CHAPTER 4: SPAWNING AGGREGATION SITES: PHYSICAL AND BIOTIC CHARACTERISTICS

4.1. Introduction

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

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

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

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

4.1.1 Aims:

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

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

4.2 Materials and Methods:

4.2.1 Study species:

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

4.2.2 Study area and study sites:

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

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

4.2.3 Broad-scale physical characteristics:

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

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

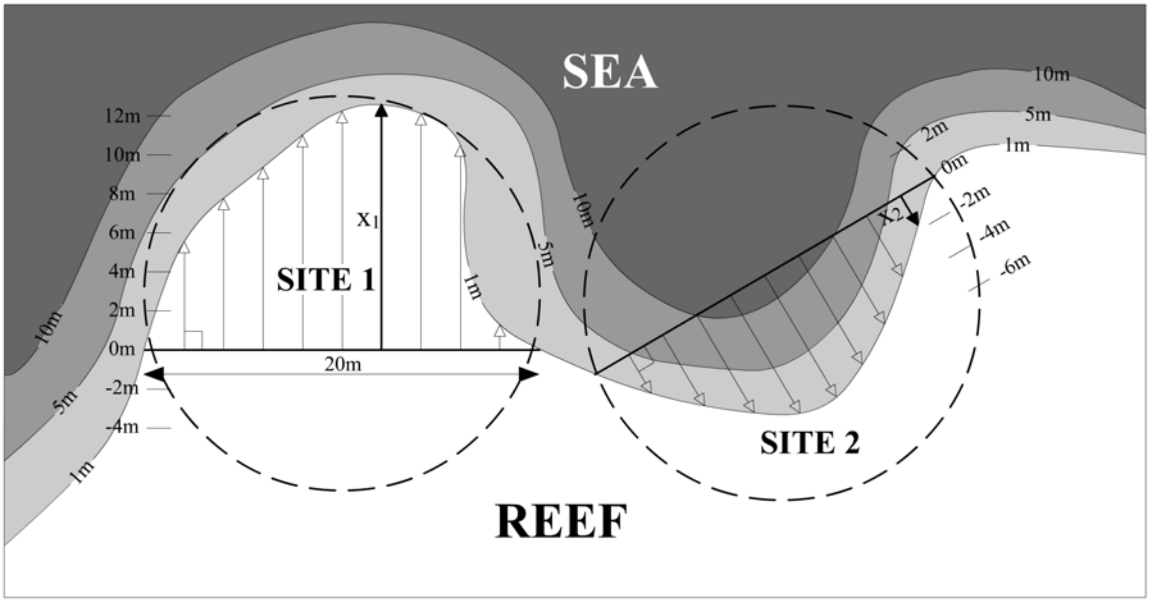


Figure 4.2. Measurement of maximum seaward projection at convex (Site 1) and concave (Site 2) areas of reef. x_1 = maximum seaward projection at Site 1; x_2 = maximum seaward projection at Site 2.

4.2.4 Fine-scale physical and biotic characteristics:

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

4.2.5 Piscivorous and planktivorous fishes:

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

4.2.6 Data analyses:

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

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

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

4.3 Results:

4.3.1 Seaward projection of reef margin:

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

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

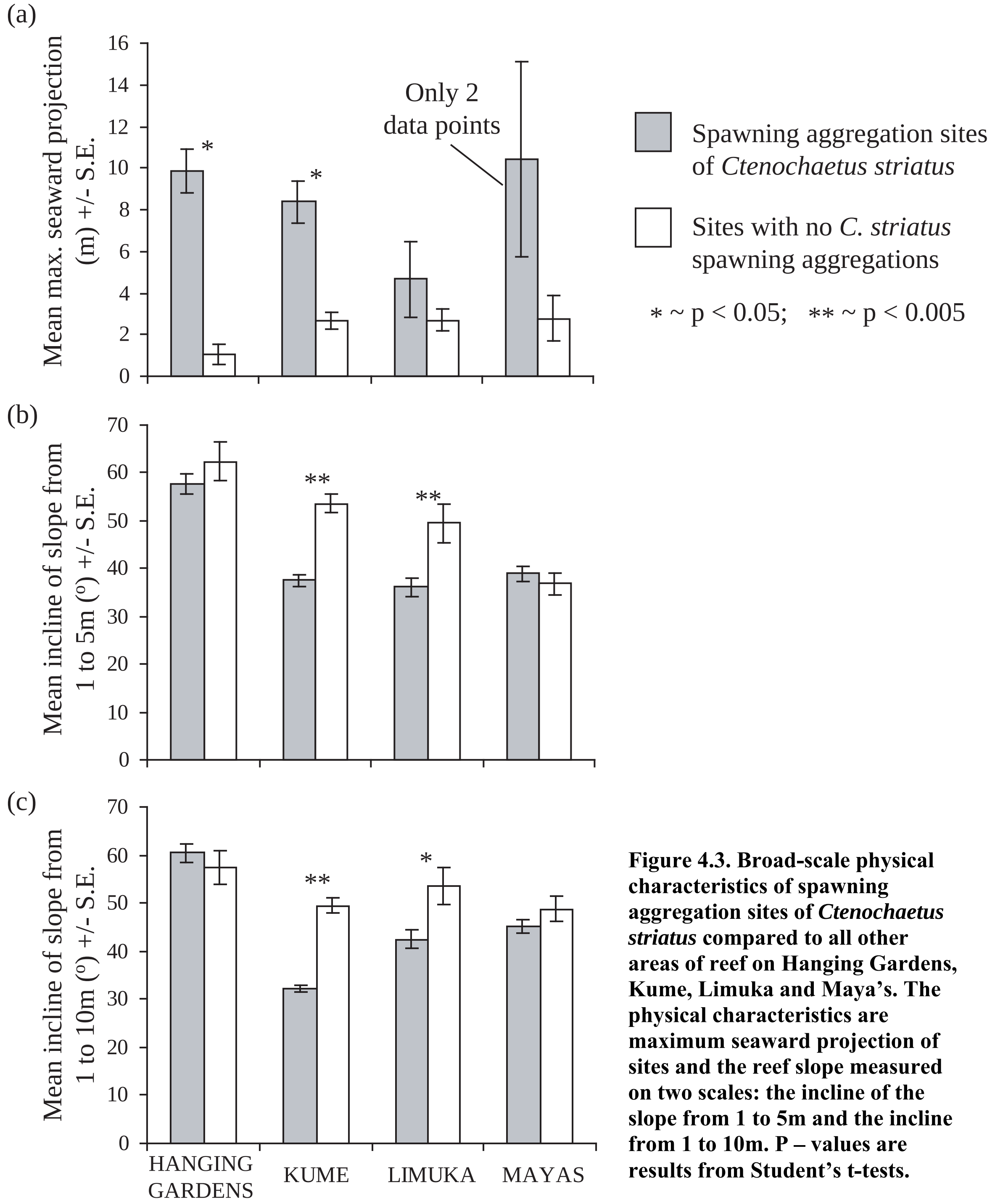


Figure 4.3. Broad-scale physical characteristics of spawning aggregation sites of *Ctenochaetus striatus* compared to all other areas of reef on Hanging Gardens, Kume, Limuka and Maya's. The physical characteristics are maximum seaward projection of sites and the reef slope measured on two scales: the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

