from other currents at the site in question. Spearman rank correlations were used to investigate relationships between: the number of species forming spawning aggregations at a site (# species) and mean current speed, # species and mean off-reef current speed, # species and proportion of currents flowing directly off-reef, and # species and the range of off-reef directions. Goodness-of-fit G-tests were used to assess whether the frequency with which currents flowed on and off-reef within sites differed between times of spawning and currents at other times. *STATISTICA 6* statistics package was used for ANOVA, t-test, and Spearman rank correlation analyses. Zar (1999) χ^2 tables were consulted for p-values of G-tests. α-levels for all analyses were 0.05.

5.3 Results:

5.3.1 General patterns of currents:

The currents recorded at all sites within reefs did not follow a pattern typically associated with a tidally driven current system: there was no reduction in current speed around peak high tide (no slack high tide), nor was there a pronounced reversal or change of flow direction from flood to ebb tide (see Figure 5.4). Mean current speed did not peak at any consistent time of the afternoon at any of the reefs (see Figure 5.5).

Although Rayleigh's tests revealed that currents flowed in discernible mean directions at Hanging Gardens and Limuka within 50% of half hourly time intervals, and ~70% of hourly tide intervals (for $z_{0.05,\ n}$ $p < 0.05$, and therefore circular distribution is not uniform), the high level of angular dispersion (1 – r) at most times indicates that there was little consistent directionality within these time intervals on these two reefs (see Figures 5.4 & 5.5). The currents at Limuka, however, flowed in a more consistent southerly direction with little angular dispersion, and with discernible means at over 85% of time intervals and over 90% of tide time intervals (see Figures 5.4 & 5.5).

5.3.2 Species recorded spawning in aggregations:

Current measurements were taken during aggregative spawning of 22 different species from 5 families: ACANTHURIDAE- *Acanthurus nigrofuscus, Acanthurus triostegus, Ctenochaetus striatus, Zebrasoma scopas;* LABRIDAE- *Bodianus mesothorax, Cheilinus fasciatus, Cheilinus trilobata, Coris gainard, Epibulis insidiator, Halichoeres hortulanus,* *Halichoeres marginatus, Halichoeres melanurus, Stethojulis trilineata, Thalassoma amblycephalum, Thalassoma hardwicke, Thalassoma lunare;* MULLIDAE- *Parupeneus barberinus, Parupeneus bifasciatus* ; POMACANTHIDAE- *Pygoplites diacanthus;* SCARIDAE- *Chlorurus bleekeri, Scarus microrhinus, Scarus quoyi.*

5.3.3 Choice of spawning aggregation sites within reefs:

The mean current speed differed significantly between sites within reefs on all reefs except Limuka [one factor ANOVA: Hanging Gardens – $F(5,359) = 4.4629$, $p < 0.001$; Limuka – $F(5,202) = 1.6059$, $p > 0.4$; Maya's – $F(5,887) = 4.0277$, $p <0.002$]. The off-reef current speed differed also significantly between sites on all reefs (one factor ANOVA: Hanging Gardens – $F(5,359) = 6.5964$, $p < 0.0001$; Limuka – $F(5,202) = 21.659$, $p <0.0001$; Maya's – $F(5,887) = 7.7038$, $p < 0.0001$]. However, the sites where *C. striatus* formed spawning aggregations did not represent choices maximizing either current speed or off-reef current speed: spawning aggregations were formed at both sites with the fastest and slowest mean current speed and off-reef current speed (see Figure 5.6). Additionally, despite significant differences in the frequencies of off-reef and on-reef currents between sites within reefs [Replicated G-test for homogeneity (Sokal & Rohlf 1995): Hanging Gardens- $G_H = 31.24$, df = 6, $p < 0.001$; Limuka- $G_H = 72.75$, df = 6, $p < 0.001$; Maya's- $G_H = 72.15$, df = 6, $p < 0.001$], spawning aggregations of *C. striatus* were formed at sites with both the highest and lowest proportions of currents flowing directly off-reef (see Figure 5.7).

Similarly, the number of species forming spawning aggregations at any site did not follow any pattern dictated by currents: non-parametric Spearman rank correlations did not reveal any significant relationship between either the mean current speed or mean off-reef current speed at a site with number of species forming spawning aggregations (mean current speed vs. # species forming spawning aggregations: Hanging Gardens- $r_S = 0.371$, $p > 0.45$; Limuka- $r_S = -0.371$, $p > 0.45$; Maya's- $r_S = 0.714$, $p > 0.1$; mean off-reef current speed vs. # species forming spawning aggregations: Hanging Gardens- $r_S = 0.829$, $p < 0.05$; Limuka- $r_S = 0.486$, $p > 0.3$; Maya's- $r_S = 0.486$, $p > 0.3$; see Figure 5.8), nor was there a significant relationship between the proportion of currents flowing directly off-reef and the number of species aggregating to spawn within reefs (proportion of currents flowing directly off-reef vs. # species forming spawning aggregations: Hanging Gardens- $r_S = 0.771$, $p > 0.05$; Limuka- $r_S = 0.373$, $p > 0.45$; Maya's- $r_S = 0.6$, $p > 0.2$; see Figure 5.9).

5.3.4 Currents at times of aggregative spawning:

T-tests conducted on both current speeds and off-reef current speeds revealed that there was no significant difference between the mean currents at times of *Ctenochaetus striatus* spawning and at other times within spawning aggregation sites (see Figure 5.10, and Table 5.1 for summary of t-tests). Williams corrected Goodness-of-fit G-tests revealed that there were no significant differences between the frequencies with which currents flowed on-reef and off-reef at times of *C. striatus* spawning from the frequencies predicted by the general pattern of currents within sites (see Figure 5.10, and Table 5.3 for summary of G-tests).

When the currents at times of aggregative spawning of all species were pooled together and analysed the results mirrored those of *C. striatus*: there were no significant differences between the currents at times of spawning and the currents at other times for current speed or off-reef current speed at any sites, and the frequency with which currents flowed directly on and off-reef did not differ from that predicted by the general pattern of currents at the site for any sites (see Figures 5.9 & 5.10, and Tables 5.2 & 5.3).

Table 5.1. Summary of t-tests between mean current speeds at times of aggregative spawning and at other times for *Ctenochaetus striatus*.

Ctenochaetus striatus		Current speed				Off-reef current speed		
Reef	Site	t	df	p		t	Df	p
Hanging Gardens	1	0.639609	101	0.523875		0.061824	101	0.950825
Hanging Gardens	3	0.034915	90	0.972225		0.063670	90	0.949374
Limuka	3	0.681557	58	0.498232		1.84754	58	0.069771
Limuka	5	0.059278	55	0.952945		0.204849	55	0.838446
Maya’s	1	0.952885	147	0.34221		.062068	147	0.289947
Maya’s	4	0.668268	227	0.50461		0.342940	227	0.731961

Table 5.2. Summary of t-tests between mean current speeds at times of aggregative spawning and at other times for all species combined.

All species		Current speed				Off-reef current speed		
Reef	Site	t	df	p		t	Df	p
Hanging Gardens	1	0.382879	101	0.702		0.605600	101	0.546139
Hanging Gardens	3	1.08511	90	0.280773		1.075639	90	0.284964
Limuka	3	0.272973	58	0.785844		1.09343	58	0.278724
Limuka	5	0.12613	61	0.900018		0.113455	61	0.910042
Maya’s	1	0.386486	147	0.699695		1.329009	147	0.185904
Maya’s	3	0.386486	125	0.699695		1.566349	125	0.119795
Maya’s	4	0.979731	227	0.328259		0.419821	227	0.675013

Table 5.3. Summary of results of Williams corrected Goodness-of-fit G-tests between the frequencies of off-reef and on-reef currents at times of spawning compared to that predicted by the general pattern of currents at the site in question. Separate tests were performed on currents at times of aggregative spawning of *Ctenochaetus striatus* and aggregative spawning of all species at all sites where sufficient observations of spawning permitted.

		Ctenochaetus striatus				All species		
Reef	Site	G_{adj}	df	p		G_{adj}	Df	p
Hanging Gardens	1	0.157158	1	>0.5		0.43646	1	>0.5
Hanging Gardens	3	0.012655	1	>0.75		0.398087	1	>0.5
Limuka	3	/	/	/		1.185579	1	>0.25
Limuka	5	0.048262	1	>0.75		0.763576	1	>0.25
Maya’s	1	/	/	/		0.6345	1	>0.25
Maya’s	4	0.124093	1	>0.5		1.051709	1	>0.25

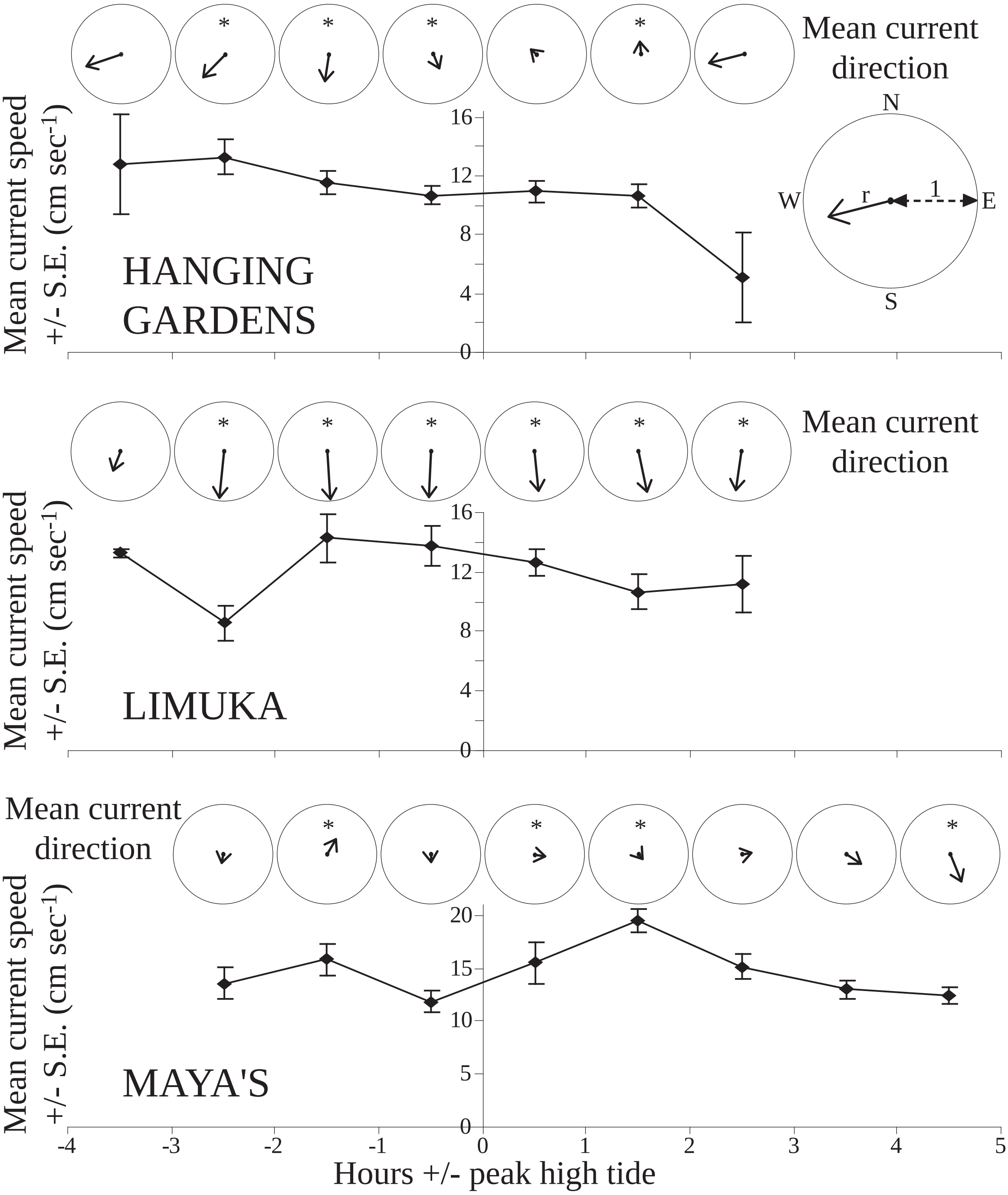


Figure 5.4. Mean current speed and direction at Hanging Gardens, Limuka, and Maya's with time +/- peak high tide. Means derived from currents measured at all sites on reefs within hourly time bins +/- peak high tide. Arrows indicate mean current direction. Length of arrow = r ; r = angular concentration; 1 - r = angular dispersion (Zar 1999); radius of circle = 1; *~ circular distribution not uniform (Rayleigh's test, $p < 0.05$). No asterisk indicates that no discernible mean direction exists.

