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.

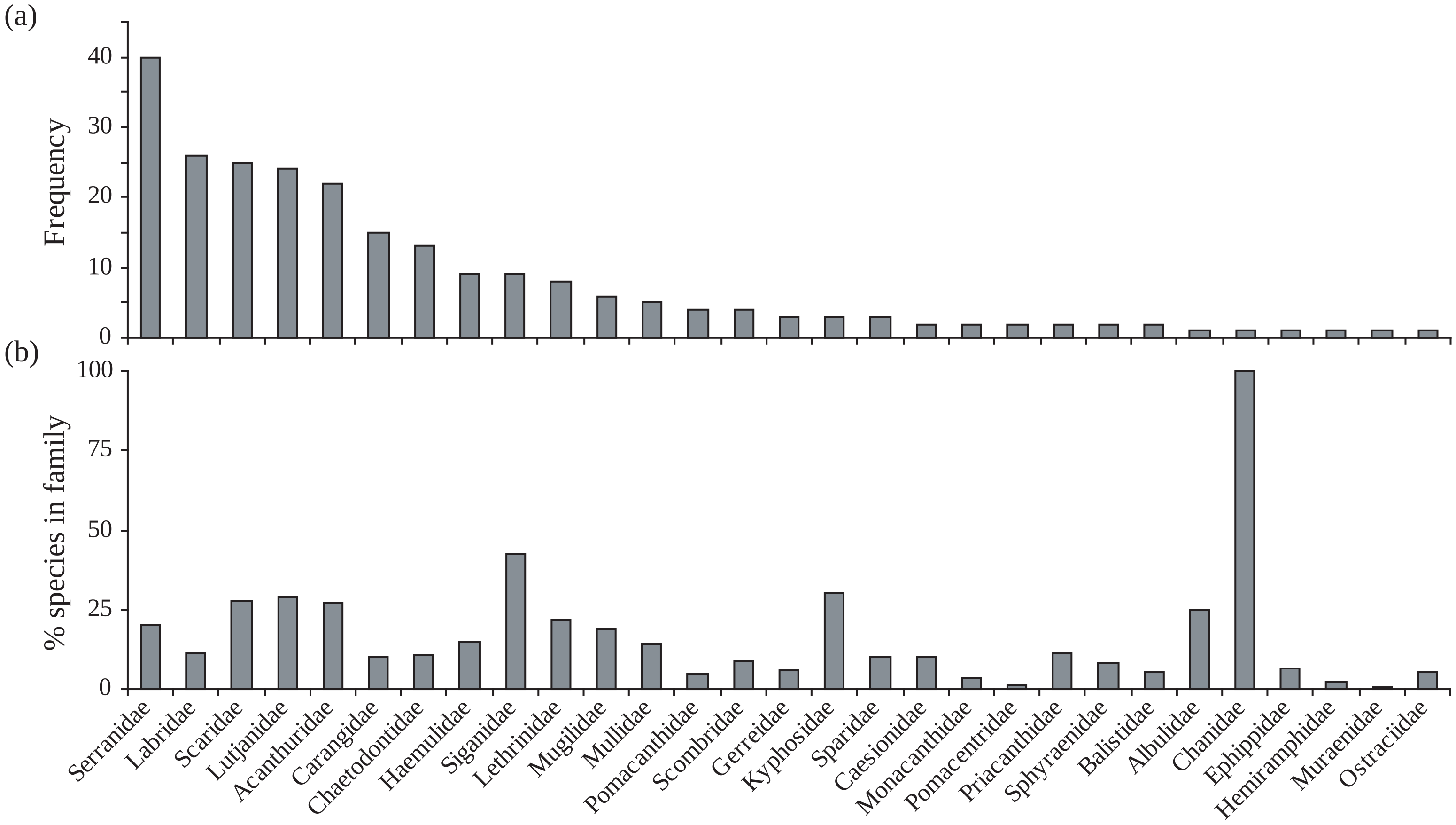

Figure 2.1.(a) The numbers of species of coral reef fishes known to form spawning aggregations from the 29 families identified in Table 2.1. (b) The percentage of coral reef fishes in each family known to form spawning aggregations. Data were compiled from Nelson (1994) and Froese & Pauly (2000).

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).