4.3.2 Reef slope:

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

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

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

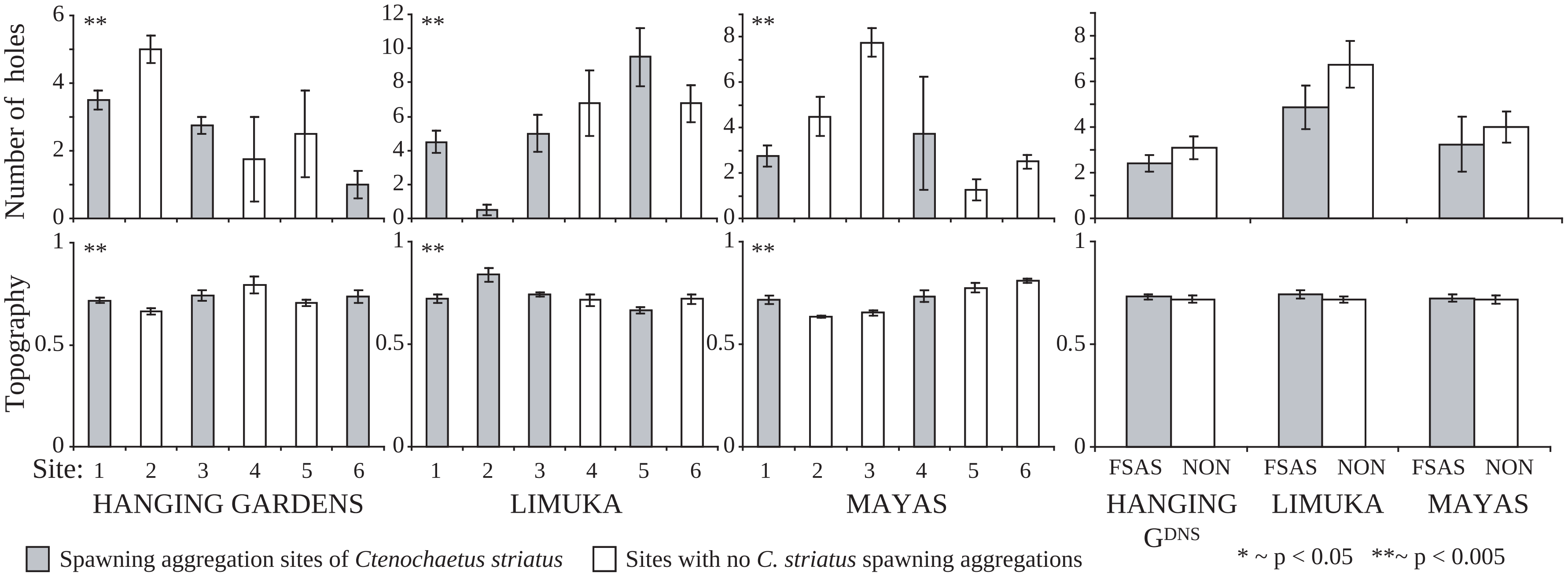


Figure 4.4. The mean number of holes in the substratum (between 6 and 20 cm maximum aperture), and topographic complexity (Topography; 1 = flat, <1 =topographically complex) +/- S.E. at all 6 sites on Hanging Gardens, Limuka and Maya's. The means for all spawning aggregation sites (FSAS) vs. sites where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

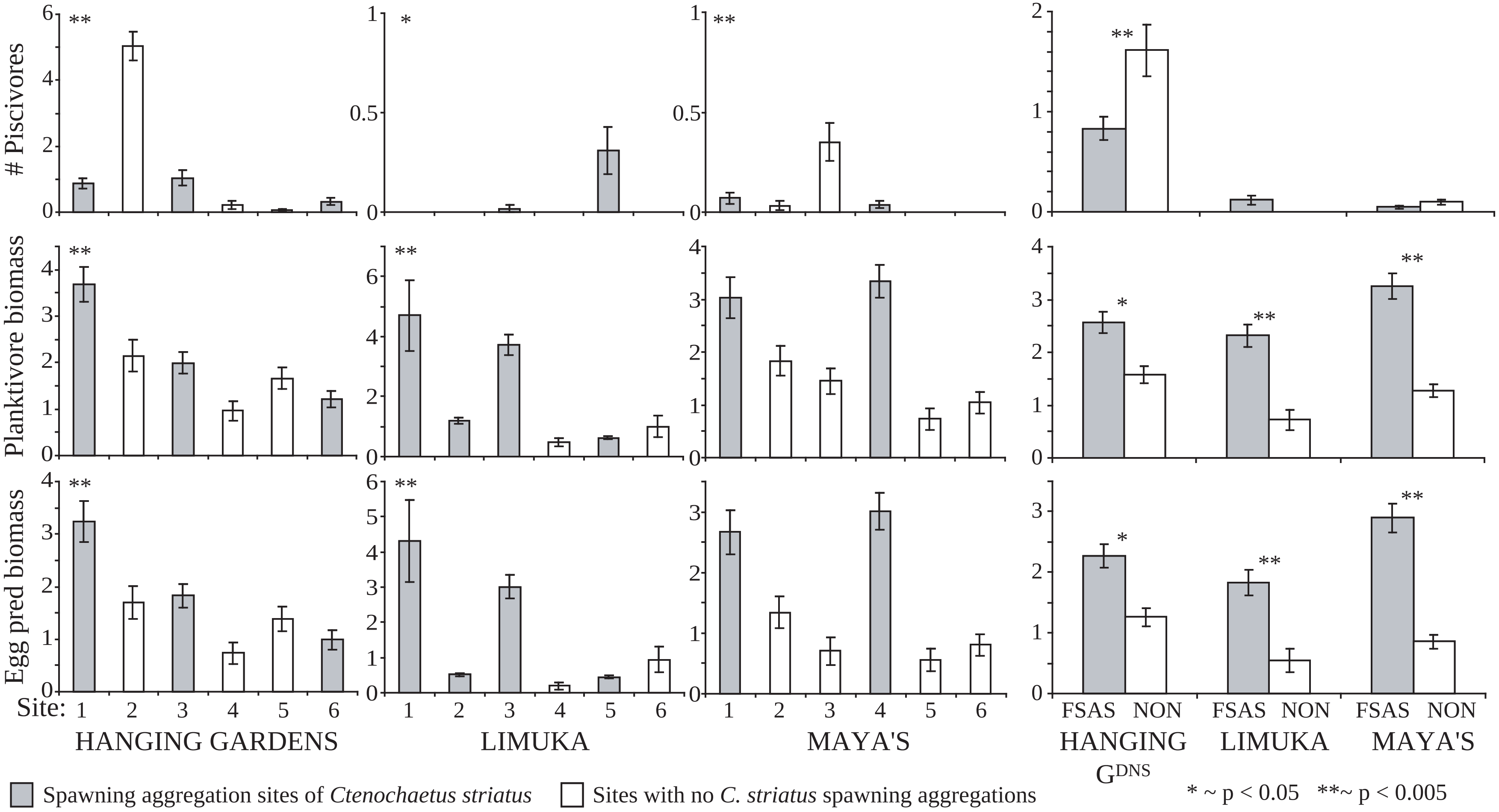


Figure 4.5. The piscivore presence (number of individuals) and planktivore biomass (kg) at study sites: the abundance of piscivores (>30cm S.L.), the estimated biomass of all planktivores, and the estimated biomass of target egg predators (Egg pred) at all sites on Hanging Gardens, Limuka and Maya's,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