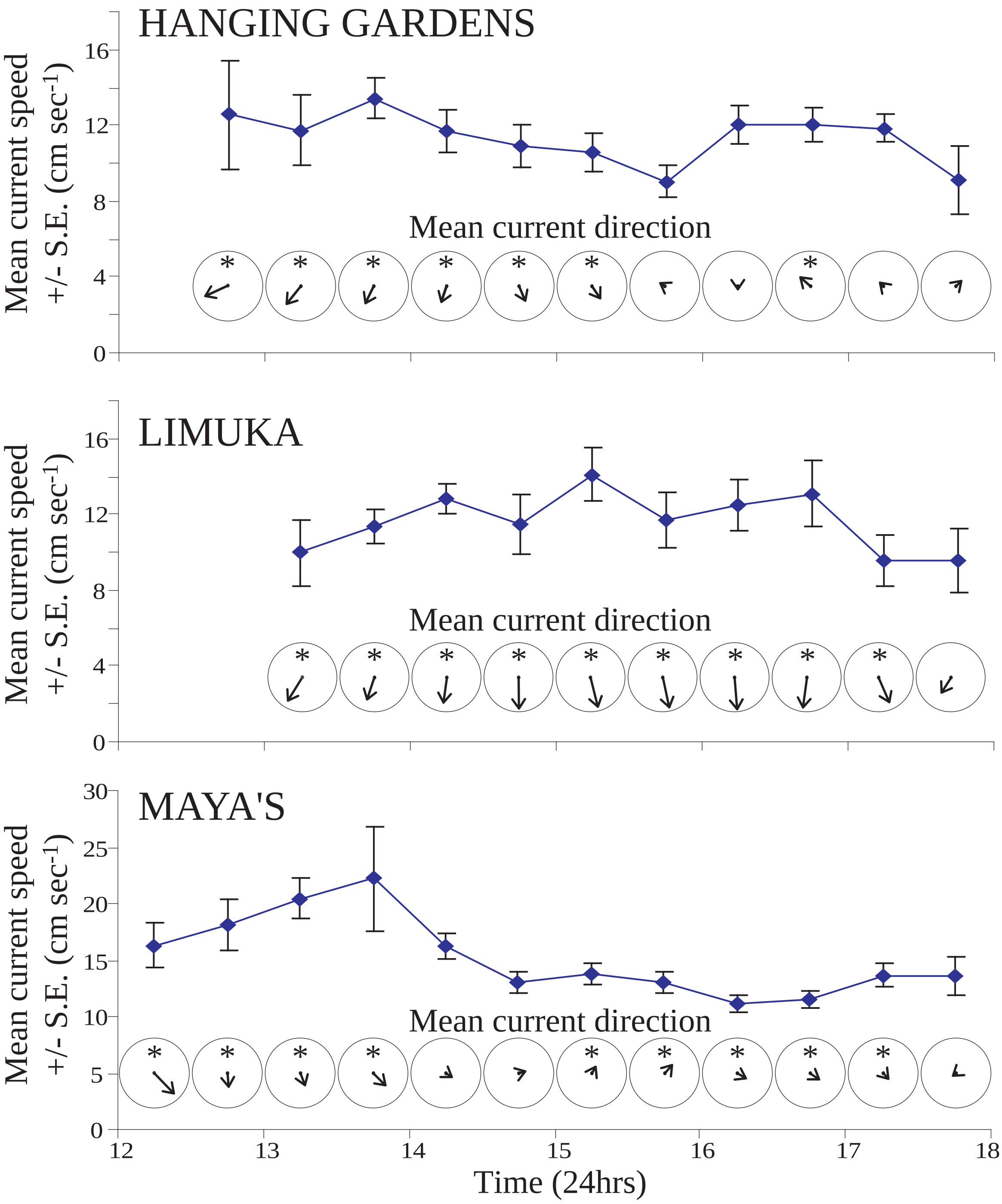


Figure 5.5. Mean current speed and direction at Hanging Gardens, Limuka, and Maya's with time. Means derived from currents measured at all sites on reefs within 30 min time bins. Key to current direction as in Figure 5.4.

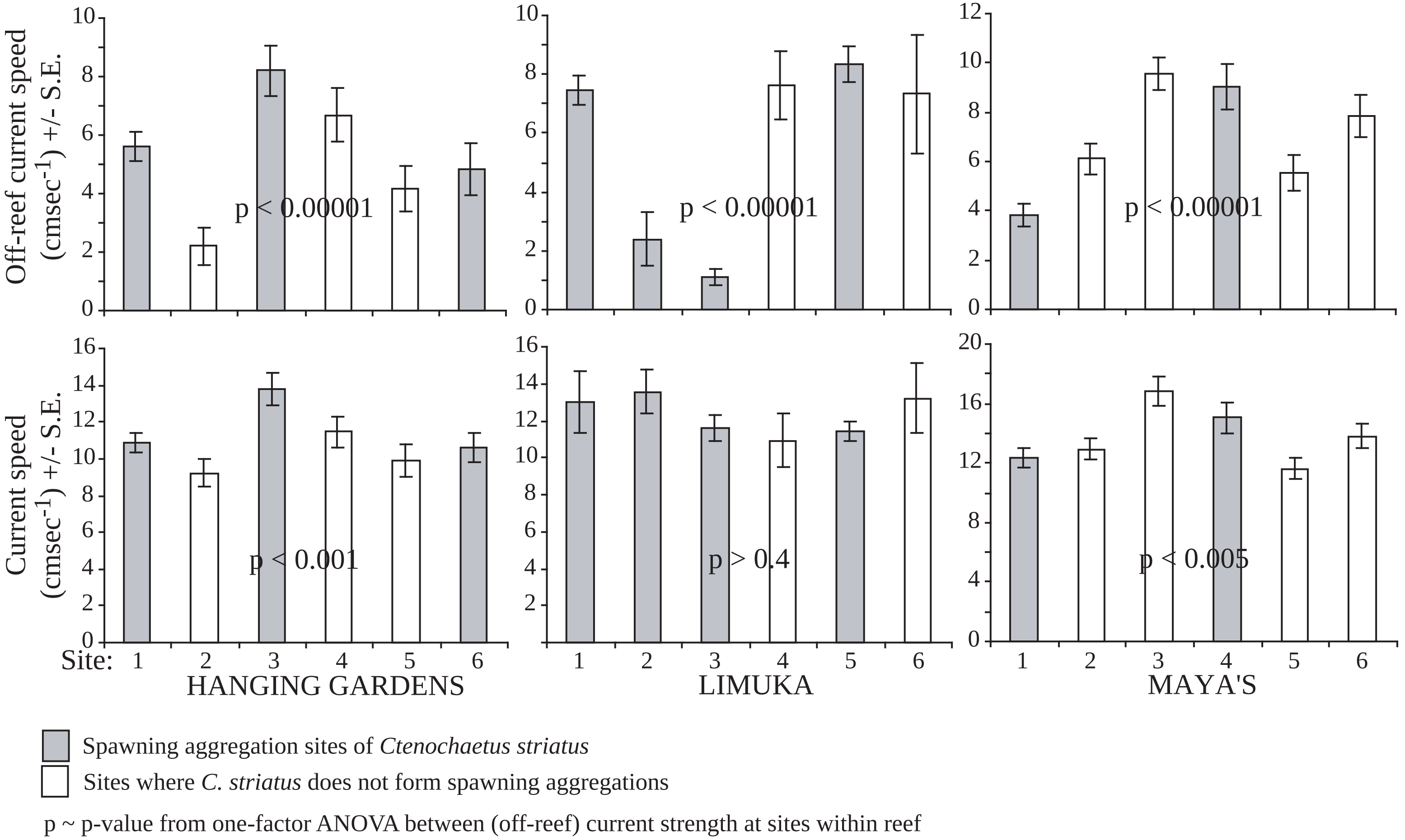


Figure 5.6. Mean off-reef current speed and mean current speed at all sites on Hanging Gardens, Limuka and Maya's. P-values are the results from single factor ANOVA's testing for equality of current speed between sites on reefs.

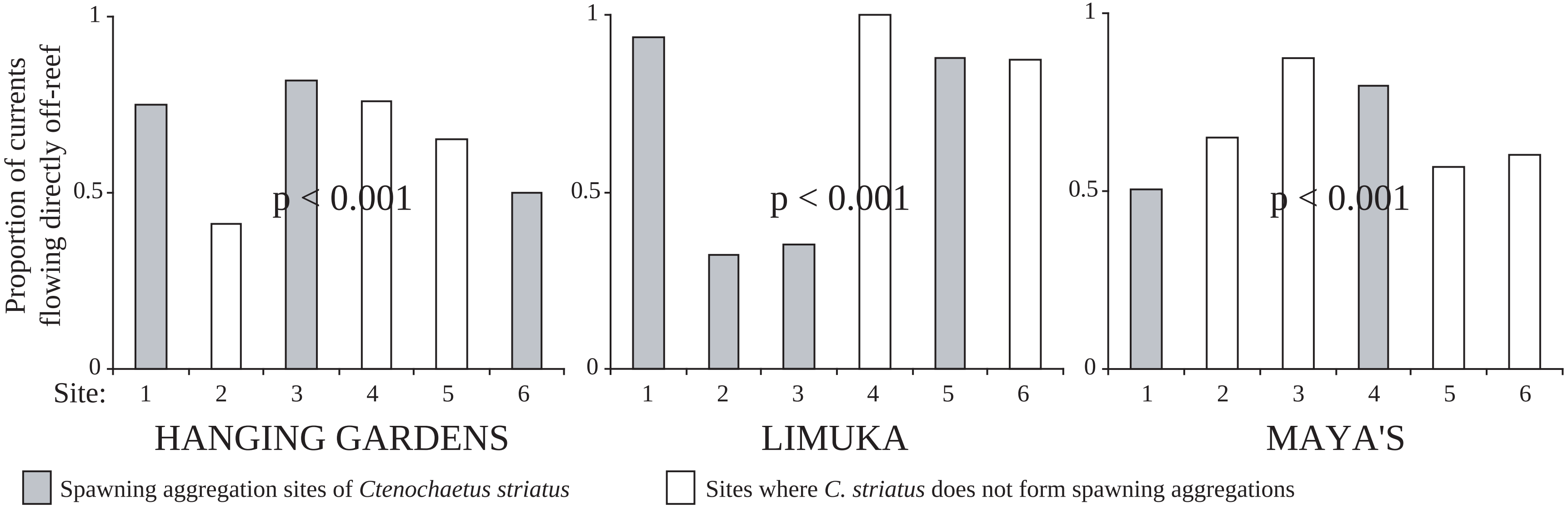


Figure 5.7. Proportion of all currents measured that flow directly off-reef at all sites on all reefs. p-values are the probability that the ratios of off-reef to on-reef currents are homogenous across sites within reefs (derived from a replicated G-test of homogeneity).