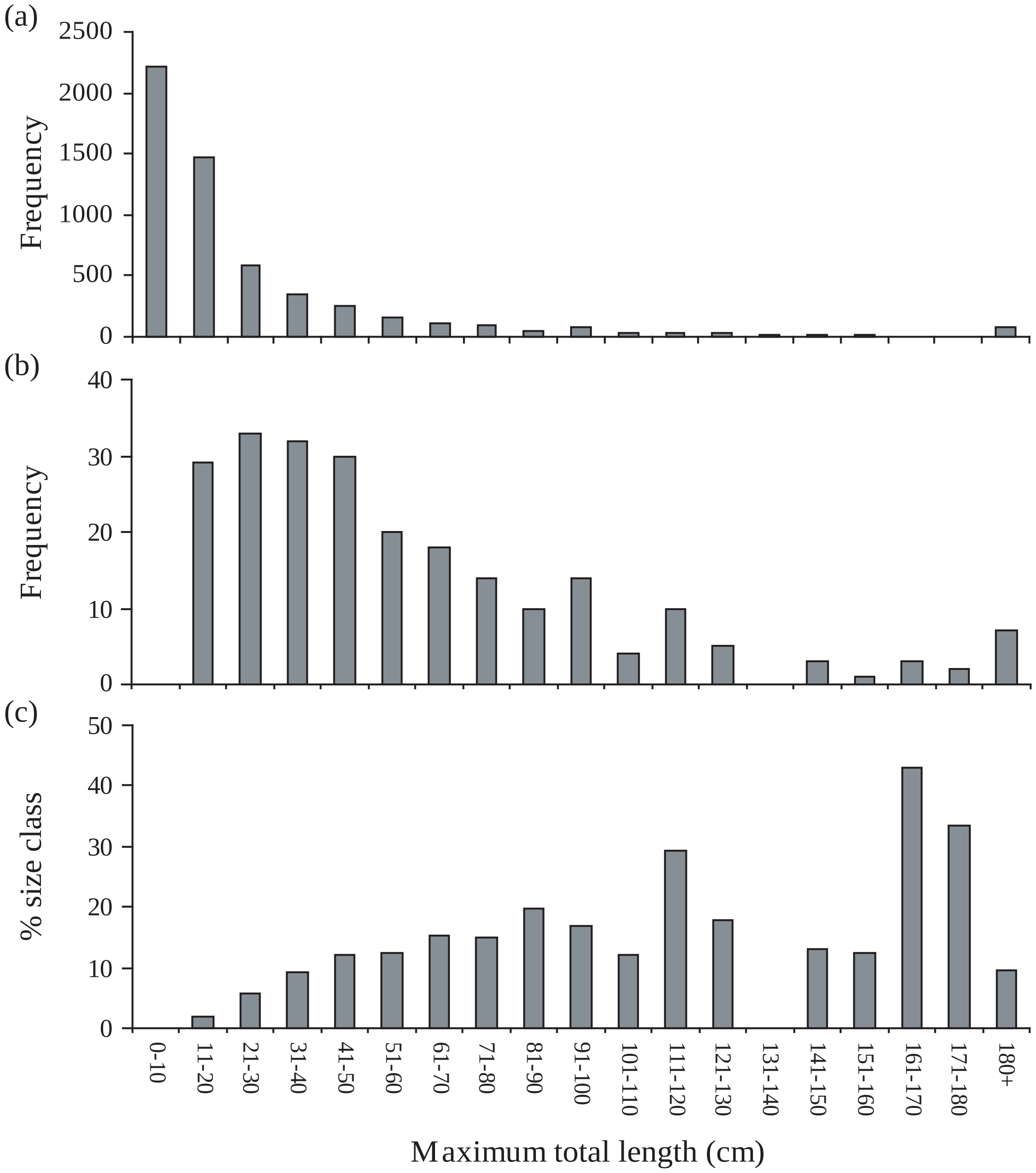

Figure 2.2.(a) Size-frequency distribution of coral reef fishes. (b) Size-frequency distribution of coral reef fishes known to form spawning aggregations. (c) The proportion of each size class represented by species known to form spawning aggregations. The total length data were compiled from sources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

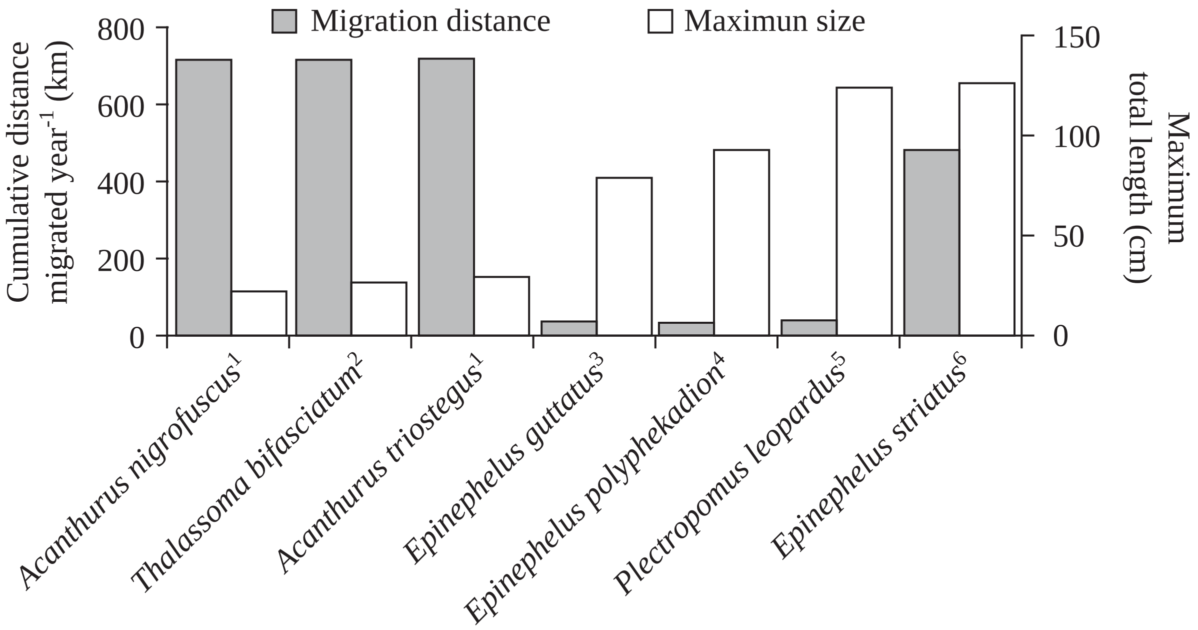

Figure 2.3. The estimated annual cumulative distance migrated by reef fishes with known migration distances to spawning aggregation sites. Cumulative distance was calculated by doubling the maximum distance that species were known to migrate to spawning aggregations, to account for return journeys, and 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).

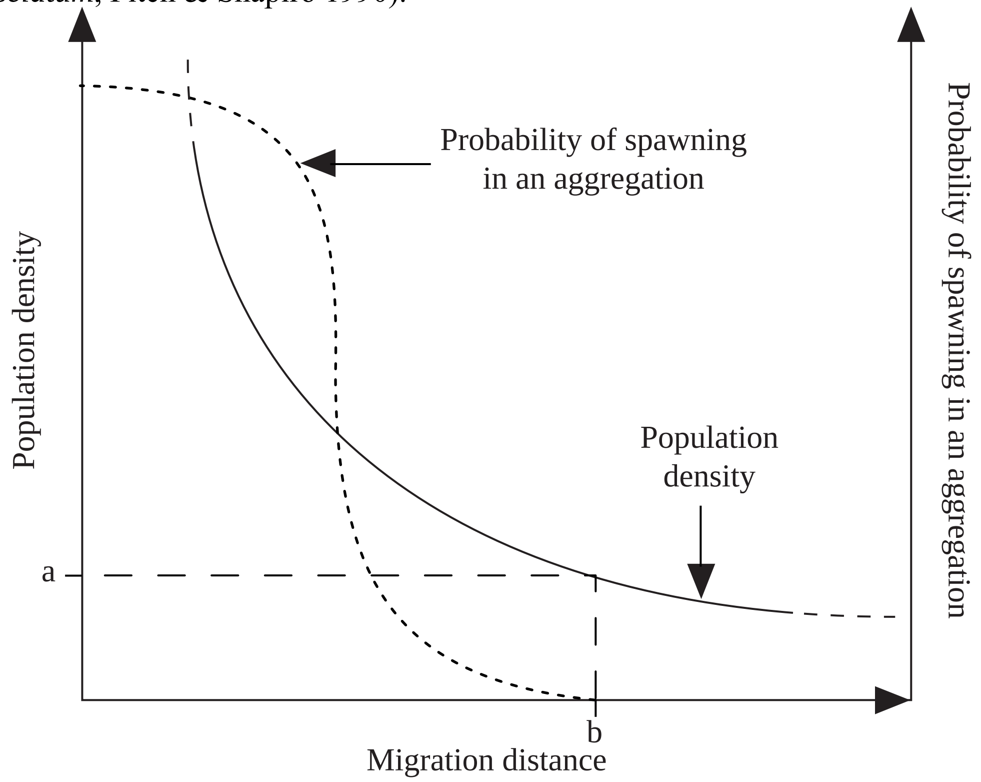

Figure 2.4. The hypothetical interrelationship between population density (full line), migration distance, and the probability that a population will form spawning aggregations (dotted line). When the population density becomes too low (a) the migration distance becomes prohibitively high (b) and spawning 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