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

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

4.3.3 Refuge from predation:

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

4.3.4 Piscivores:

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

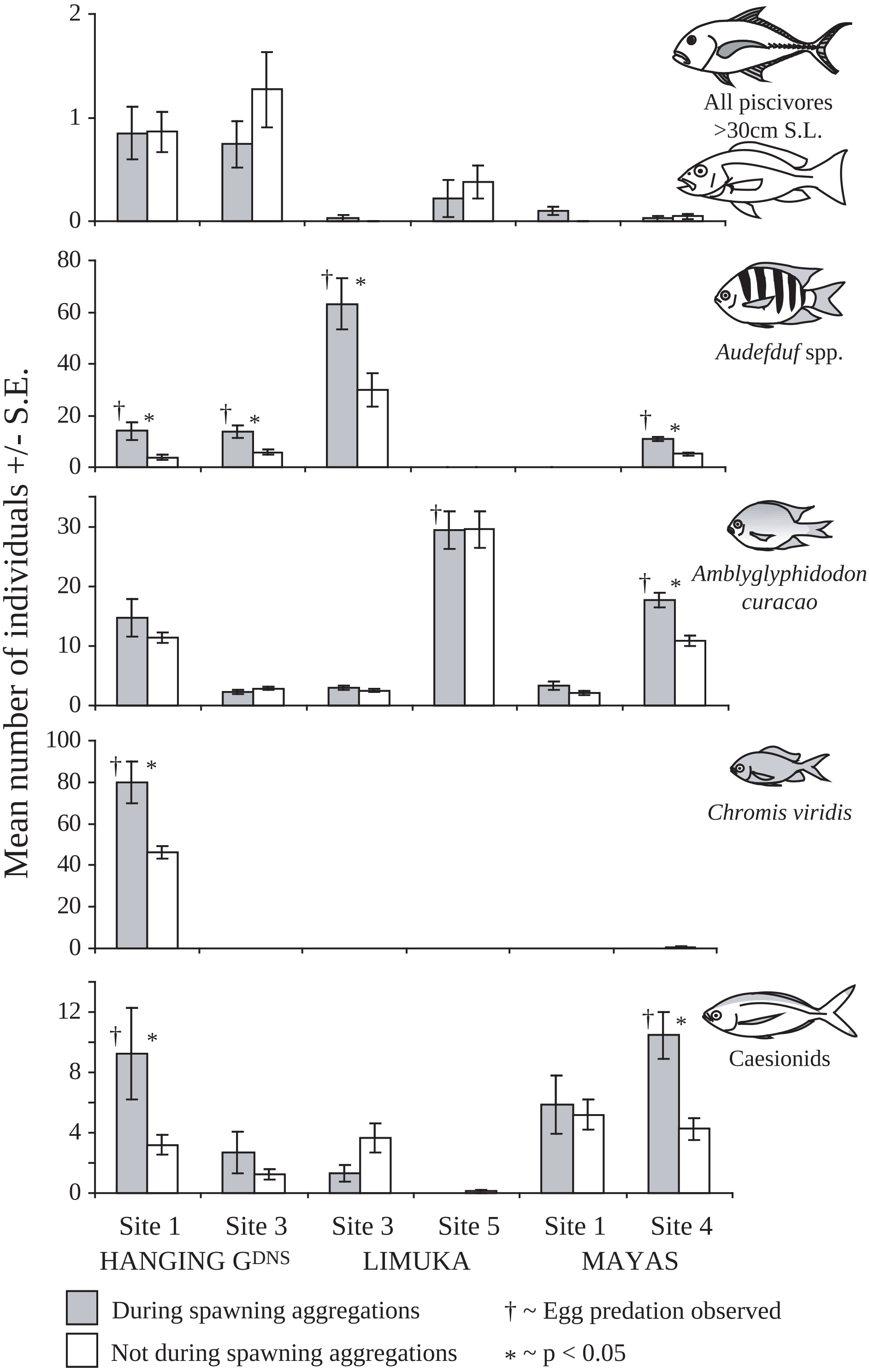


Figure 4.6. The abundance of piscivores and target egg predators at spawning aggregation sites at times when spawning aggregations are formed and at times when they are not. Only piscivores >30cm S.L. were included. Target egg predators illustrated are *Abudefduf* spp., *Amblyglyphidodon curacao*, *Chromis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

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

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

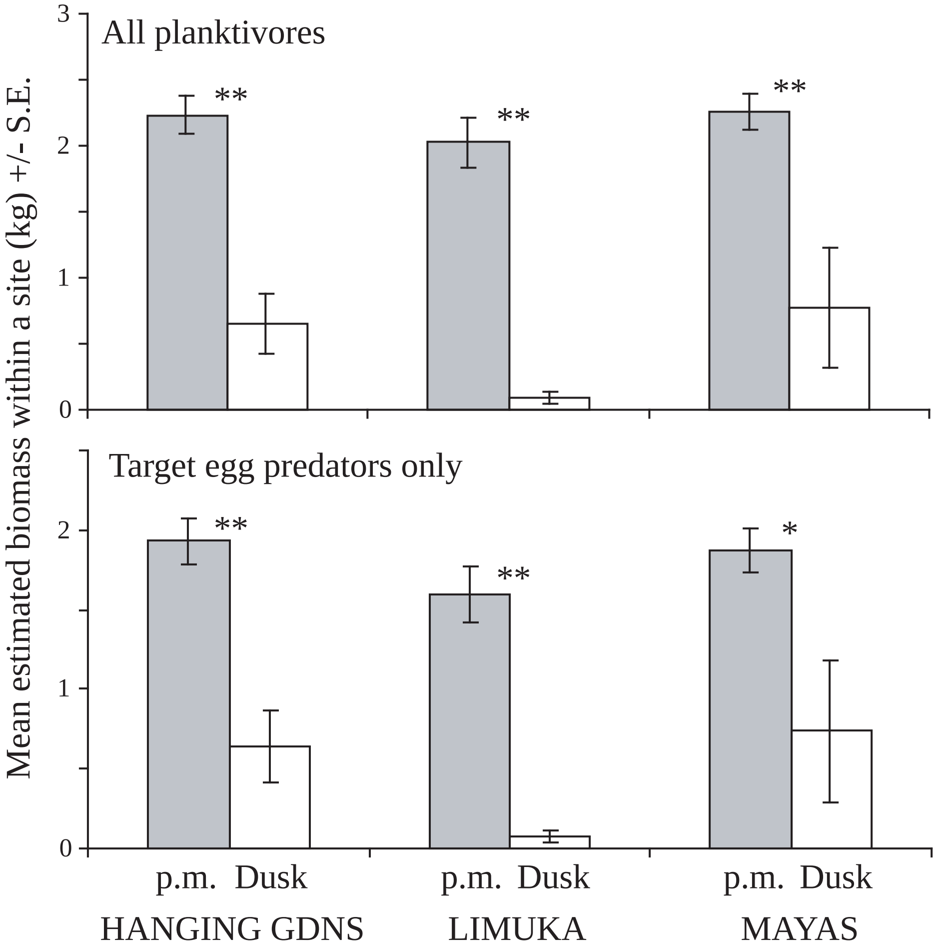


Figure 4.7. Mean estimated biomass of all planktivores and target egg predators only at times in the afternoon (p.m.) and at dusk (17:45 – 18:20 hrs). Means derived from data from all sites within reefs. * ~ $p < 0.05$; **~ $p < 0.005$. p – values are results of Student's t-tests between mean biomass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