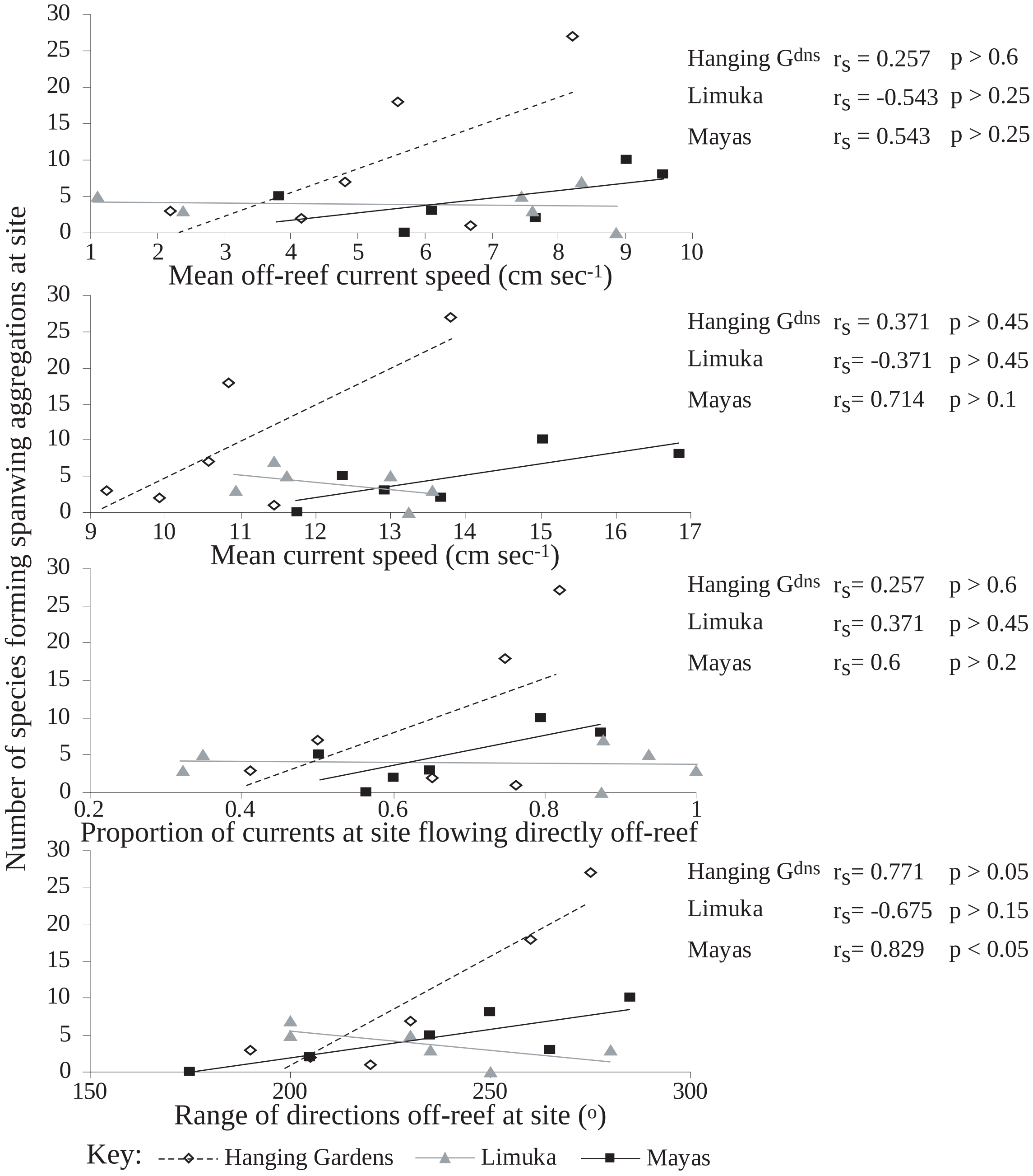


Figure 5.8. Relationship between characteristics of the currents measured, range of directions off-reef, and number of species forming spawning aggregations at a site. r_S and p-values are results of Spearman rank correlations.

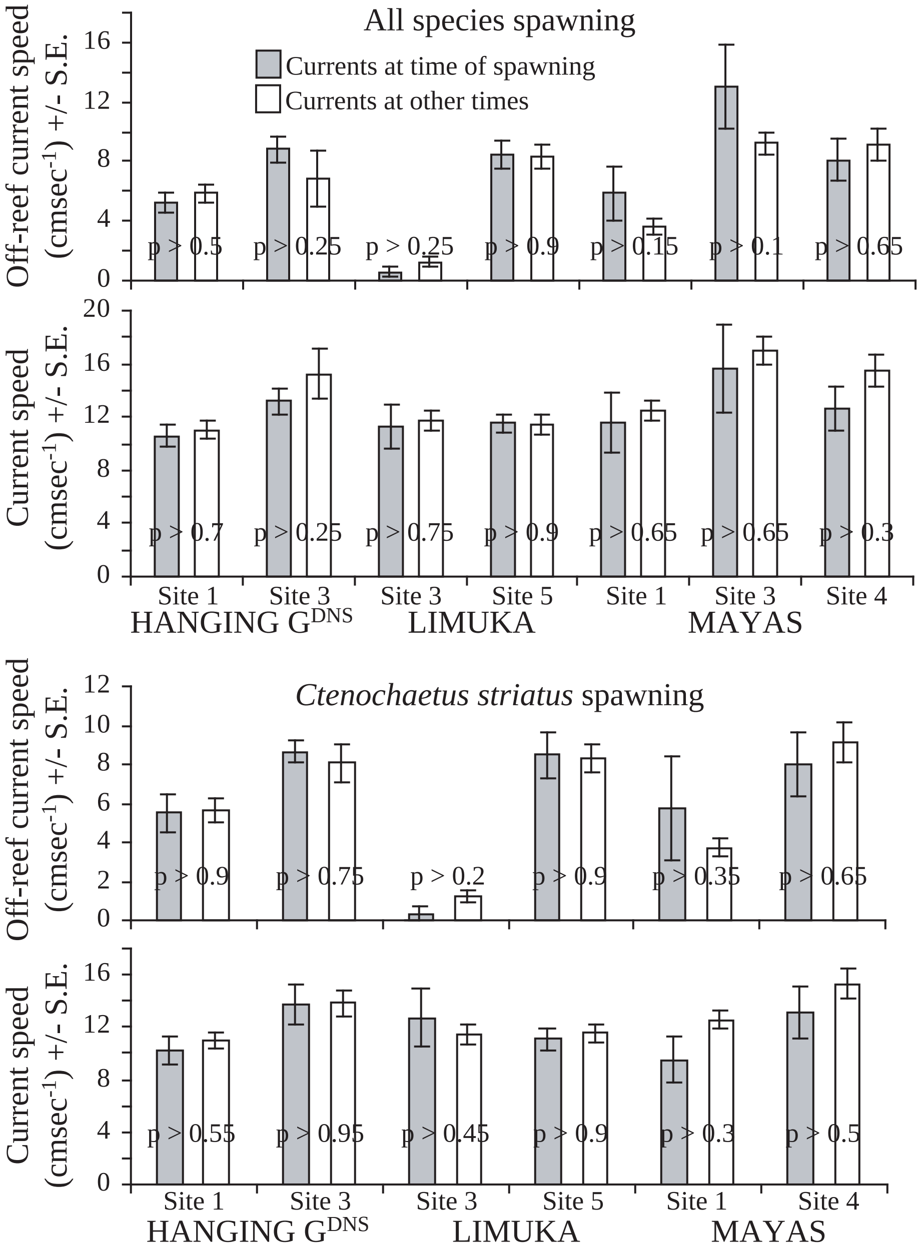
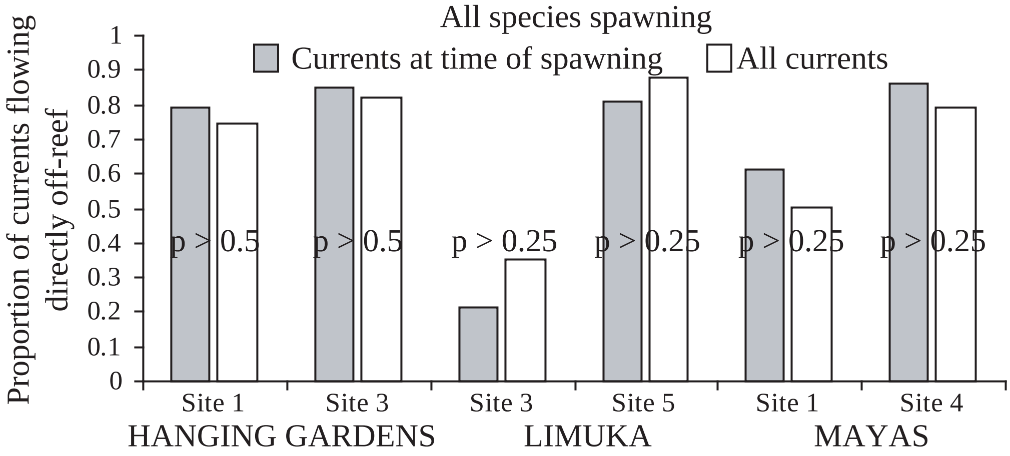


Figure 5.9. The currents at time of spawning by all species and *Ctenochaetus striatus* alone compared to other currents recorded at that site. Sites were omitted if insufficient data were available. The p-values are the results of t-tests between the mean currents recorded at the time of spawning and the mean of currents at other times at that site.



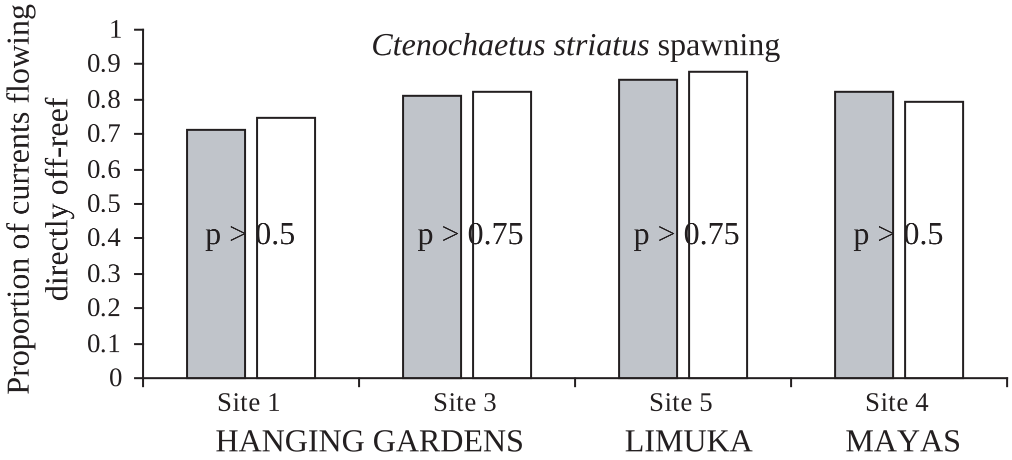


Figure 5.10. Proportion of currents flowing directly off-reef at time of spawning compared to all currents at site for all species and Ctenochaetus striatus. p- values are the results of Williams-corrected goodness-of-fit G-tests between the frequencies of spawning with off-reef and on-reef currents with the frequencies predicted by the general pattern of currents at the site in question. Only sites with sufficient data for G-tests are displayed.