Species	Depth (m)	Reef Feature						Reference
		Outer Reef Edge	Channel/ Passage	Promontory/ Bommie	Down-Current Margin	Seaward Projection	Other	
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).

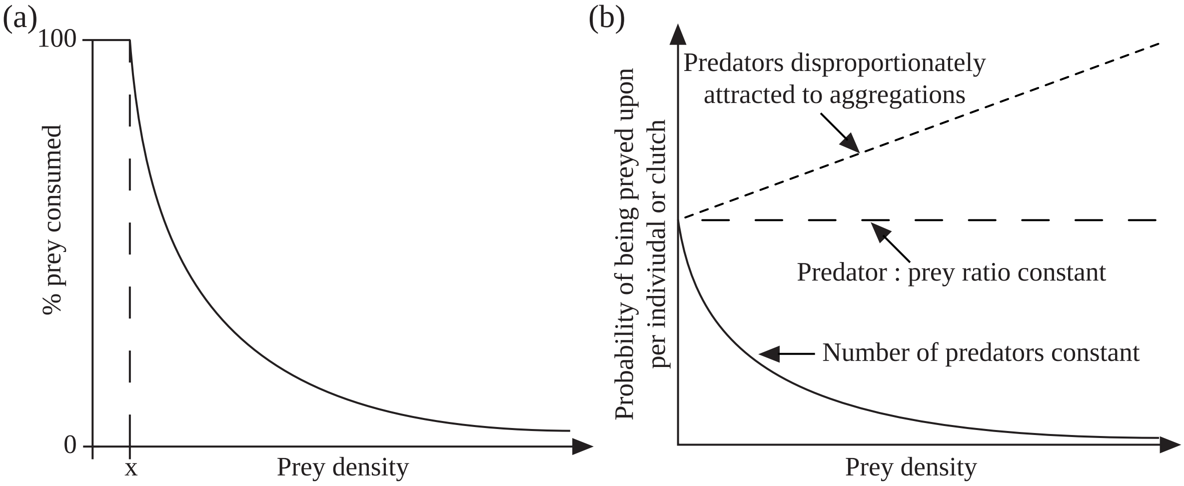

Figure 2.5. (a) The predator satiation hypothesis: the relationship between prey density and the percentage of the prey population that will be consumed. Predators become satiated having consumed x prey. (b) The probability of prey (spawning fish or pelagically released egg) being preyed upon, with increasing 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^{o}30’S 150^{o}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.

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

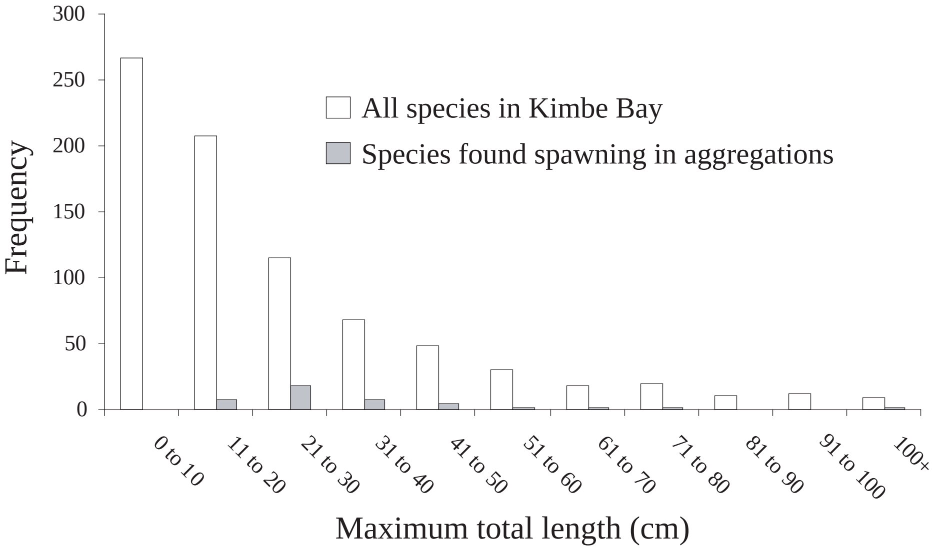

Figure 3.7. Size frequency distribution of all species of reef fish in Kimbe Bay and those found forming spawning aggregations. Sizes from Froese & Pauly (2000), and species presence from Allen & Munday (1996).

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.