4.3.5 Planktivores:

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

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

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

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

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

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

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

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

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

4.4 Discussion:

4.4.1 Seaward projections and reef slope:

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

4.4.2 Refuge from predation:

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

4.4.3 Piscivores and planktivores:

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

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

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

4.4.4 Continued spawning despite predation of eggs:

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

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

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

4.5 Conclusion

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

CHAPTER 5: SPAWNING AGGREGATIONS AND CURRENTS

5.1 Introduction

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

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

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

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

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

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

5.1.1 Aims

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

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

5.2 Materials and Methods:

5.2.1 Study species:

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

5.2.2 Study area:

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

5.2.3 Current Measuring Device:

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

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

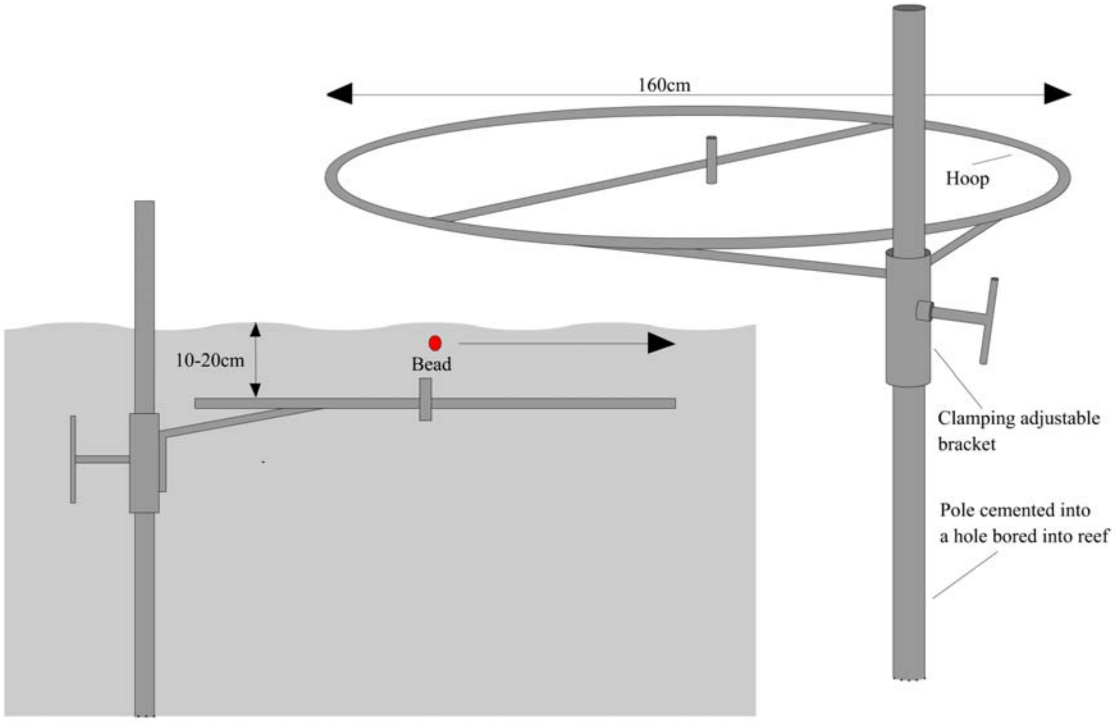


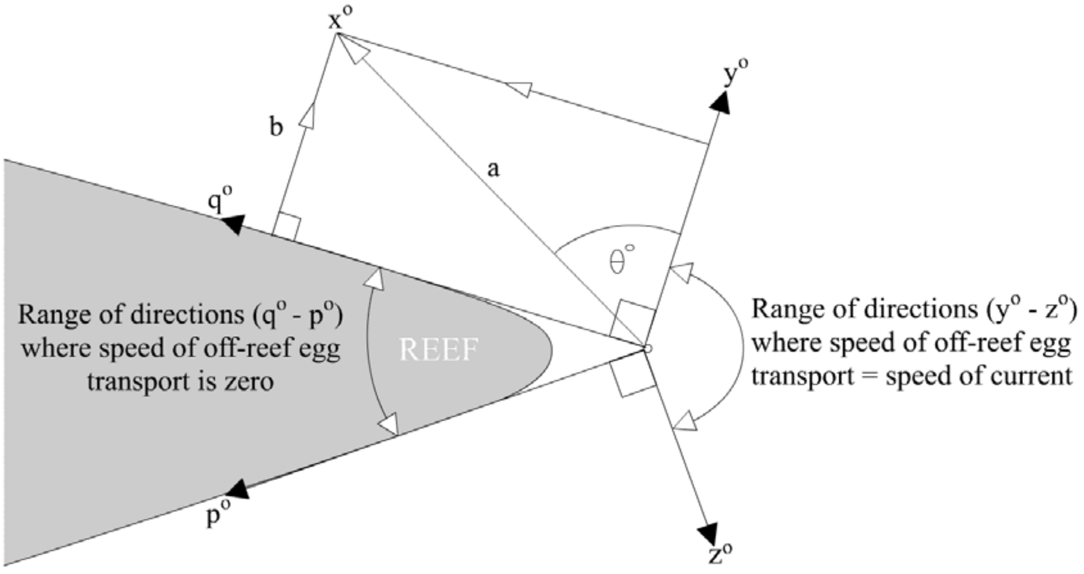
Figure 5.2. Current measuring device

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

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

5.2.4 Off-reef current speed:

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



Eggs spawned pelagically in a current with a speed of "a" and a direction of "x^o" have an off-reef speed of "b", where $b = a\cos\theta$

Figure 5.3. Calculation of off-reef current speeds.

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

5.2.5 Study Sites:

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

5.2.6 Data Collection:

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

5.2.7 Data analyses:

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

5.3 Results:

5.3.1 General patterns of currents:

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

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

5.3.2 Species recorded spawning in aggregations:

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

5.3.3 Choice of spawning aggregation sites within reefs:

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

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

5.3.4 Currents at times of aggregative spawning:

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

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

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

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

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

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

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

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

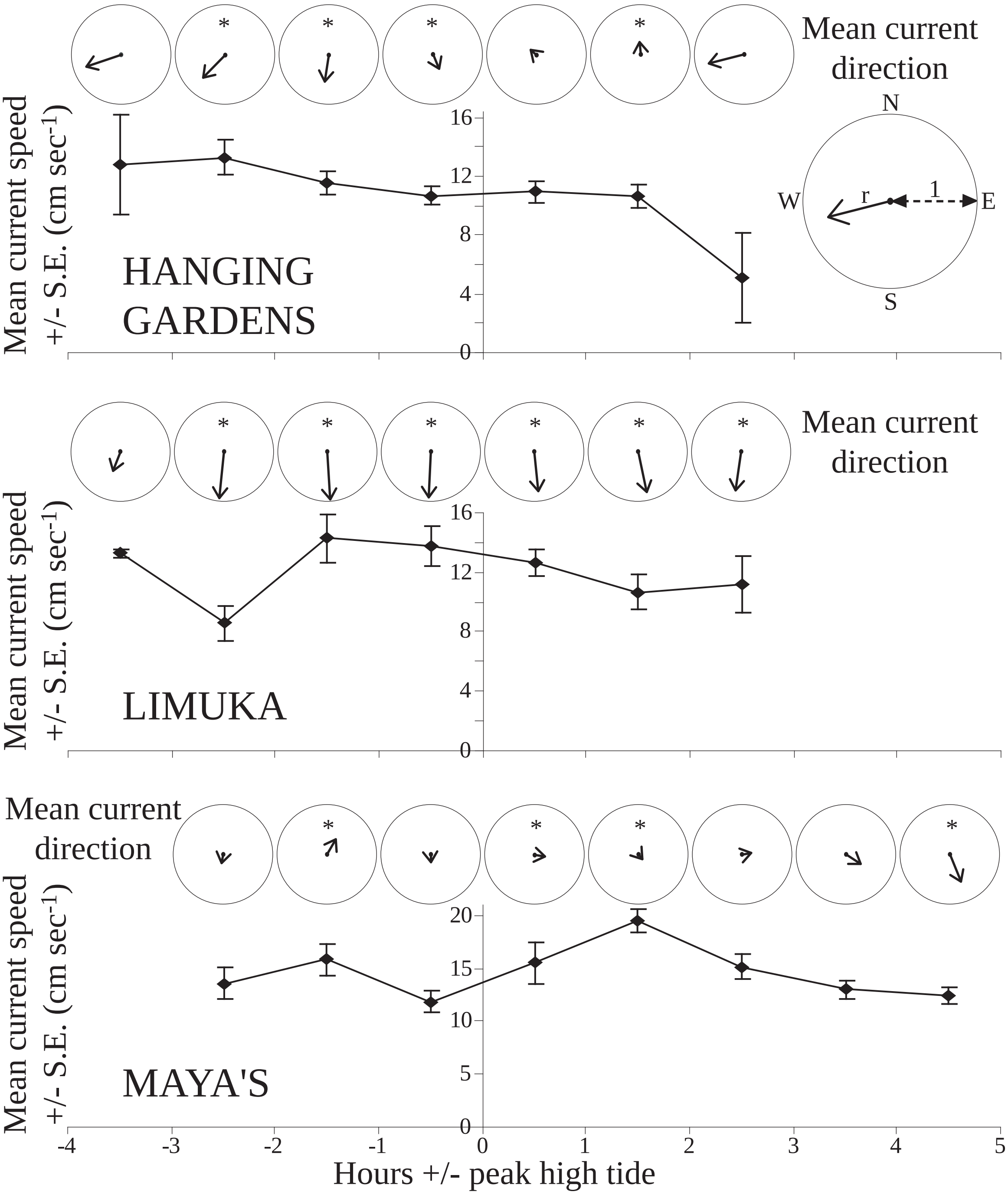


Figure 5.4. Mean current speed and direction at Hanging Gardens, Limuka, and Maya's with time +/- peak high tide. Means derived from currents measured at all sites on reefs within hourly time bins +/- peak high tide. Arrows indicate mean current direction. Length of arrow = r ; r = angular concentration;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