5.4 Discussion

None of the predictions of the egg predation and prey dispersal hypotheses were supported by the results of this study: neither the location nor the time of spawning appeared to enhance the rapid transport of eggs off-reef into deeper water, nor did they enhance the rapid dispersal of gamete clouds. Thus, the fish forming spawning aggregations on the reefs studied did not utilize currents in order to reduce the loss of their eggs to planktivores. These results contrast the sizeable but largely speculative support for the egg predation paradigm (see reviews in Hensley et al. 1994 & Shapiro et al. 1988). It is therefore important to ask why this is so, and whether the conclusions drawn from these results are applicable beyond the limited geographic scale of this study.

There are three possible explanations to why the results do not support the egg predation and prey dispersal hypotheses. Firstly, the survival of eggs may not be enhanced in the manners predicted by the hypotheses. Secondly, despite the potential to enhance offspring survival, coral reef fish may not be able to predict where and when favourable currents occur and thus cannot adapt locally to them. Thirdly, the location and timing of spawning may be dictated by factors other than currents that have greater influence over an individual’s fitness. Each of these three alternatives is addressed below.

5.4.1 Can currents enhance the survival of eggs?

The egg predation hypothesis is based on arguments that seem irrefutable: the longer an egg remains in the predator-rich environment of a reef, the more likely it is to be consumed. Thus, the higher survival rate of eggs spawned in faster currents flowing more rapidly off-reef appears to be incontestable. However, the spawning behaviour of certain species questions this assumption: some species display markedly different spawning behaviour within the same reef, with some individuals migrating to the outer edge of the reef to spawn whilst others spawn within their feeding areas (e.g. *Thalassoma bifasciatum*, Fitch & Shapiro 1990, and see Shapiro et al. 1988 for other species). Eggs spawned at the reef edge will spend less time in the shallow planktivore-rich environment and are therefore assumed to suffer lower rates of predation. However, it is unlikely that the non-migratory strategy would persist if an alternative strategy ensured the survival of a greater number of eggs. Whilst no species in the present study displayed both migratory and non-migratory strategies, it is necessary to question whether the chances of an egg being consumed really are proportional to the time they spend drifting over shallow water environments, especially on the study reefs where planktivores are largely restricted to the reef crest.

Fertilized pelagic eggs are buoyant (Randall 1961a, Lagler et al. 1977), and thus may be afforded spatial refuge from planktivorous fishes and invertebrates. Sessile planktivorous invertebrates cannot feed on organisms at the surface (except perhaps during extreme low tides), and planktivorous fishes seldom feed at the surface (Emery 1973, Hobson 1974, Hobson & Chess 1978), except when attracted to highly distinctive objects floating there (personal observation). Most planktivorous reef fishes need to locate their prey visually in order to feed (Hobson 1991), and, accordingly, eggs floating near the surface may be relatively undetectable to many of these fish and only favoured prey items when found in conspicuously high densities immediately following spawning. The predatory threat faced by planktonic eggs may therefore be largely restricted to the brief period shortly after they are spawned, a notion supported by observations of the feeding behaviour of egg predators from the previous chapter. Research into the relative concentration of prey items in the gut contents of planktivores, and the stratification of feeding activity and prey concentrations in the water column would greatly assist in answering these questions.

If predation pressure is limited to the brief period when eggs are found at high densities, then the potential influence of currents on the survival of eggs as predicted by the egg dispersal hypothesis is greatly enhanced. However, any benefit to egg survival derived from increased current speeds may be confounded by the reduced fertilisation success suggested to be suffered by eggs spawned into faster currents (Petersen et al. 1992, Sancho et al. 2000b, Petersen et al. 2001), a well described phenomenon in other taxa (Pennington 1985, Denny & Shibata 1989, Levitan & Young 1995, Lasker et al. 1996, Coma & Lasker 1997), but likely to play a limited role in the present system where currents are relatively weak.

5.4.2 Are coral reef fish able to predict currents?

In the present study, fish did not exploit currents in order to reduce the loss of eggs to predators. One possible explanation is that favourable currents were unpredictable. Broad-scale movements of surface waters are likely to be predictable with respect to tidal patterns, or, in systems where tidal movements are small and currents are wind-driven, with respect to time of day. However, the scale at which currents may limit egg loss in the manners predicted by the egg predation and prey dispersal hypotheses is considerably finer than that at which currents may be predictable. Local currents are greatly affected by local winds (Warner 1997). This is especially true for the uppermost layer of the water column in which buoyant fertilised eggs are likely to be found. Small-scale random wind and storm events are characteristic features of tropical seas, and are highly unpredictable as will be the currents they produce. In the present study currents were not predictably stronger during flood and ebb tides compared to slack tides nor in association with any particular time of day, nor was there predictable directionality to currents with tidal or diel rhythms. It is highly unlikely that spawning behaviour can be locally adapted to currents if the currents themselves are not predictable.

5.4.3 Are spawning sites and times dictated by factors other than currents?

Despite favourable currents having the potential to increase the survival of pelagically spawned eggs, other factors may play more of a dominant role in determining where and when species spawn. The magnitude of this role is not only determined by the degree to which a factor influences an individual’s inclusive fitness, but also by the degree to which an individual is able to exploit this factor to its advantage. For example, currents may influence egg survival more than any alternative factor, but if individuals are unable to predictably exploit favourable currents, then the location and timing of spawning is likely to take advantage of other factors that can be predictably exploited and results in the greatest overall benefits to the individuals concerned. Such factors may not be directly related to offspring survival and include feeding patterns of adults, feeding patterns of competitors, as well as predatory threats to adults and eggs.

For example, aggressive defence of feeding territories dominates the daytime behaviour of the surgeonfish *Acanthurus lineatus* (Robertson & Polunin 1981, Choat & Bellwood 1985, Robertson & Gaines 1986, Craig 1996). This effort would be wasted if *A. lineatus* were to migrate to spawn at times when its herbivorous competitors are active. This may explain why *A. lineatus* is known concentrate spawning around dawn (Johannes 1981, Robertson 1983, Craig 1998, and see Chapter 3). Thus, time of spawning appears to be dictated by competition in *A. lineatus* (Robertson 1983) rather than currents. However, in the present study, no other species spawns at times so clearly dictated by such a factor. The results from this study and those of previous chapters indicate that, for most species, there is no intrinsic advantage to the timing or location of spawning the time of spawning.

5.4.4 Location and time of spawning: intrinsically adaptive or cues for synchrony?

Warner (1997) outlined results of an investigation into the currents into which *Thalassoma bifasciatum* spawned eggs. Spawning was most strongly correlated with times of highest tide and lunar phase, and not with local current conditions. He concluded that local physical characteristics were unpredictable and that spawning in association with high tide and lunar phase were adaptive responses to currents when viewed in the broader geographical context of the population. However, the fact that a pattern exists is not proof in itself that the pattern is adaptive (Shapiro et al. 1988). An equally plausible explanation is that lunar and tidal cues merely serve to synchronise spawning unambiguously (Colin & Clavijo 1978). Such synchrony is important in order to limit the time an individual spends in reproductive activities, and because of the multiplicative benefits intrinsic to spawning in aggregations (see Chapter 3 and Claydon 2004). Thus, the location and time of spawning documented in this study may serve as cues to synchronise aggregative spawning rather than cues to synchronise the release of eggs into favourable currents.

5.4.5 Broader implications of study:

It is necessary to assess whether conclusions drawn from this study are relevant to pelagically spawning coral reef fish throughout tropical seas, or restricted to the geographic scale of the study. Whilst certain characteristics may be shared by all reefs, enormous variation exists across regions. For example, the influence of currents on the survival of pelagically spawned eggs on the reefs in Kimbe Bay may be small compared to those spawned on reefs in other locations. On the study reefs, planktonic eggs are at risk in the relatively narrow bands of planktivores found at the reef crest and at the most shallow areas of the steeply sloping reef walls. The reef flat is largely devoid of planktivorous fishes and invertebrates, and exposed at spring low tides. In other locations, such as the San Cristóbal Reef Platform in Puerto Rico where Hensley et al. (1994) tracked the movement of pelagically spawned eggs, reefs consist of shallow but permanently submerged reef platforms extending over large areas. Whilst less site-attached planktivorous fishes may also concentrate in narrow zones at the reef edge similar to those found in Kimbe Bay (Hobson 1972, 1973, 1974), eggs passing over the reef platforms are possibly subjected to constant predatory pressure of a kind that is absent on the reefs of the present study. On the San Cristóbal Reef Platform some *Thalassoma bifasciatum* spawning sites were over 200m away from water over 6m deep in any direction (Hensley et al. 1994). In Kimbe Bay, spawning was never observed further than 5m away from water of such depths. Therefore, the influence of currents over an egg's survival may be considerably different depending on the characteristics of the reefs from which they are spawned. At other locations predation pressure has the potential to be a stronger force driving selection. However, many of the observations from Hensley et al.'s study (1994) also contradict the egg predation and prey dispersal hypotheses.

5.5 Conclusion

The fishes forming spawning aggregations on the reefs studied did not appear to utilise currents in order to reduce the loss of eggs to planktivorous predators. This is unsurprising in the light of the unpredictable nature of local currents. This study questions the validity of the egg predation “virtual paradigm” on both empirical and theoretical grounds. Future investigators should exercise more caution before concluding that a relationship exists between the location and timing of pelagic spawning and the currents into which eggs are spawned, especially if the currents in question are not measured directly, but inferred from lunar phase, state of tide or time of day. Despite large differences in the potential role of currents on egg survival between reefs in different regions, the conclusions of this study may be applicable to species other than *Ctenochaetus striatus* and to locations other than Kimbe Bay because of their theoretical basis.

CHAPTER 6: SPAWNING AGGREGATIONS OF REEF FISH: PATTERNS OF MIGRATION

6.1 Introduction

Coral reef fishes display strongly site-attached behaviour: whilst the limited movements of small reef fishes are well documented [e.g. coral-dwelling gobies (Patton 1994, Munday et al. 1997), anemonefish (Fautin & Allen 1992), and other pomacentrids (Sale 1971, Robertson & Lassig 1980)], most reef fish of all sizes appear to forage within restricted home ranges (Sale 1998, Chapman & Kramer 2000) and sleep in specific sites of shelter, with many individuals consistently returning to the same crevices or caves (Hobson 1973, Sluka 2000, Eristhee & Oxenford 2001). However, such site-attachment does not preclude extensive movements within home ranges (Chapman & Kramer 2000), the dimensions of which can be expansive, e.g. >20,000m^2 for *Epinephelus striatus* (Bolden 2002). Nor does site-attachment preclude daily migrations of over 1km between sites of shelter and feeding areas (Hobson 1973, Mazeroll & Montgomery 1998). However, the most impressive movements in adult reef fishes are undertaken by the over 240 species from 29 families presently known to migrate to form spawning aggregations (see Chapter 2). *E. striatus* has been documented migrating over 200km between home ranges and spawning aggregation sites (Carter et al. 1994, Bolden 2000).

An individual's patterns of migration to spawning aggregations are likely to be influenced by a number of factors, including its size, its sex, and the distance of its home range from aggregation sites. Migration incurs energetic costs and may expose individuals to greater risks of predation: movement is energetically expensive, and time migrating represents time not spent feeding in preferred areas, or for some fish, time not spent feeding at all (Warner 1995). Individuals migrating may be exposed to an increased risk of predation due to the conspicuous nature of movement, and because of reduced familiarity with potential shelter outside of home ranges (Chapman & Kramer 2000). The further an individual migrates, the greater the energetic cost of migration and the more the individual is exposed to predators. With a finite energy budget, the more energy that is spent migrating, the less resources that can be dedicated to growth and gametogenesis.