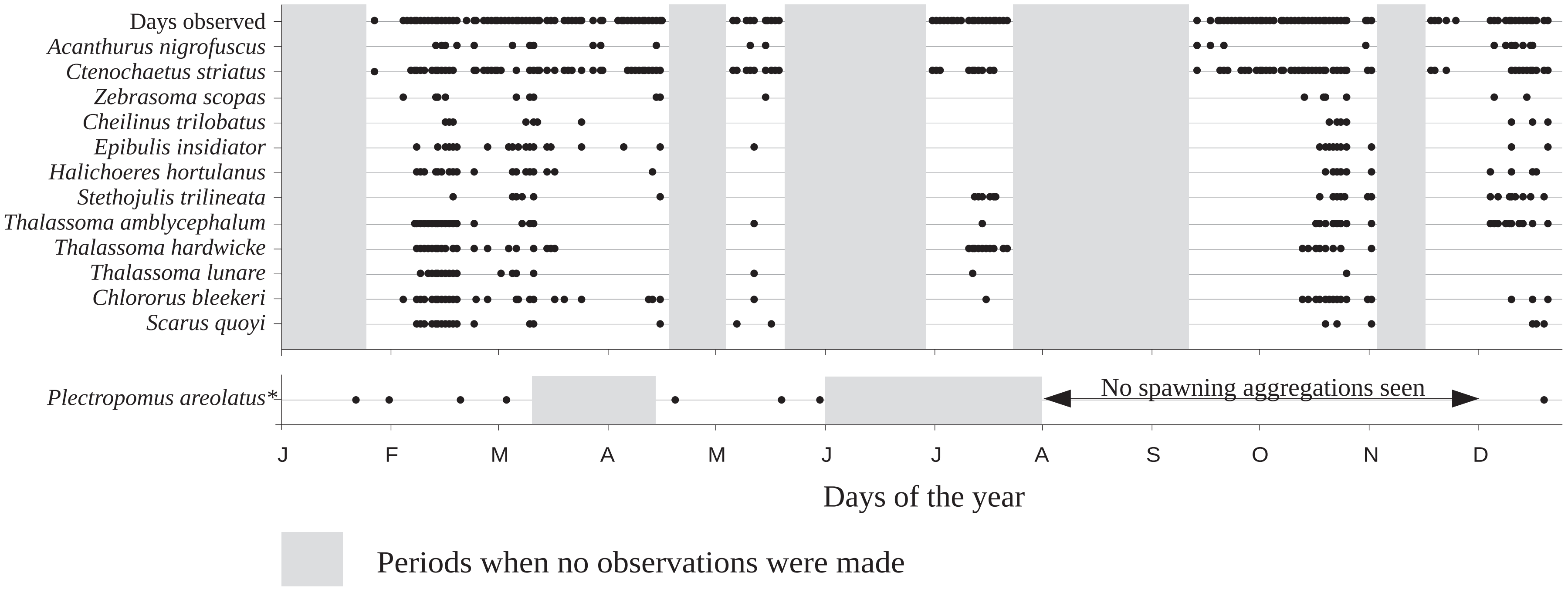

Figure 3.8. Annual patterns of spawning activity in different species of reef fish. Observations were made over 3 years (2001-2004). *~ spawning never witnessed but probable spawning aggregations observed; data for *Plectropomus areolatus* **were collected on a limited number of occasions during 2003-2004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

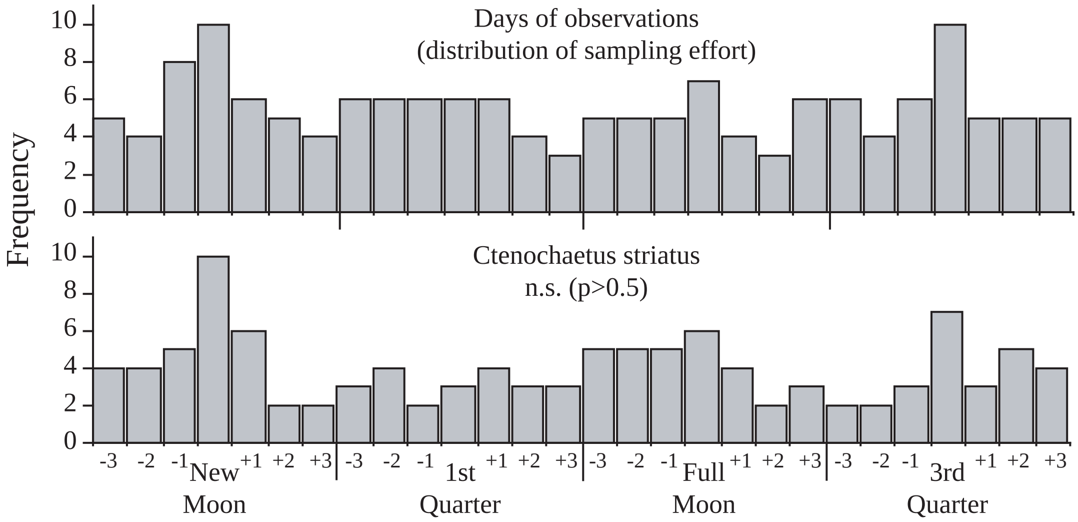

Figure 3.9. Lunar spawning patterns in *Ctenochaetus striatus*. Williams-corrected goodness-of-fit G-tests compared frequency of spawning on days of the lunar month with the frequency with which observations were made. n.s. ~ no significant difference between observed and expected frequency (alpha =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