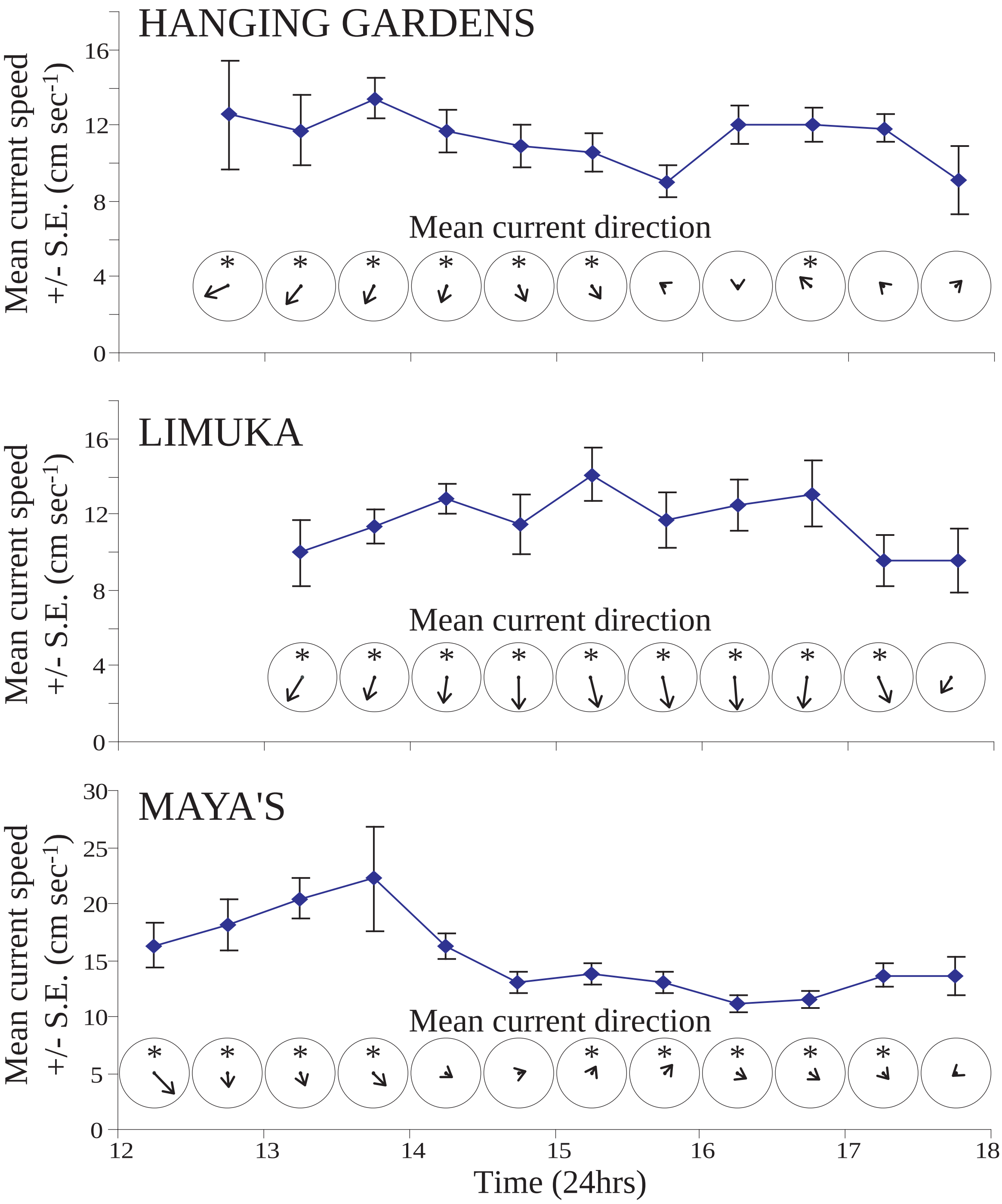


Figure 5.5. Mean current speed and direction at Hanging Gardens, Limuka, and Maya's with time. Means derived from currents measured at all sites on reefs within 30 min time bins. Key to current direction as in Figure 5.4.

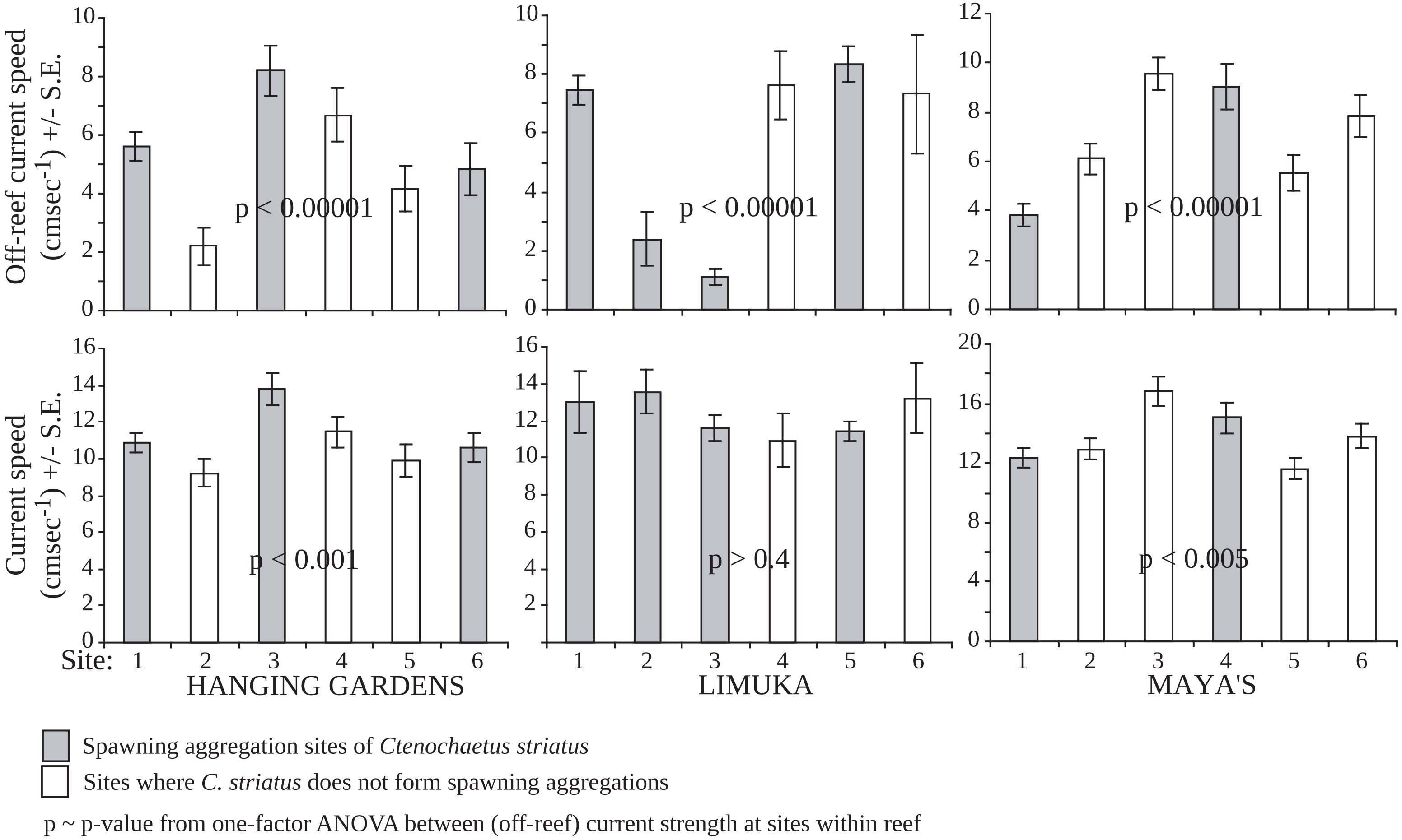


Figure 5.6. Mean off-reef current speed and mean current speed at all sites on Hanging Gardens, Limuka and Maya's. P-values are the results from single factor ANOVA's testing for equality of current speed between sites on reefs.