Therefore, it is predicted that individuals with home ranges situated closer to the site in which they spawn aggregativley will migrate more frequently than those migrating further distances. Both the risk of predation and the proportional cost of movement are reduced in larger individuals (Roff 1991, Domeier & Colin 1997). Therefore, larger individuals are expected to be able to migrate further (as documented for a tropical wrasse, Shibuno et al. 1993) and more frequently than smaller ones. Additionally, because spermatogenesis is less costly than oogenesis (Schärer & Robertson 1999), it is also predicted that males will migrate more frequently than females, and that males will be prepared to migrate further distances to spawn.

The choice of the spawning aggregation site to which an individual migrates is likely to be influenced by the size of the spawning aggregations in question (the number of conspecifics aggregating). It has been proposed that spawning in aggregations is intrinsically beneficial, increasing an individual's range of potential mates, and reducing predation on eggs and spawning adults by overwhelming predators with prey (see Chapter 2 and Claydon 2004). These theoretical benefits are multiplicative: the larger the aggregation, the greater the range of potential mates and the less chance there is that an adult or its offspring will be preyed upon. Therefore, individuals are expected to migrate further distances to larger spawning aggregations.

Despite a considerable number of reef fishes being documented as migrating to spawn in aggregations (see Chapter 2), most research has concentrated on the aggregations themselves rather than migrations to them. Consequently, for most of these species, little is known about their patterns of migration beyond the fact that, by definition, they must have migrated from somewhere to form aggregations. The few notable studies that have addressed the question of migration have done so by focussing on limited numbers of individuals and few spawning aggregation sites (Myrberg et al. 1988, Shibuno et al. 1993, Warner 1995, Zeller 1998, Bolden 2000).

6.1.1 Aims:

The aims of this study are to investigate the patterns of reef fish migration to spawning aggregations. Specifically, the study explores the relationship between an individual's size and sex, the distance of its home range from spawning aggregation sites, and the size of the spawning aggregations formed.

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Figure 6.1. Study reefs of Kume, Hanging Gardens and Maya's accessed from the Mahonia na Dari Research and Conservation Centre (MND), Kimbe Bay, New Britain, Papua New Guinea. The location of spawning aggregation sites of *Ctenochaetus striatus* on the study reefs are indicated by white circles.

6.2 Methods:

6.2.1 Study area and study species

All fieldwork was conducted on the inshore reefs accessible from the Mahonia na Dari Research and Conservation Centre, Kimbe Bay, New Britain, Papua New Guinea. Fieldwork focussed on the migratory patterns of the “lined bristletooth” surgeonfish, *Ctenochaetus striatus*, on 3 reefs, Hanging Gardens, Kume and Maya’s. On the study reefs, *C. striatus* has a maximum S.L. of 16cm and is known to form spawning aggregations in the afternoon, with spawning occurring over a site-specific 2 hour period. The location of spawning aggregation sites on the study reefs had been identified previously, with 4, 15 and 2 sites on Hanging Gardens, Kume and Maya’s respectively (see Figure 6.1). In over 1000 hours of observations undertaken over 3 years, *C. striatus* was never observed spawning outside of aggregations on any of the inshore reefs of Kimbe Bay.

6.2.2 Tagging and determining positions of resighted individuals:

A number of *C. striatus* individuals were tagged on each study reef (59 on Hanging Gardens, 304 on Kume and 43 on Maya’s) so that their patterns of movement could be observed. Fish were caught in fence nets, sexed by stripping gametes, measured (S.L.), and tagged with brightly coloured beads sewn on to three areas of the dorsal region. In this fashion, each of the 406 individuals tagged were identifiable by unique tag codes (see Figure 6.2). Where possible, fish were caught from locations with a representative range of distances from spawning aggregation sites. However, the precise location of capture was dependent on where nets could be successfully deployed, and restricted to areas of reef where individuals were present.

Figure 6.2. ***Ctenochaetus striatus*** **tagged with beads attached in 3 locations through the musculature along the dorsal fin margin.**

Highly visible numbered markers were deployed at intervals of 20m around the reef crest of all study reefs. On each reef, the first marker deployed was taken as the origin and the x, y coordinates (metres east and metres north of the origin respectively) of each subsequent marker was calculated by means of trigonometry, knowing its distance and bearing from other markers. Using these markers as reference points, it was also possible to determine the x,y coordinates of tagged individuals by measuring their distances and bearings from the closest marker. In this fashion, the location of individuals could be calculated to a resolution of under 1m.

In this study, the home range of an individual that migrates to spawn in an aggregation is defined as *the geographical area occupied by an individual over which all activities other than those associated with reproduction occur*. It was necessary to determine whether *Ctenochaetus striatus* had spatially restricted home ranges, and to record the location and dimensions of the home ranges of tagged individuals in order to calculate the distances they migrated to spawn. Because *C. striatus* was observed forming spawning aggregations exclusively in the afternoon on the study reefs, a tagged individual's home range was established from the x,y coordinates of resightings before midday. It was prohibitively time-consuming to follow the activities of tagged individuals over prolonged periods of time. It proved more productive to swim around the reef recording the positions of all tagged fish, repeating this over a number of days, and thus establishing a record of x,y coordinates for each individual. The size of an individual's home range was determined by a linear measure: the maximum distance between an individual's home range x,y coordinates, referred to as the *maximum dimension* of the home range. This linear measure was used as opposed to the more standard technique of calculating the area of the polygon of resightings (Mohr 1947) for two reasons: firstly, such a distance can be directly compared to migration distance, whereas a measure of area cannot, and secondly, whilst limited home range resightings are likely to underestimate the area of an individual's home range, a linear measure is less affected. An individual's mean position within its home range was also calculated, hereafter referred to as its *mean home range position*.

In the afternoon, patterns of migration were recorded by focussing effort to obtain resightings on spawning aggregation sites. The location of tagged individuals within spawning aggregations was recorded along with the number of conspecifics aggregating. This enabled the degree of spawning site fidelity to be determined. The distance an individual migrated was calculated from its mean coordinates within the spawning aggregation and its mean home range position. The relationships between the frequency with which individuals migrated, the distance migrated, their sex, and their size were explored, as was the relationship between the maximum distances individuals were known to migrate and the size of the spawning aggregations to which they migrated.

Resightings were performed over 49 days on Hanging Gardens, 22 days on Kume, and 11 days on Maya's, between September 2003 and January 2004.

6.2.3 Data analyses:

A Kolmogorov-Smirnov 2-sample test was used to investigate whether the size frequency distribution of males differed significantly to that of females. Student's t-tests were used to test for differences between: (1) the size of individuals migrating to the closest spawning aggregation site with the size of those migrating to sites further away, and (2) the spawning frequency of males to that of females. Due to excessive deviations from normality, Mann-Whitney U-tests were used to compare the size of individuals seen in spawning aggregations with the size of individuals resighted on more than 3 occasions but never seen in aggregations. Separate Mann-Whitney U-tests were performed for males and females. Pearson product-moment correlation coefficients were calculated to test for associations between: (1) the size of spawning aggregations and the maximum distance that individuals migrated to them, (2) individuals' migration frequencies and their migration distances, and (3) individuals' migration frequencies and their body sizes (S.L.). Males and females were treated separately in all correlations. All statistical procedures followed Sokal & Rohlf (1995), and α-levels for all analyses were 0.05.

A model system with high but incomplete spawning site fidelity (individuals migrate to one spawning aggregation site 99% of the time and an alternative site only 1% of the time) was used to assess the likelihood of recording the patterns of complete fidelity to spawning sites observed in the present study by chance alone. Binomial theorem was used to calculate this probability.

6.3 Results:

6.3.1 Tagging overview:

The 406 *Ctenochaetus striatus* tagged ranged in size from 94 to 150mm S.L. Stripping released gametes from 62% of fish caught, 98% of these released sperm. Whilst only 4 individuals released eggs during stripping, all fish not releasing gametes were also considered to be adult females This assumption was considered to be valid for a number of reasons: all individuals caught were from a sexually mature size range, as evidenced by observing spawning by the smallest individuals as well as by individuals not releasing gametes during stripping. The females that released eggs were caught exclusively during spawning aggregations or whilst migrating to them. Nets were seldom deployed at such times, and thus the majority of females were stripped at times when eggs would not be released, whereas sperm was forthcoming from males at all times of capture. Thus 235(58%) individuals tagged were male, 151(37%) were female, and 20(5%) individuals suffered excessive pressure on the abdomen during capture for sex to be reliably determined. Despite considerable overlap in sizes, the size frequency distribution of males differed significantly to that of females (Kolmogorov-Smirnov 2-sample test: $D_{(235,151)} = 0.336$, $p < 0.001$; see Figure 6.3).

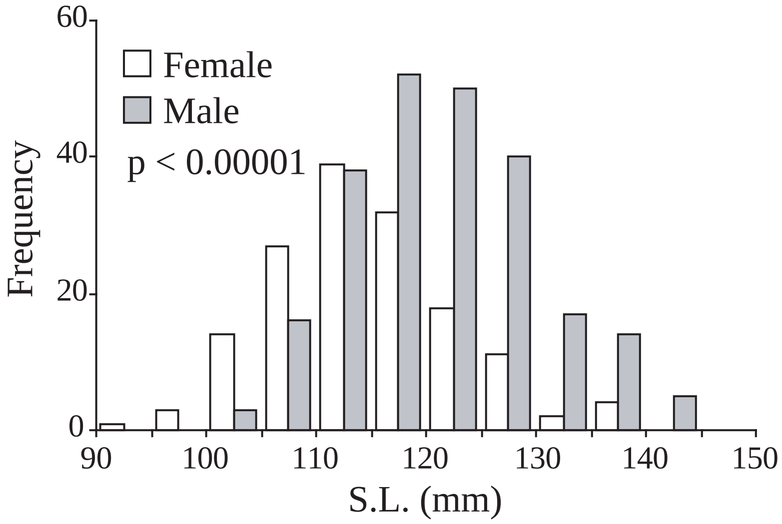

Figure 6.3. Size frequency distribution of tagged *Ctenochaetus striatus*. p-value is the result of a Kolmogorov-Smirnov 2-sample test between the S.L. of males and females.

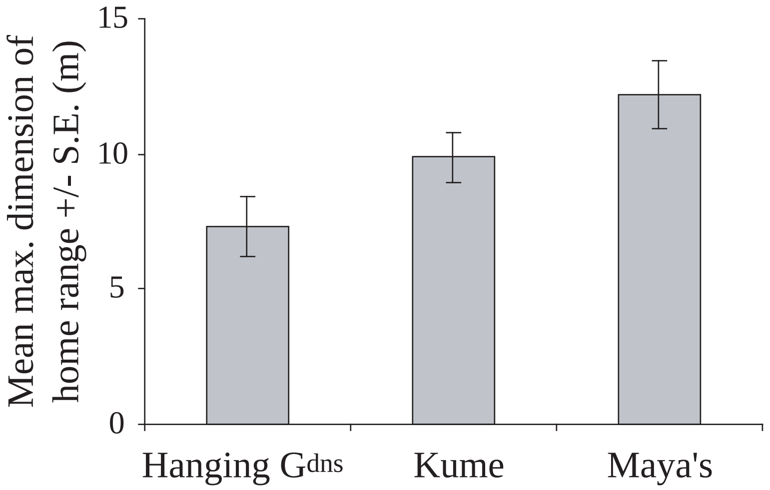

Figure 6.4. The mean maximum dimension of the home ranges of tagged individuals resighted on Hanging Gardens, Kume and Maya's. Units are metres.