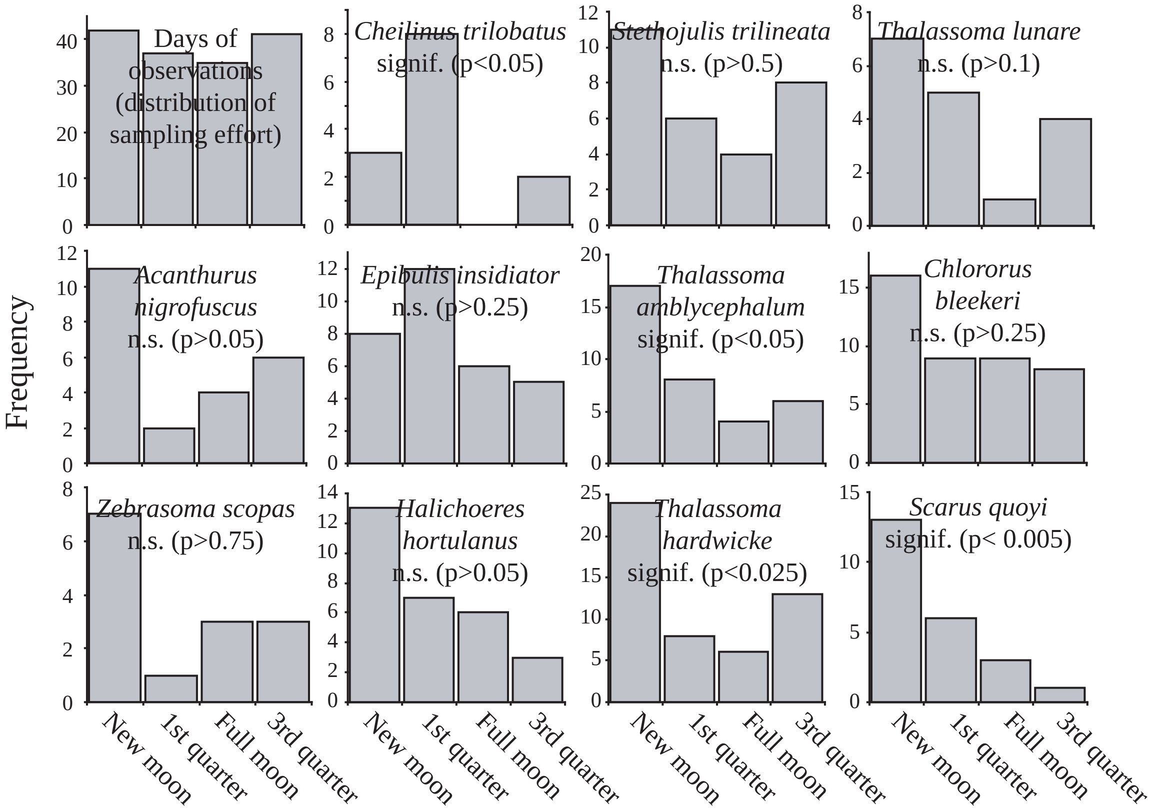

Figure 3.10. Lunar spawning patterns of reef fish species. Williams-corrected goodness-of-fit G-tests compared frequency of spawning during lunar quarters with the frequency with which observations were made. n.s. ~ no significant difference between observed and expected frequency; signif. ~ observed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

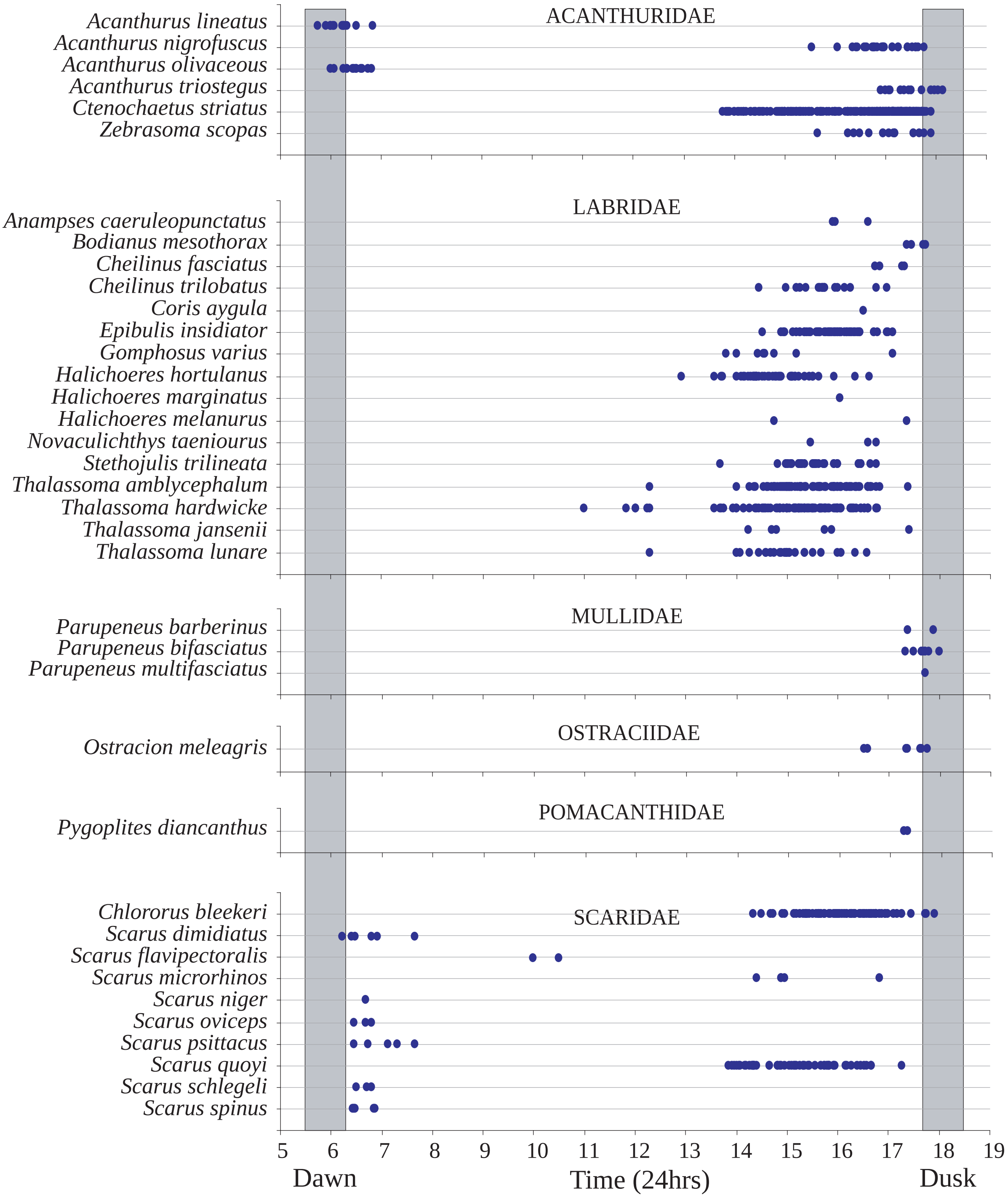

Figure 3.11. Diel patterns of spawning in species of reef fish. Shaded columns represent dawn (05:30 - 06:15) and dusk (17:45 - 18:30).