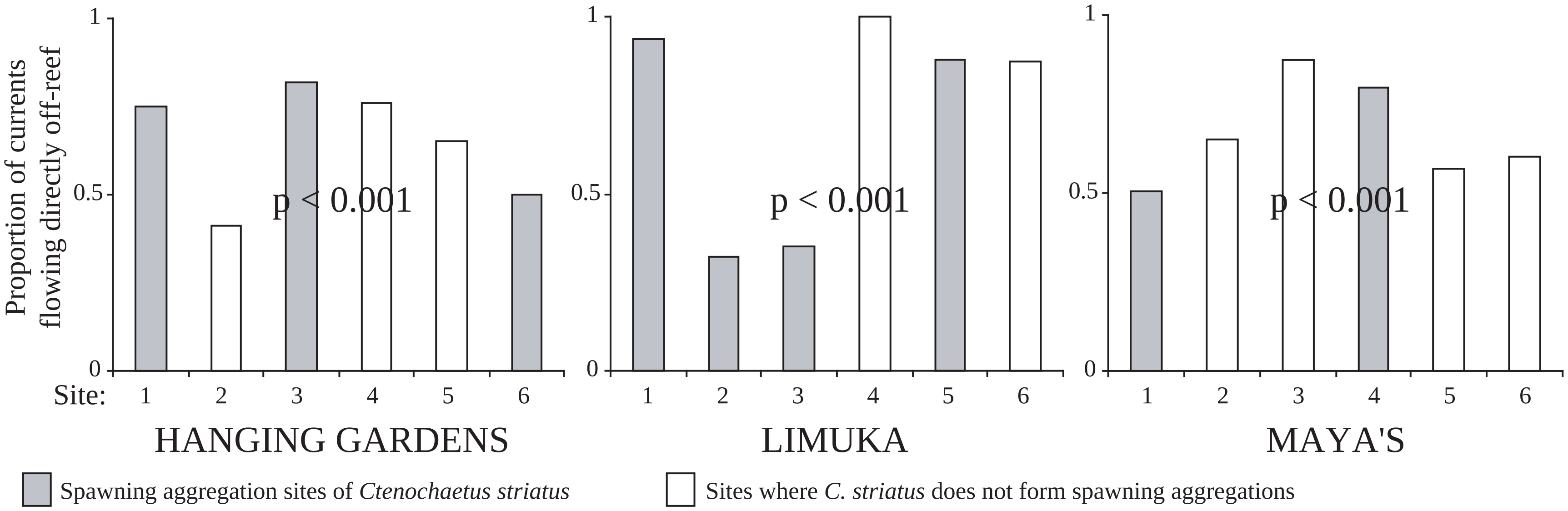


Figure 5.7. Proportion of all currents measured that flow directly off-reef at all sites on all reefs. p-values are the probability that the ratios of off-reef to on-reef currents are homogenous across sites within reefs (derived from a replicated G-test of homogeneity).

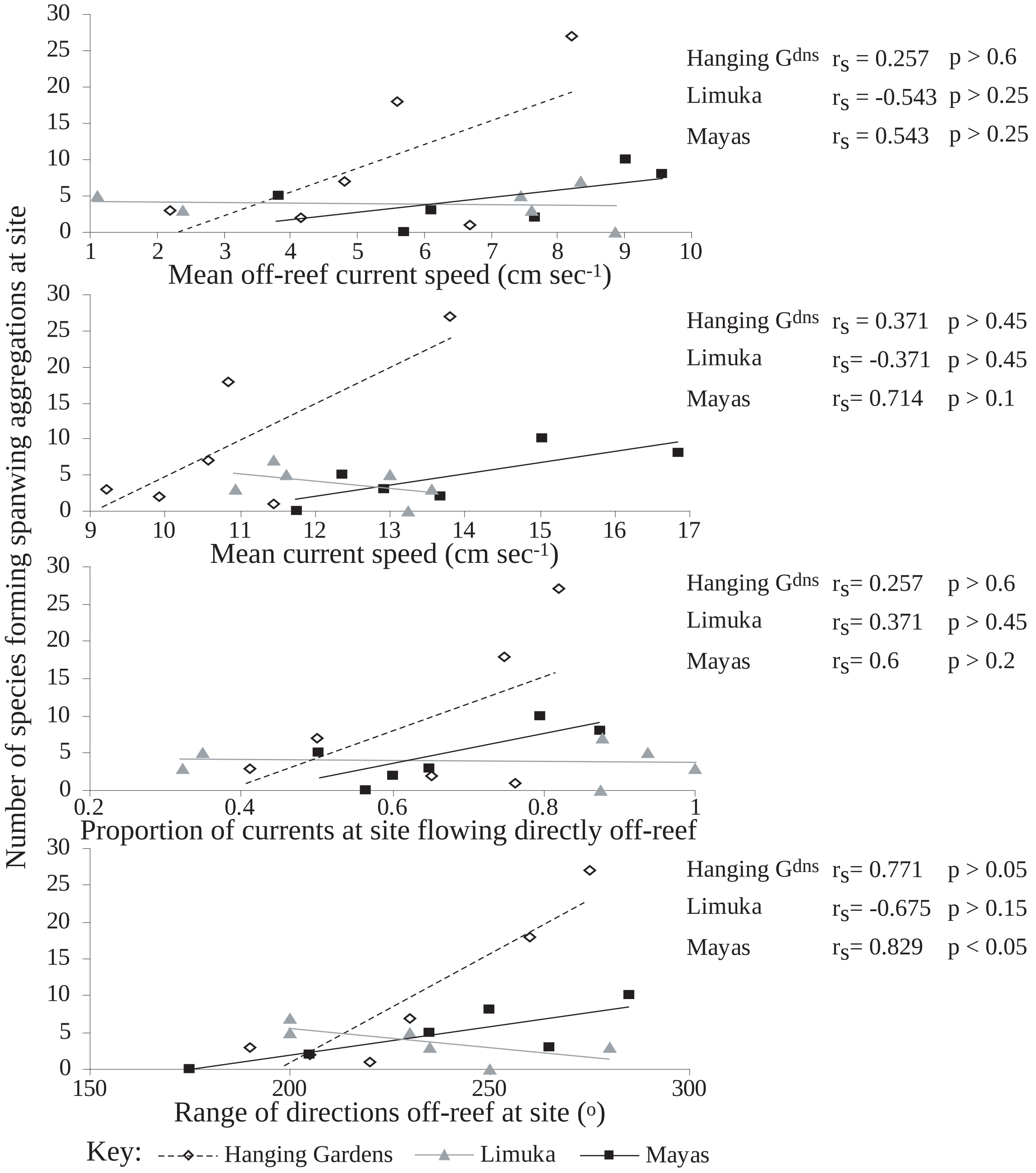


Figure 5.8. Relationship between characteristics of the currents measured, range of directions off-reef, and number of species forming spawning aggregations at a site. r_S and p-values are results of Spearman rank correlations.