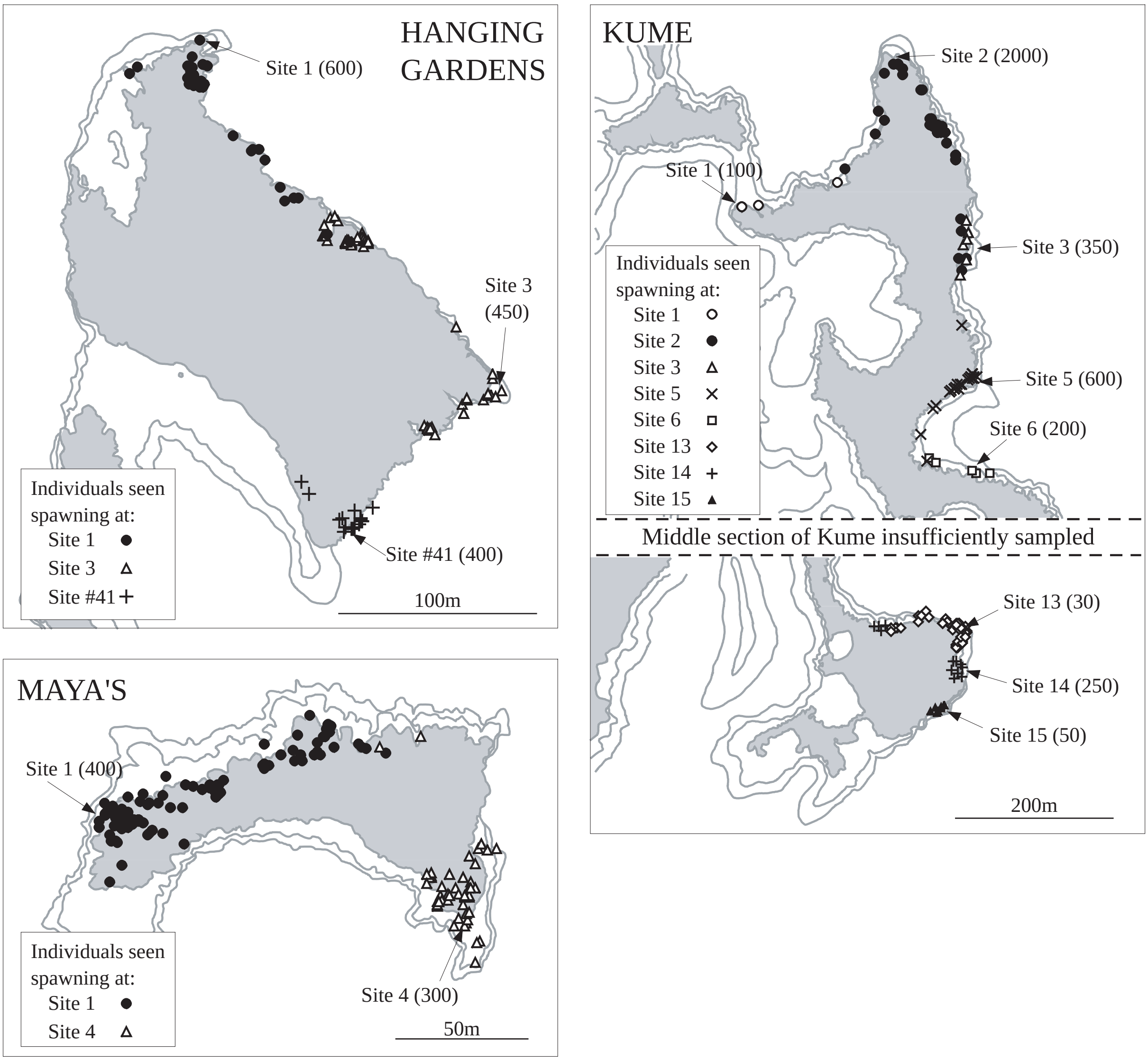

Figure 6.5. The locations of tagged *Ctenochaetus striatus* individuals seen spawning in aggregations on Hanging Gardens, Kume and Maya's reefs. Each symbol represents a single resighting of tagged individuals seen spawning in aggregations at the site. The positions plotted are resightings of individuals both whilst aggregating to spawn and whilst in their home ranges. Only individuals seen spawning are plotted. The value in parentheses is the maximum number of individuals in the spawning aggregation at the respective site. Site names correspond to those given in Chapter 3.

6.3.2 Home ranges and spawning migrations:

On Hanging Gardens 81% of tagged individuals were resighted, with 72% on Maya’s and 44% on Kume. The rate of tag returns for Kume was misleadingly low due to limited sampling effort on the mid section of this reef. Tagged individuals were consistently resighted within a limited home range. The mean maximum dimension of home ranges was less than 13m on all three study reefs (see Figure 6.4). However, this was probably an overestimate caused by individuals venturing outside their home ranges during occasional flight from observers.

In total, tagged fish were witnessed in spawning aggregations on a total of 549 occasions. On Hanging Gardens 73% of resighted tagged individuals were observed spawning in aggregations, with 74% from Maya’s and 45% from Kume. These individuals ranged from those having home ranges overlapping the site in which they spawned to those migrating up to 291m to spawn. Migration was not a conspicuous activity. Individuals migrated in small (<20 individuals), loose groups, and not in the distinctive “trails” described in other species (Robertson 1983, Myrberg et al. 1988, Warner 1995). Intermittent, feeding was observed both during migrations and whilst at spawning aggregation sites. The distance an individual migrated was largely determined by the location of its home range and the location of the nearest spawning aggregation site: whilst home ranges overlapped between individuals migrating to different spawning aggregations, over 92% of individuals migrated to the spawning aggregation sites closest to their mean home range positions (see Figure 6.5). The 9 individuals that migrated elsewhere always migrated to sites with larger spawning aggregations: 8 males migrated to the site where the largest spawning aggregation on Kume was formed (Site 2, 2000 individuals), a journey of up to 203m further than that to the closer aggregation site (Site 3, 350 individuals), and a female was observed migrating an additional 34m to the largest spawning aggregation on the southern section of Kume (Site 14, 250 individuals), rather than to a closer site (Site 13, 30 individuals). There was no significant difference in the size (S.L.) of individuals migrating to the closest site and those migrating further (Student’s t-test: t-value = 0.0015, df = 111, $p > 0.99$; see Figure 6.6.a).

The maximum distance that any tagged individual was known to migrate to a spawning aggregation site was significantly correlated to the maximum size (number of individuals) of the aggregation for males ($r = 0.91$, $p < 0.05$) but not for females ($r = 0.49$, $p > 0.05$; see Figure 6.7). However, the significant result for males was largely dependent on one data point from the largest aggregation. An individual's spawning aggregation site fidelity was absolute: of the 65 tagged individuals seen spawning on multiple occasions, none spawned at more than one site. Despite many of the individuals being recorded spawning only twice, the probability that individuals used alternative sites on limited occasions is extremely low: the probability of the documented pattern of spawning site use being recorded in a system where individuals spawn at an alternative site only 1% of the time is less than 0.01.

6.3.3 Spawning frequency:

The spawning frequency of individuals was calculated for tagged individuals from Hanging Gardens only (insufficient sampling days of spawning aggregations prevented such analysis on the other reefs). Males spawned significantly more frequently than females (Student's t-test: t-value = 2.09, df = 29, $p < 0.05$; see Figure 6.6.c), spawning on average more than once every 2 days for males as opposed to once every 3 days for females. For both males and females, there was no significant correlation between the frequency with which individuals migrated and migration distance (males, $r = 0.06$, $p > 0.05$; females, $r = 0.21$, $p > 0.05$; see Figure 6.7). However, migration frequency was significantly correlated with body size in females ($r = 0.72$, $p < 0.05$), but not males ($r = 0.37$, $p > 0.05$; see Figure 6.7). A number of individuals were resighted on numerous occasions but never seen spawning. For both males and females, there was no significant difference between the size (S.L.) of these individuals and the size of those observed migrating to spawn (Mann-Whitney U-test: males, $U_{(24,5)} = 31$, $p > 0.05$; females, $U_{(10,6)} = 24$, $p > 0.5$; see Figure 6.6.b).

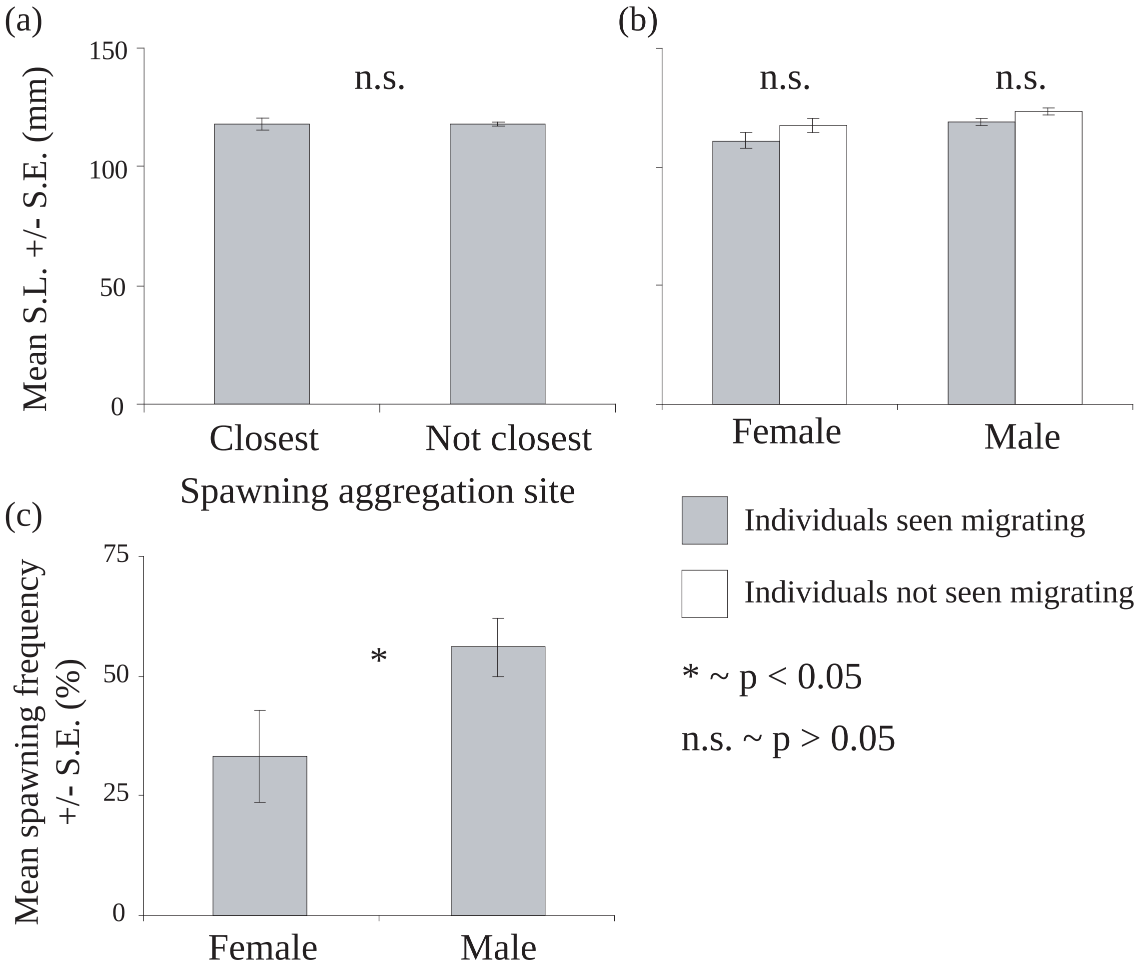

Figure 6.6. (a) The mean sizes (S.L.) of tagged individuals migrating to the spawning aggregation site closest to their mean home range and those migrating to sites further away. (b) The mean sizes of tagged males and females seen spawning and those resighted on more than 3 days but never seen spawning. (c) The mean spawning frequency of males and females seen spawning on Hanging Gardens. Spawning frequency is the % of days that individuals were seen spawning out of the number of days that the aggregation site to which they migrate was monitored. p-values for size of individuals migrating to the closest spawning aggregation site vs. sites further away and for the frequency of spawning in females vs. males are the results of Student's t-tests. p-values for size of females and males seen migrating vs. those not seen migrating are results of Mann-Whitney U-tests.