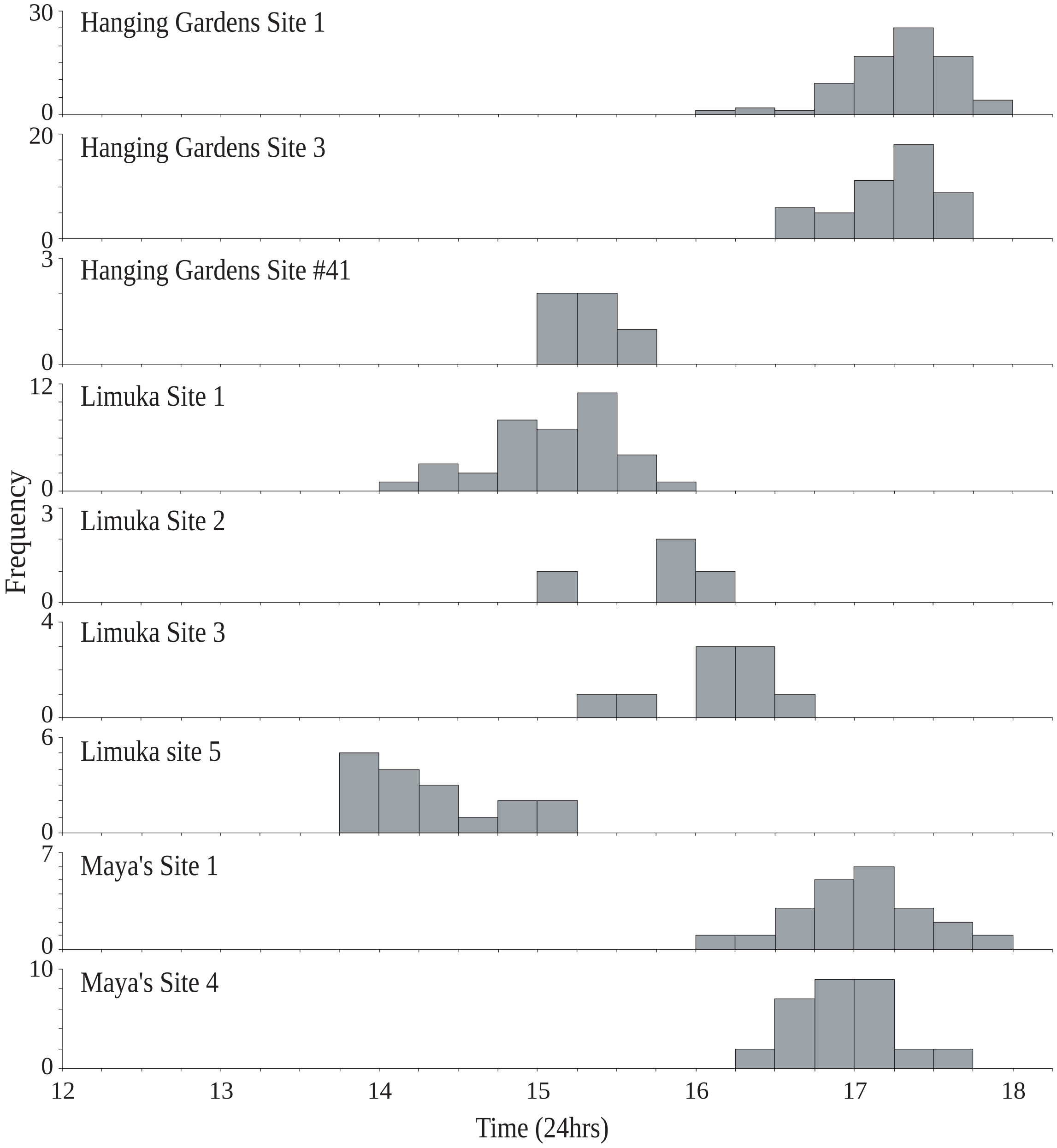

Figure 3.12. Diel patterns of spawning in *Ctenochaetus striatus* at different sites on Hanging Gardens, Limuka, and Maya's. Spawning times differ significantly between sites (one-way ANOVA: F(7,161) = 19.77, p<0.001).

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.

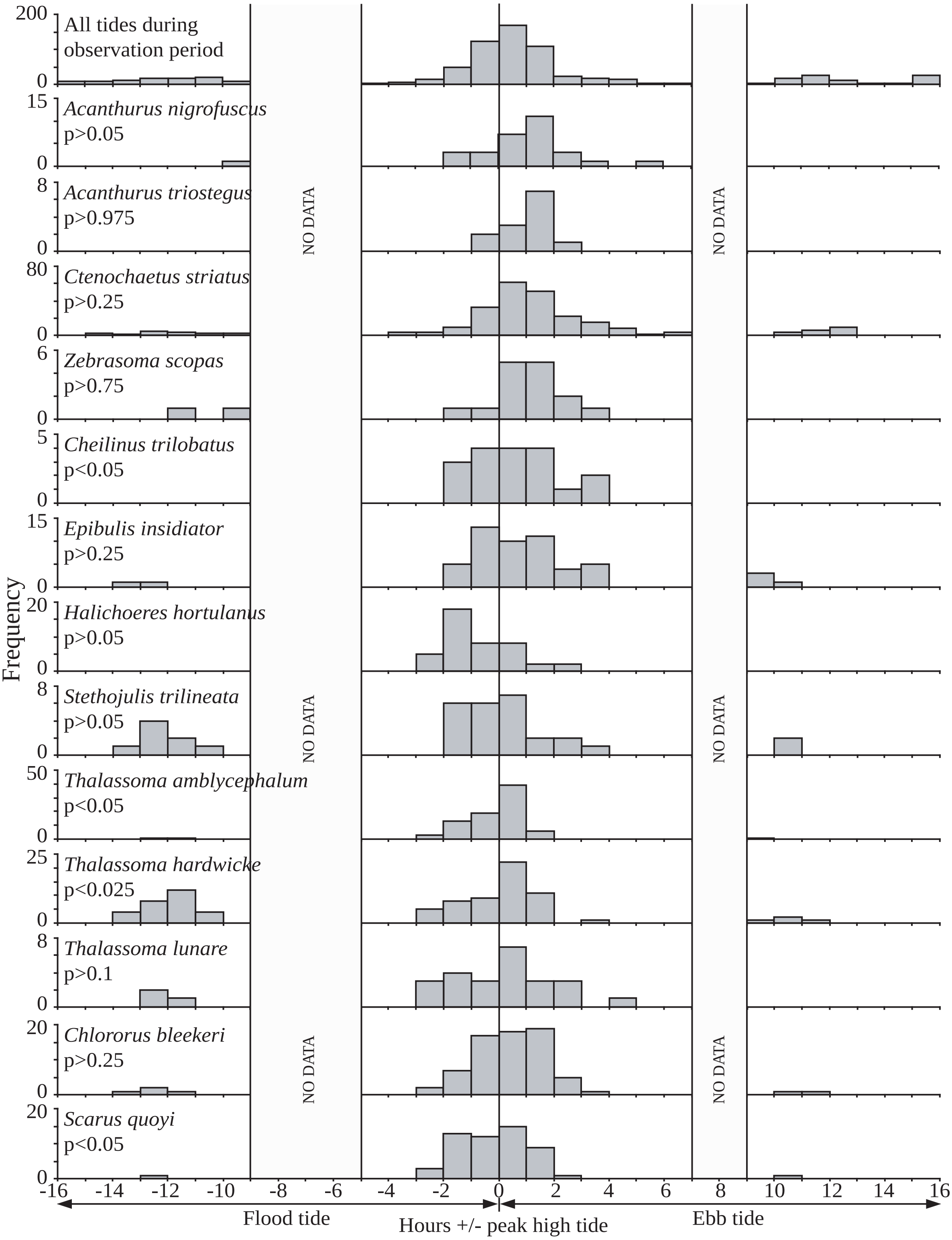

Figure 3.13. Tidal patterns of spawning in species of reef fish. Frequency ~ number of days spawning seen during time interval +/- peak high tide. p ~ resultant probability from Williams corrected goodness-of-fit G-tests that observed distribution differs from that expected from the species' known diel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