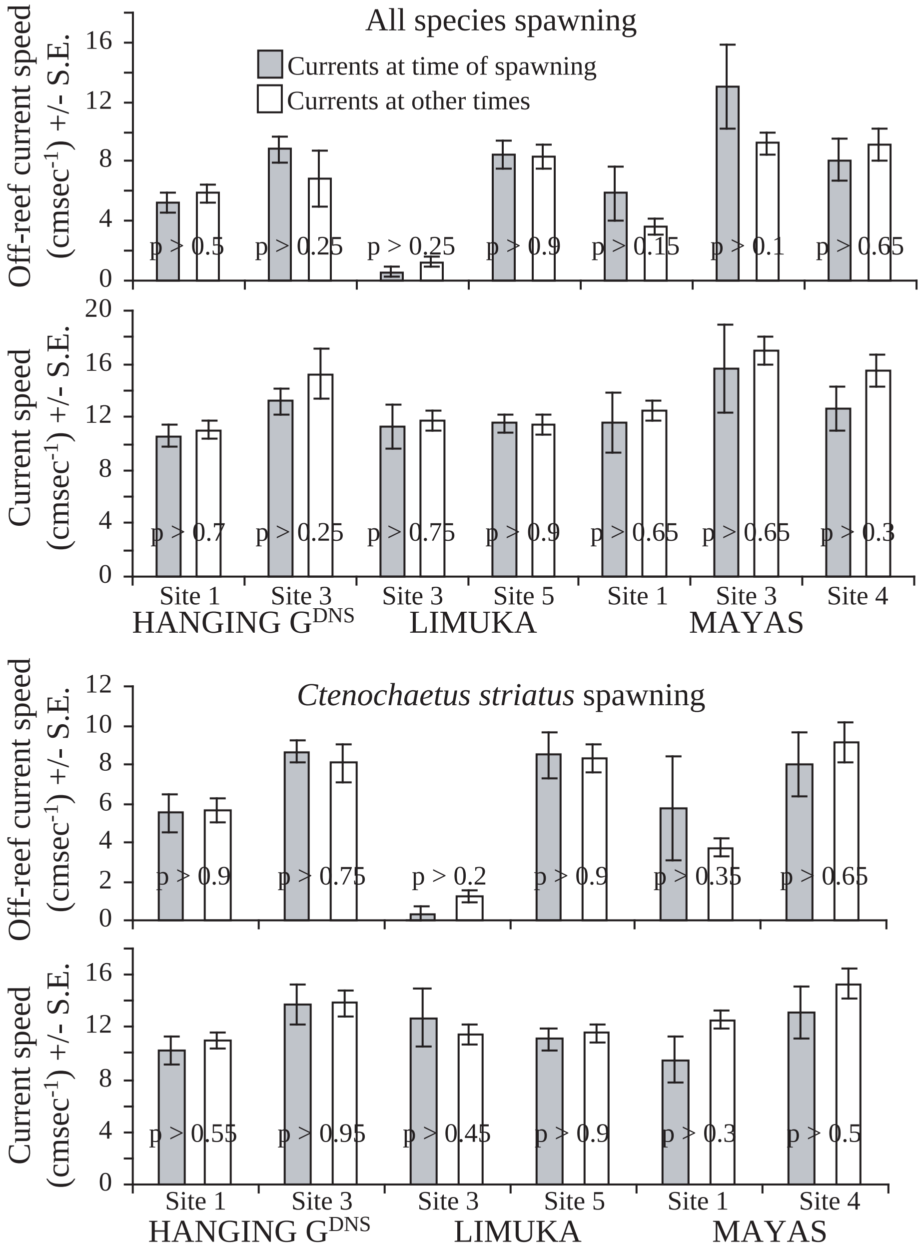
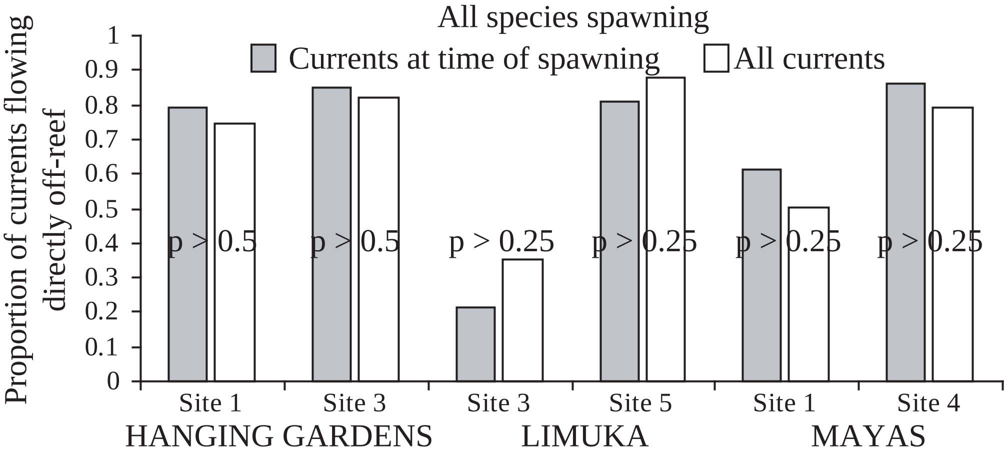


Figure 5.9. The currents at time of spawning by all species and *Ctenochaetus striatus* alone compared to other currents recorded at that site. Sites were omitted if insufficient data were available. The p-values are the results of t-tests between the mean currents recorded at the time of spawning and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



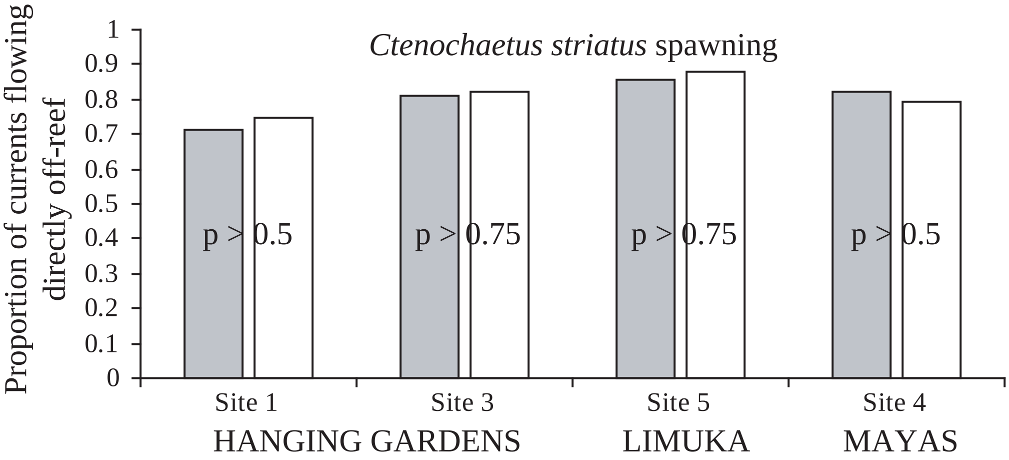


Figure 5.10. Proportion of currents flowing directly off-reef at time of spawning compared to all currents at site for all species and Ctenochaetus striatus. p- values are the results of Williams-corrected goodness-of-fit G-tests between the frequencies of spawning with off-reef and on-reef currents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

5.4 Discussion

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

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

5.4.1 Can currents enhance the survival of eggs?

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

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

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

5.4.2 Are coral reef fish able to predict currents?

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

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

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

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

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

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

5.4.5 Broader implications of study:

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

5.5 Conclusion

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

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

6.1 Introduction

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

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

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

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

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

6.1.1 Aims:

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

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

6.2 Methods:

6.2.1 Study area and study species

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

6.2.2 Tagging and determining positions of resighted individuals:

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

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

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

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

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

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

6.2.3 Data analyses:

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

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

6.3 Results:

6.3.1 Tagging overview:

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

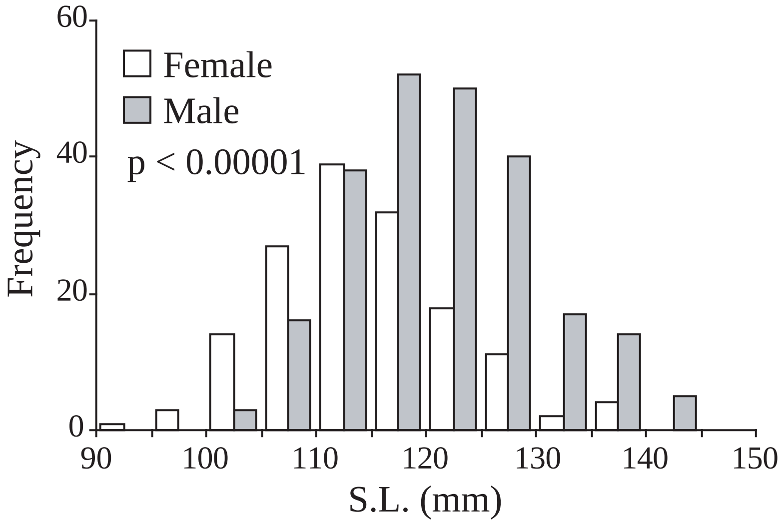

Figure 6.3. Size frequency distribution of tagged *Ctenochaetus striatus*. p-value is the result of a Kolmogorov-Smirnov 2-sample test between the S.L. of males and females.

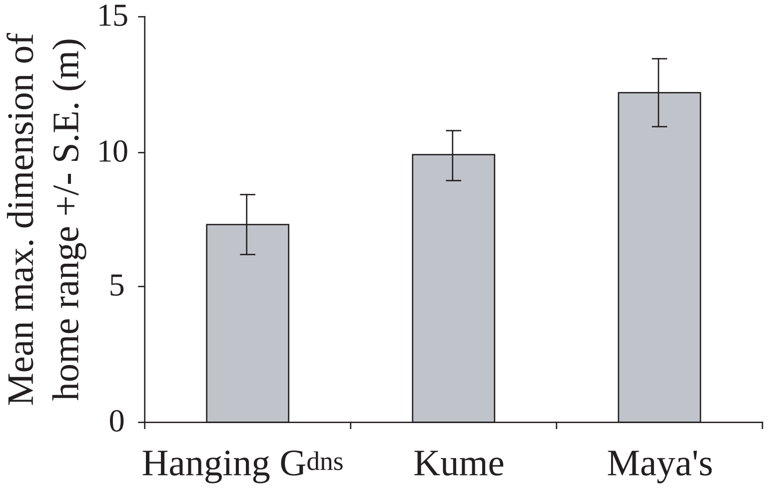

Figure 6.4. The mean maximum dimension of the home ranges of tagged individuals resighted on Hanging Gardens, Kume and Maya’s. Units are metres.