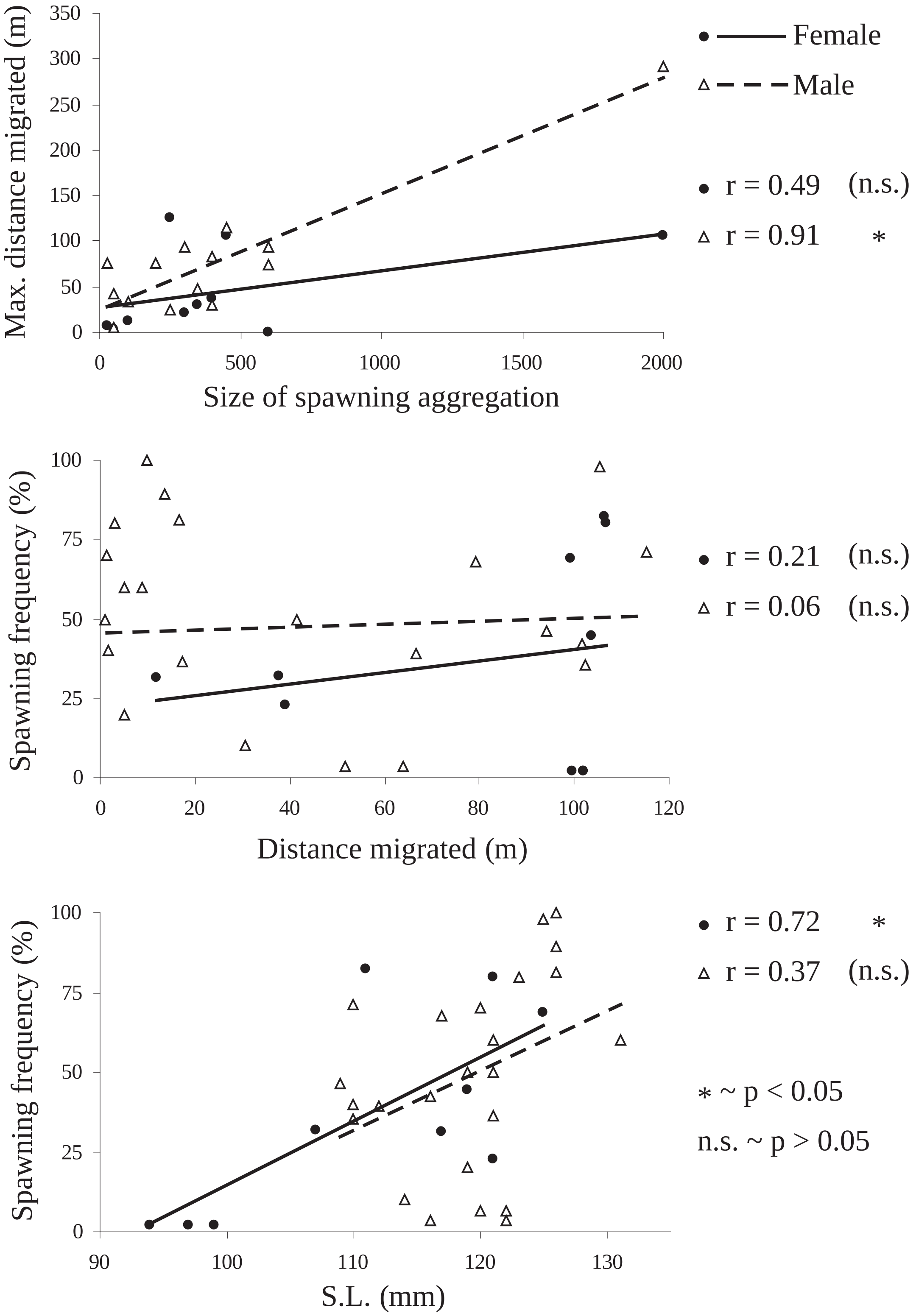

Figure 6.7. The relationship between the size of spawning aggregations and the maximum distance that any tagged individual migrated to spawn there (data from all reefs); the relationship between the distance individuals migrated and the frequency with which they migrated to spawn in aggregation (data from Hanging Gardens only); The relationship between size (S.L. mm) and spawning frequency of individuals (data from Hanging Gardens only). r ~ product-moment correlation coefficient.

6.4 Discussion

An individual’s sex, its size, the distance of its home range from spawning aggregation sites and the number of conspecifics in spawning aggregations all appeared to affect the patterns of migration of *Ctenochaetus striatus* to varying degrees, but not necessarily in the manners predicted. Males migrated to spawn more frequently than females. This is to be expected because the greater cost of producing eggs compared to sperm prevents females from spawning as frequently as males, and is a pattern displayed by other species of reef fish (Schärer & Robertson 1999). Albeit only significant in females, the correlation between an individual’s size and the frequency with which it migrated to spawn was also expected because this supports the notion that migration incurs costs, either in terms of energetic expenditure or increased risks of being preyed upon, and that these costs are proportionately less for larger individuals (Roff 1991, Domeier & Colin 1997).

The theoretical costs of migration are proportional to the distance migrated. Therefore, males, having invested less on gametogenesis than females, and larger individuals, with proportionately less costly movement than smaller ones, are predicted to be able to migrate further than females and smaller individuals. However, migration distance was primarily determined by the proximity of an individual’s home range to the closest spawning aggregation site, and not by an individual’s sex or size. Additionally, the greater costs of migrating further did not reduce the frequency with which individuals undertook these larger migrations, a pattern also noted for *Thalassoma bifasciatum*, a species documented migrating over 5 times further (Warner 1995). These observations suggest that the costs of migration are not substantial enough to influence spawning patterns in these species. Why then do larger individuals migrate more frequently than smaller ones? The answer could lie in the costs of gametogenesis rather than the costs of migration: although no data support such a notion, gametogenesis may be proportionally more expensive for smaller individuals and thus they are unable to spawn on as many days as larger individuals, in the same way that females spawn less frequently than males.

Individuals were also predicted to migrate further to larger spawning aggregations because of the multiplicative benefits of spawning in an aggregation with larger numbers of conspecifics. Support for this prediction is mixed: contrary to the prediction, most individuals migrated to the spawning aggregation sites closest to their home ranges, regardless of the size of the spawning aggregation to which they migrated. However, the few individuals that migrated to sites other than those closest to their home ranges, followed the predicted pattern by always migrating to sites with larger spawning aggregations. Additional support for this prediction came from a significant positive correlation between the maximum distance that any males were recorded to migrate to a spawning aggregation site and the maximum size of the aggregation in question (although this relationship was largely dependent on one data point). However, this relationship can also be explained more simply: on reefs with relatively uniform population densities, larger spawning aggregations will necessarily draw individuals from a larger catchment area.

In general, the costs of migration appear to play a limited role in determining patterns of spawning documented in this study. Sex and body size are more dominant factors. However, the costs of migration may play a more substantial role in the spawning patterns of other aggregatively spawning species, especially those that migrate several kms (e.g. *Epinephelus striatus*, Carter et al. 1994, Bolden 2000). In *Thalassoma bifasciatum*, the frequency of migrations to spawning aggregations was also observed to be independent of migration distance (Warner 1995). However, the higher feeding rates of individuals migrating from further away suggest that more energy is required to maintain spawning frequency with increasing migration distance in this species (Warner 1995). Unlike *Ctenochaetus striatus*, *T. bifasciatum*, was not observed feeding during migrations or whilst at spawning aggregation sites, and individuals migrated considerably longer distances than those in the present study (>1500m vs. <300m). Thus even the longest distances over which *C. striatus* migrated may be too short to incur a significant cost, especially whilst feeding is maintained, albeit at a reduced rate.

6.4.1 Non-reproductive individuals:

Both Zeller (1998) and Samoilys (1997) concluded that reproduction in *Plectropomus leopardus* did not occur exclusively at spawning aggregation sites. In the present study, a number of tagged adults were also consistently seen within home ranges but never seen in spawning aggregations. Whilst individuals' ages were never assessed, and the possibility that some were sexually immature cannot be excluded, all individuals fell within a sexually mature size range, and many of the individuals not observed spawning were confirmed to be male from the release of milt during tagging. It is also possible that these individuals spawned outside of aggregations or in locations not sampled. However, this seems unlikely: in over 1000hrs of observations of *Ctenochaetus striatus* on the inshore reefs of Kimbe Bay, *C. striatus* was never witnessed spawning outside of aggregations. Furthermore, over a period of more than 2½ years attempts were made to record the reproductive activities of all pelagically spawning species of fish on Maya's and Hanging Gardens. It is therefore exceedingly unlikely that some spawning locations of *C. striatus* remained undiscovered after exhaustive search on these relatively small reefs. It must therefore be concluded that some of the tagged adults did not reproduce during this study.

Why individuals should forgo reproduction is unknown, but this has also been noted in other species of reef fishes (see Sadovy 1996). Individuals that did not migrate to spawning aggregations were found in home ranges that overlapped those of tagged individuals seen spawning. Thus, no obvious mechanism prevented migration: these individuals were not found at locations on the reef prohibitively long distances away from spawning aggregations; they were not prevented from migrating by areas of habitat that served as effective natural barriers to such movement (see Chapman & Kramer 2000); they were likely to have been exposed to the same social stimuli that may have triggered reproductive behaviour in individuals that did migrate to spawn. All tagged individuals were of an adult size range and many of the individuals not seen migrating released sperm at the time of capture. Whether these individuals forgo reproduction indefinitely is unknown.

6.4.2 Cost-benefit optimisation vs. tradition:

The fidelity displayed by individuals in the present study to a single spawning aggregation site has also been documented for other species of surgeonfish (Myrberg et al. 1988) and larger species such as the coral trout, *Plectropomus leopardus* (Zeller 1998). However, it is presently not known whether such spawning site fidelity is widespread amongst aggregatively spawning species. In the present study, most individuals migrated to the spawning aggregation sites closest to their home ranges, although a limited number migrated to sites further away, a pattern also displayed by *P. leopardus* (Zeller 1998). If spawning site choice were determined purely by cost-benefit optimisation, then catchment areas of spawning aggregations would be more clearly delineated: all individuals with home ranges within a certain radius of a spawning aggregation would migrate to the same site. The length of this radius and the subsequent boundary between the catchment areas of two adjacent spawning aggregation sites would be determined by a trade-off between the costs of migrating to the sites and the site-specific benefits of spawning there. This does not appear to happen. Therefore, the site at which an individual decides to spawn is likely to be determined by an alternative mechanism.

Warner (1988b, 1990b) concluded that the location of spawning aggregation formation in *Thalassoma bifasciatum* was maintained by tradition. Therefore, the site at which an individual spawns can be regarded as a culturally inherited trait. An individual learns this trait from following the behaviour of adults found in home ranges overlapping its own (Colin 1996, Bolden 2000). In an uncertain future, seeking alternative sites in which to spawn is risky compared to continuing to migrate to a site at which spawning success is proven. Additionally, individuals may be unaware that alternative spawning aggregation sites exist, having only learnt the location of the one site to which they migrate. Thus, individuals spawn at the same site repeatedly, regardless of the potential increase in reproductive success that may be gained from spawning at alternative sites. In a system where migration routes are distinctive and where individuals migrate in conspicuous trails, as documented for some surgeonfishes (Robertson 1983, Myrberg et al. 1988) and a wrasse (Warner 1995), all recruits within an area are likely to learn the location of the same spawning aggregation site. However on the study reefs, *Ctenochaetus striatus* did not form such trails, but rather migrated in small, inconspicuous groups. In such a system, tradition has the potential to maintain differential spawning site use by individuals with overlapping home ranges.