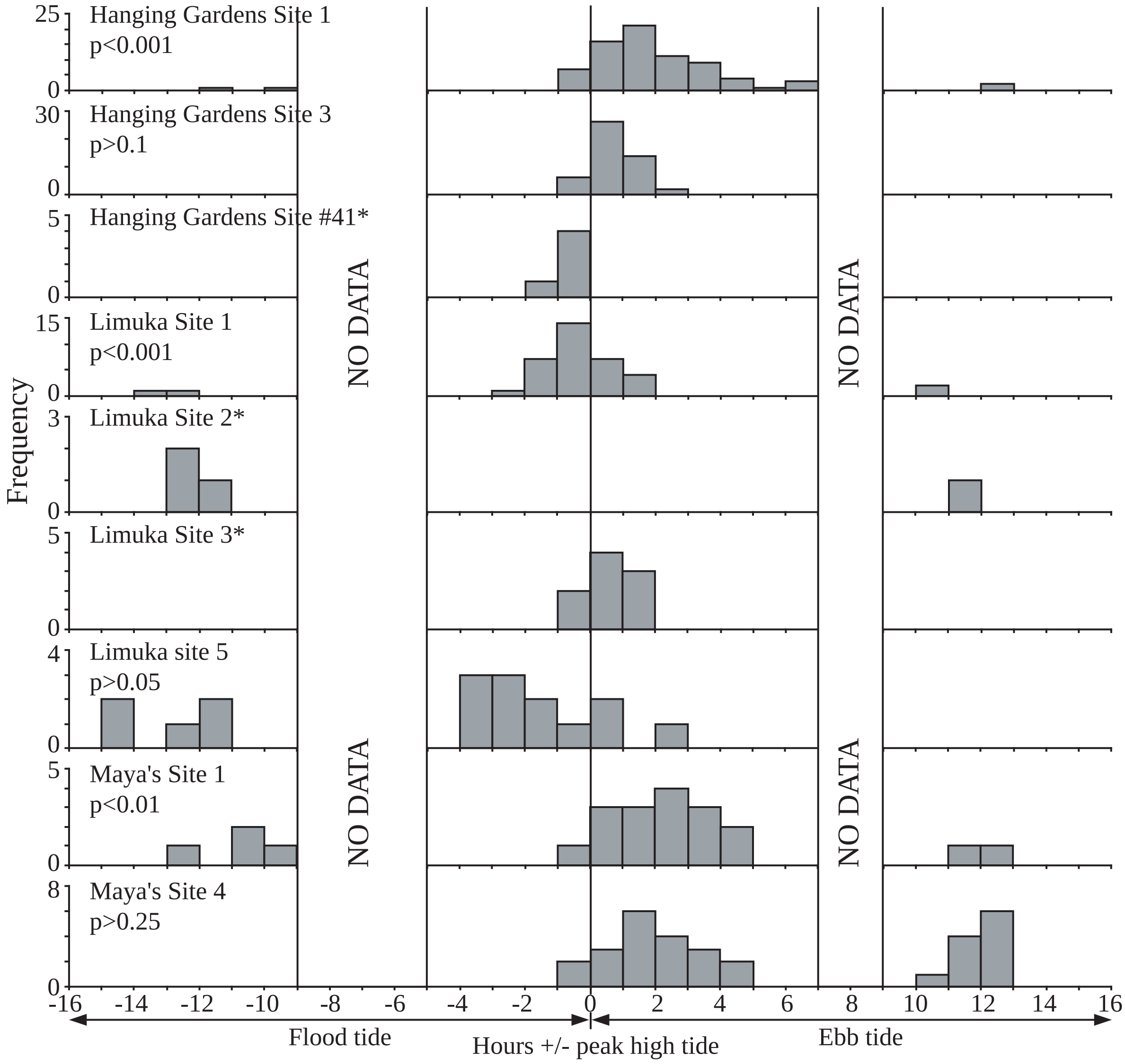

Figure 3.14. Tidal patterns of spawning in *Ctenochaetus striatus* at different sites. Frequency ~ number of days spawning seen during time interval +/- peak high tide. p ~ resultant probability from Williams-corrected goodness-of-fit G-tests that observed distribution differs from that expected from 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.