6.4.3 Metapopulations

Regardless of the mechanisms responsible, spawning aggregation site fidelity has important implications for population biology. The individuals migrating to each spawning aggregation site represent a separate subpopulation. Whilst these subpopulations may overlap geographically, reproduction occurs exclusively within subpopulations. A network of these subpopulations forms a metapopulation, with connectivity between subpopulations maintained not by adult migration but by larval recruitment. On the Great Barrier Reef, such connectivity was found to be far reaching for *Ctenochaetus striatus* (Doherty et al. 1995), and thus a metapopulation is likely to consist of a number of subpopulations from multiple reefs. Within such a system, recruitment to a wide area of reef may originate from a limited number of disproportionately successful subpopulations.

6.5 Conclusion:

The results of this study suggest the sites at which *Ctenochaetus striatus* individuals spawn are determined by tradition rather than cost-benefit optimisation. Patterns of migration to spawning aggregations appear to be dictated by an individual's sex, its size and the location of its home range. The spawning migrations of *C. striatus* were too short to incur costs substantial enough to influence the spawning behaviour of individuals.

CHAPTER 7: GENERAL DISCUSSION

7.1 Synthesis of results:

Only a small proportion of the species of reef fish in Kimbe Bay were seen forming spawning aggregations. These species were all larger than 10cm maximum T.L, and all but one spawned pelagically. Such patterns are consistent with the characteristics of the relatively few species known to form spawning aggregations globally (see Chapter 2 and Claydon 2004). However, whilst not widespread in terms of species, spawning aggregation formation was widespread in both time and space: (1) being formed consistently at times ranging from dawn to dusk, (2) being formed on a near-daily basis, year-round and (3) being formed at multiple sites within close proximity to one another. Spawning aggregation formation was not a density dependent phenomenon: species from both high and low density populations formed spawning aggregations, and the numbers of conspecifics in these aggregations ranged from 3 to 2000.

The patterns of aggregative spawning in this study did not appear to reduce the threats posed by predators on spawning adults or their pelagic eggs. Spawning did not occur at sites with reduced piscivorous or planktivorous predators, and the physical characteristics of these site did not appear to offer greater refuge from predators. Although spawning aggregations were formed more often at areas of reef projecting seawards, current data demonstrated that spawning did not occur at sites or times where and when eggs were more readily swept off reefs away from planktivores, nor was the loss of eggs to predators reduced by faster currents dispersing gamete clouds more rapidly. Despite no discernible intrinsic advantage from the location, *Ctenochaetus striatus* displayed remarkable fidelity to spawning sites that was largely determined by which spawning aggregation site was closest to an individual’s home range.

One of the principal aims of this dissertation was to characterise the location and timing of spawning aggregation formation. Being beyond the scope of this study, a number of characteristics of potential benefit to spawning adults or their young were not investigated, such as: whether the broader-scale currents into which eggs are entrained enhance larval survival, larval dispersal or recruitment back to natal reefs. However, albeit largely restricted to *Ctenochaetus striatus* in Kimbe Bay, one common theme arising from the results is that spawning aggregations do not appear to be formed at sites and times that are intrinsically advantageous. Whilst previous chapters have addressed these results specifically, this chapter explores the mechanisms by which the sites and times of spawning aggregation formation could become adaptive, and discusses directions for future research.

7.2 Adaptation in spawning aggregation formation:

It is counterintuitive to suggest that the location and timing of aggregative spawning are arbitrary: firstly, the same decisions about where and when to spawn appear to made independently by a number of conspecifics (sometimes in excess of 100,000, Smith 1972) migrating from distinctive geographic areas; secondly, individuals migrate considerable distances (Carter et al. 1994, Bolden 2000) in order to spawn at what are presumed to be more preferable sites; and thirdly, often a number of different species form spawning aggregations at the same site (Moyer 1989, Colin & Bell 1991, Carter et al. 1994, Johannes et al. 1999, Sancho et al. 2000b, Domeier et al. 2002, Whaylen et al. 2004). The logical conclusion that the site and time of spawning are adaptive becomes increasingly convincing with greater numbers of conspecifics in aggregations, larger catchment areas of spawning aggregations (and thus larger range of sites from which to choose, and increasing distances that some individuals migrate) and greater numbers of other species that also form spawning aggregations at the same site. If certain physical characteristics of sites or the assemblages of fish found there can increase the survival of pelagically spawned eggs or spawning adults, then it is logical to assume that aggregative spawners would evolve behavioural traits that exploit these characteristics to enhance inclusive fitness.

7.2.1 Resource assessment

It is hard to imagine how individuals would be able to make a choice between spawning sites and times based on an assessment of their potential to enhance fitness. Such an assessment would require individuals to experience all potential sites within an aggregation's catchment area at all times and make a choice accordingly. This is obviously impossible. An assessment based on location alone is also unlikely: an individual's limited home range reduces its experience to a small proportion of all potential sites within the catchment area. The larger the catchment area the more implausible such an assessment becomes. This directly contradicts the intuitive argument that the larger the catchment area, the more likely that the characteristics of the spawning aggregation site are adaptive.

Additional observations further limit the possible role of resource assessment in spawning aggregation formation. The length of time over which spawning aggregations are known to be formed at particular sites appears to be limited only by how long ago the aggregation was first discovered, and by whether the population of fish forming the aggregation is eventually depleted by overfishing (e.g. 12 yr, Warner 1988; 12-28 yr, Colin 1996; over 50 yr, Aguilar-Perera 1994; and even centuries, Johannes & Riepen 1995). It is unlikely that the same site remains unfalteringly the most beneficial location from which to spawn at every spawning event over centuries, especially in the dynamic environment of coral reefs (Connell et al. 1997). Warner (1988b) demonstrated that for *Thalassoma bifasciatum* sites of spawning aggregation formation were maintained by tradition. The longevity of spawning aggregation sites across species indicates that tradition is a mechanism maintaining site choice amongst aggregatively spawning reef fish in general. Once a spawning aggregation is established, the inertia to change appears to be too great regardless of the potential benefit to individuals that may be gained by changing spawning location and/or time. Theoretically, successive local extinctions would lead to the eventual location and timing becoming adaptive by chance, but such extinctions may be prevented by the nature of open populations. Thus, genetic differentiation at such fine scales is unlikely and therefore may not lead to locally adaptive sites and times of spawning.

7.2.2 Behavioural "rules of thumb"

The evolution of behavioural "rules of thumb" has been proposed as a mechanism leading to locally adaptive behaviours (Warner 1997). Thus, spawning aggregation site choice and time of spawning could be adaptive with regard to a certain characteristic (e.g. currents) not from resource assessment or local genetic differentiation, but from responses to a number of simple, generally applicable behavioural rules that make use of physical and temporal factors that serve as proxy estimates of better locations and times to spawn. Such rules could include: migration to the most down-current point on a reef/series of reefs or, in the absence of a consistent up-current/down-current distinction, migration to the most prominent seaward projection of reef, or another easily distinguishable reef feature that has the potential to enhance the transport of eggs off-reef, and spawning at a specific time of day, state of tide or moon phase during which currents are likely to enhance the movement of eggs away from reefs. Once a spawning aggregation has been established at a particular site, this site is thereafter used traditionally. Successive generations may learn the location and time of spawning by the behaviour of adults in the area of the reef to which they recruit, and thus inherit these behavioural traits traditionally. Spawning aggregation formation by a number of species at the same site could be explained by species having similar "rules of thumb". However, provided these "rules of thumb" ensure the survival of sufficient numbers of offspring over the geographic scale of a metapopulation, the behaviours they dictate are likely to persist despite being mal-adaptive at a number or even majority of locations: i.e. a ratio of one source to more than one sink in the metapopulation framework. The potential of such a scenario has important implications for fisheries and wildlife management, and in particular for the design of marine protected areas.

It has been suggested throughout this dissertation that the site and time of spawning aggregation formation are not adaptive beyond serving as unambiguous cues that synchronise aggregative spawning (Colin & Clavijo 1988, Claydon 2004, and see Chapter 2). The selective advantage lies not in when and where spawning takes place but in the aggregative phenomenon itself. The selection of such cues could operate at the level of the species or the region. In such a system, distinguishing whether spawning behaviour is determined by “rules of thumb” or synchronising cues is likely to be prohibitively difficult due to the overlap in the resultant spawning behaviour. However, the site-specific diel spawning patterns displayed by *Ctenochaetus striatus* suggest that the time of spawning of some species is not governed exclusively by genetically determined processes. Whilst this excludes “rules of thumb”, the temporal cues to which *C. striatus* responded may be chosen arbitrarily on a site-by-site basis and adhered to by tradition, rather than being determined genetically.

In the light of this theoretical discussion it is unsurprising that the results of this study show no intrinsic advantage to the site and time of spawning aggregation formation. The only mechanism that could drive such selection, behavioural “rules of thumb”, would reveal such advantages at regional scales and thus remain undetected by this study. However, it seems more likely that the site and time of spawning were not intrinsically adaptive, but merely served as cues synchronising spawning aggregation formation in time and space.

7.3 Future research

Most commercially important species of coral reef fish form spawning aggregations (Domeier & Colin 1997). In many locations fishing has targeted spawning aggregations because CPUE is high and because aggregations are formed at the same site with predictable periodicity. Unfortunately, fishing spawning aggregations has often led to the removal of unsustainable quantities of fish, leading to the collapse of stocks and the cessation of spawning aggregation formation (Sadovy & Eklund 1999, Domeier et al. 2002, Claydon 2004). Whilst this sequence of events is well documented, the mechanisms by which they occur are not. Insight into these mechanisms has been prevented largely by the logistics of studying these species: individuals migrate large distances, some over 200km, e.g. *Epinephelus striatus* (Carter et al. 1994, Bolden 2000), and most form spawning aggregations once per lunar month over a limited season (see Chapter 2, Domeier & Colin 1997, and Claydon 2004). Using smaller, more frequently spawning species that migrate shorter distances (e.g. *Ctenochaetus striatus*) as biological models presents opportunities to investigate spawning aggregations in a fashion that would otherwise be logistically difficult.

The use of such models is especially appropriate for manipulative studies when commercially targeted species are vulnerable. For example, C. *striatus* could be used to investigate patterns of migration and spawning site fidelity following differential fishing pressure on spawning aggregations within a network of such aggregations, and simulating the effect of placing some spawning aggregation sites within marine protected areas. Hitherto unanswered questions could be addressed: what is a population's threshold density below which individuals cease to migrate to spawning aggregations (see Colin 1996, Claydon 2004, and Chapter 2)? Does intensive fishing that depletes a subpopulation and reduces the size of its spawning aggregation also cause individuals to migrate to alternative spawning aggregation sites? If a subpopulation is fished to such an extent that the spawning aggregation is no longer formed, what happens when the subpopulation is then allowed to recover? This approach will complement research on many species of commercially important reef fishes, and lead to more effective management of exploited stocks. The advent of sophisticated acoustic tracking and data logging technologies will greatly facilitate such research.

APPENDICES

Appendix 1: Publications arising from PhD project:

Whilst Chapters 3 to 6 have been submitted for peer-reviewed publication, the following paper arising during the PhD project has been published, and is reproduced in full in this appendix:

Claydon, J. A. B. 2004 Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanography and Marine Biology: An Annual Review* **42**, 265-302.

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