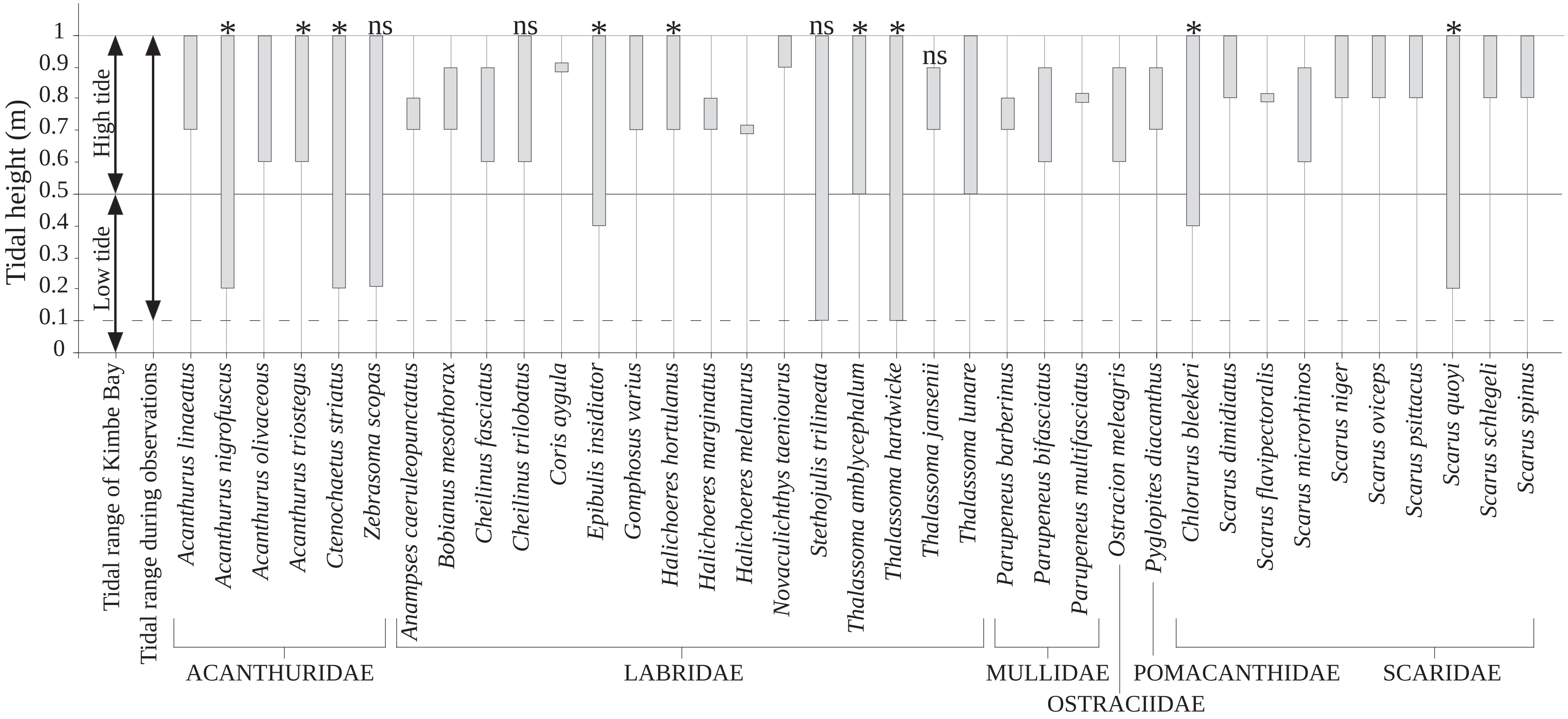

Figure 3.15. Tidal heights over which species of reef fish spawned. Where sufficient data permitted, a Williams-corrected goodness-of-fit G-test was used to compare the distribution of tidal heights over which a species spawned to that predicted by its diel spawing interval on the days observations were 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.

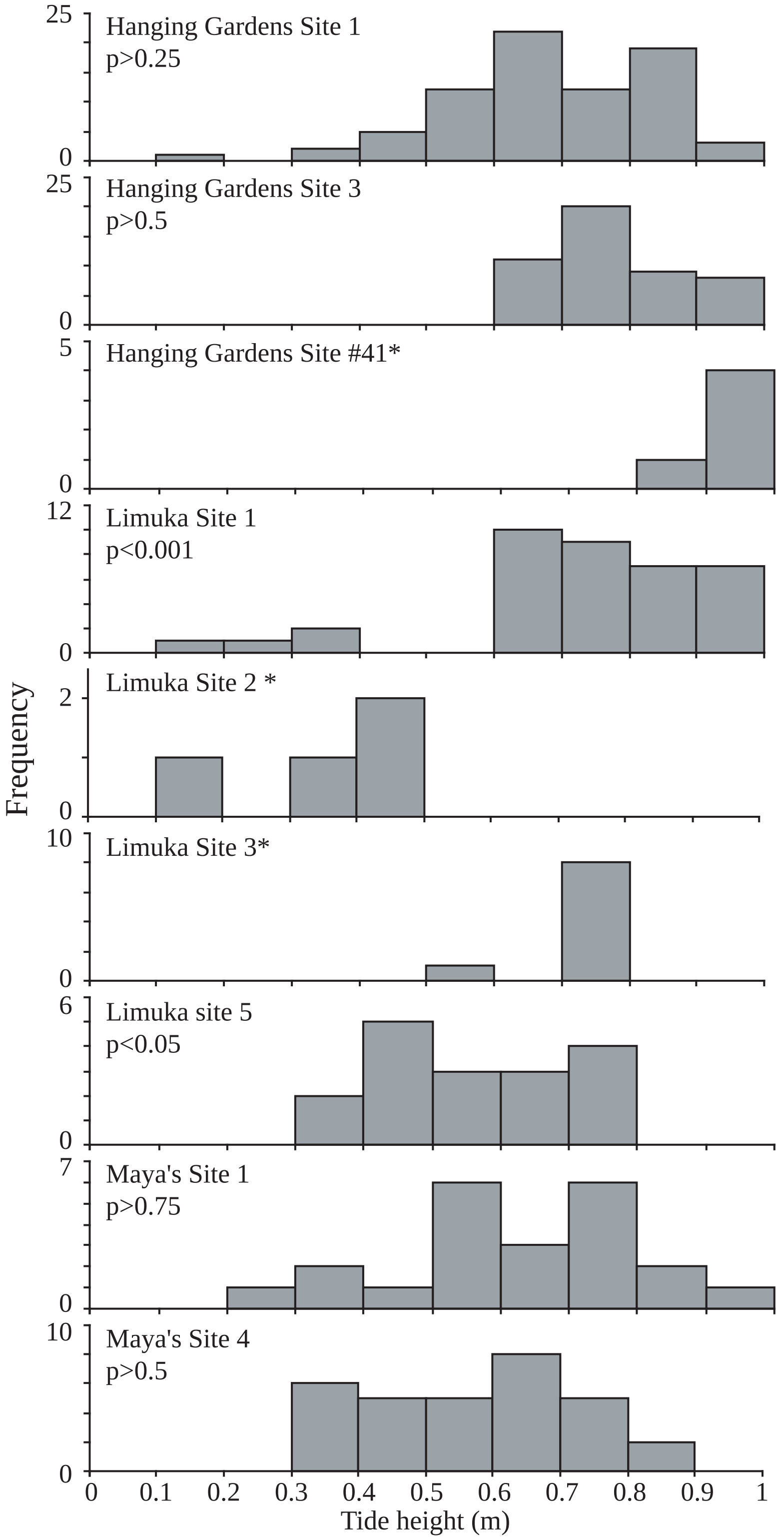

Figure 3.16. Tidal heights over which *Ctenochaetus striatus* spawned at different sites on Hanging Gardens, Limuka and Maya's. Where sufficient observations permitted, Williams-corrected goodness-of-fit G-tests were used to compare the distribution of tidal heights over which spawning occurred to that 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.