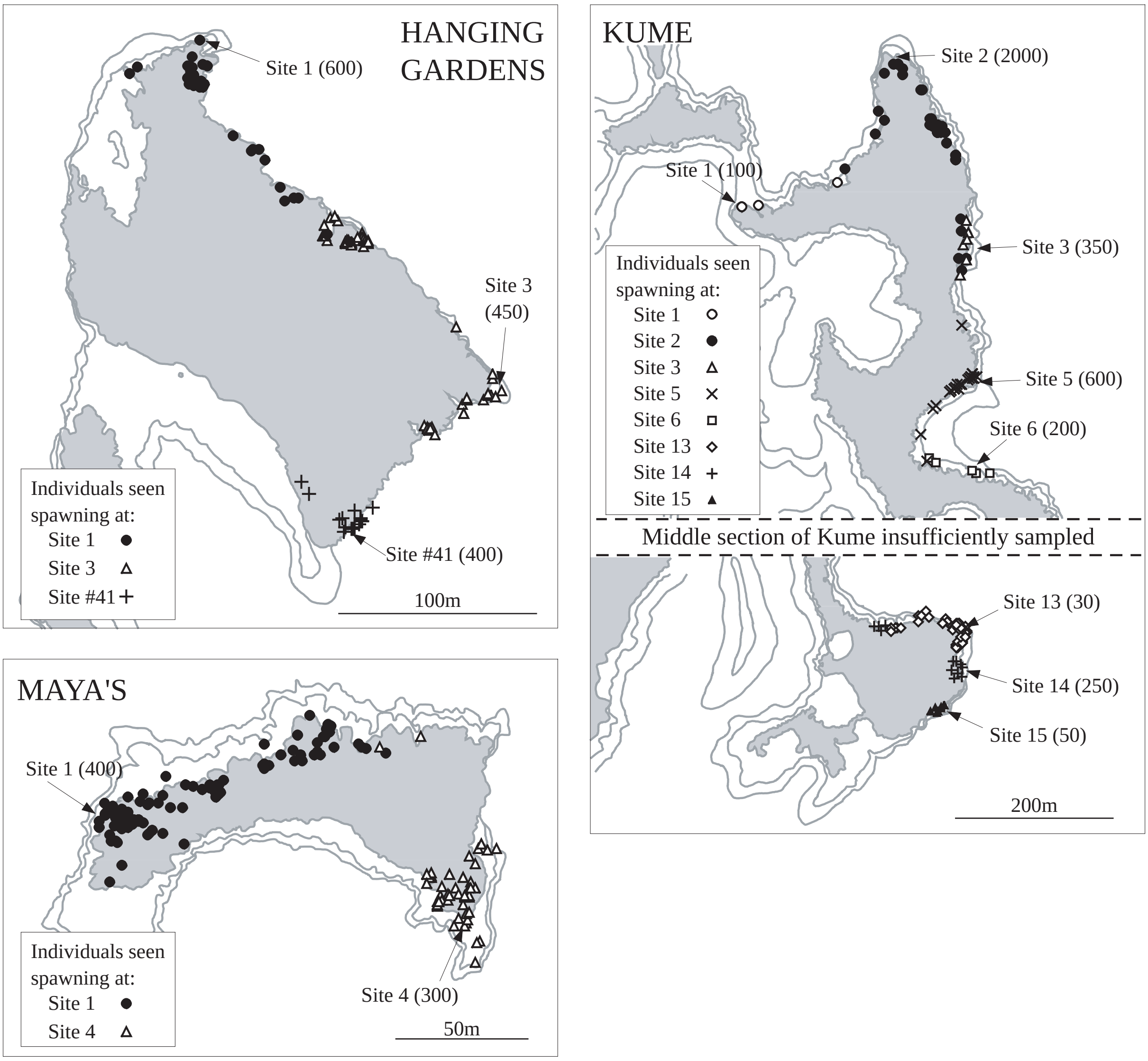

Figure 6.5. The locations of tagged *Ctenochaetus striatus* individuals seen spawning in aggregations on Hanging Gardens, Kume and Maya's reefs. Each symbol represents a single resighting of tagged individuals seen spawning in aggregations at the site. The positions plotted are resightings of individuals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

6.3.2 Home ranges and spawning migrations:

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

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

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

6.3.3 Spawning frequency:

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

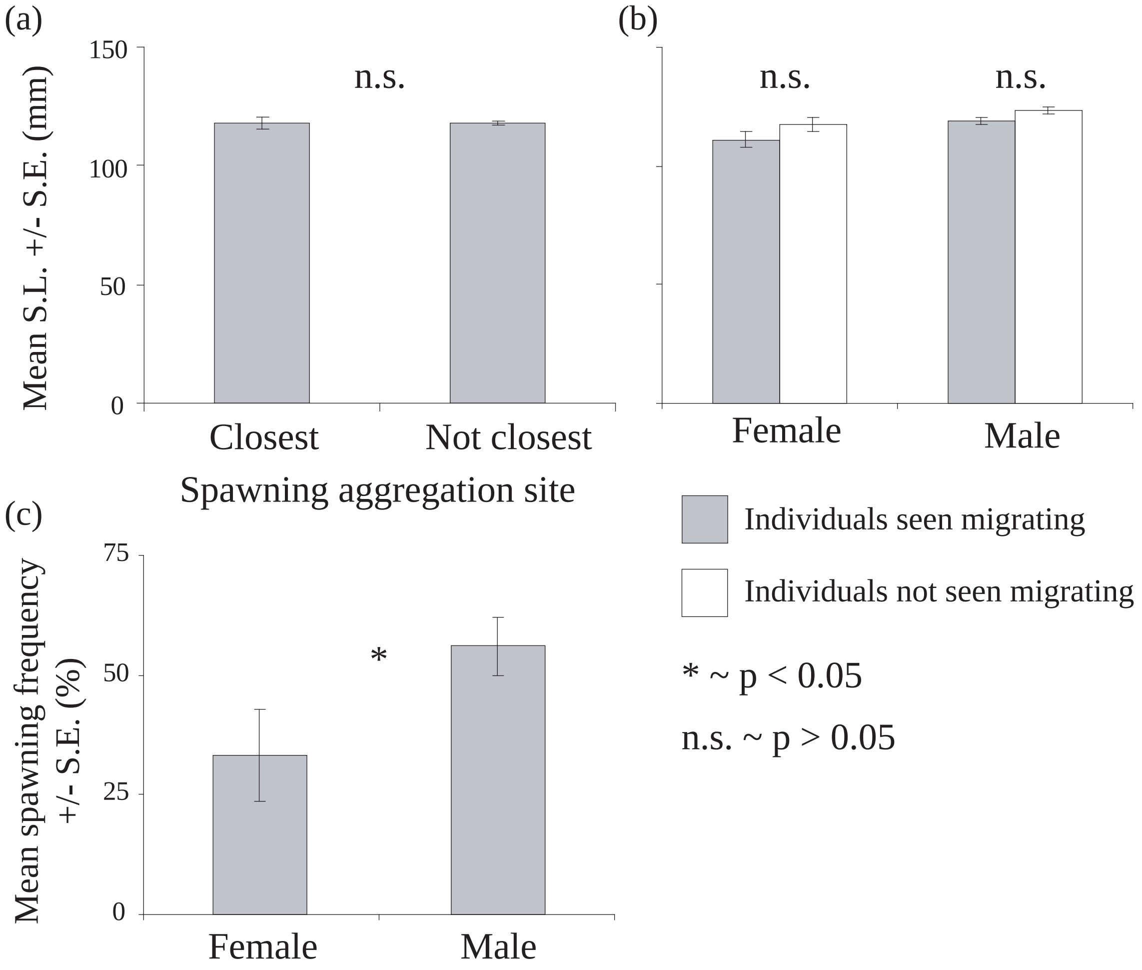

Figure 6.6. (a) The mean sizes (S.L.) of tagged individuals migrating to the spawning aggregation site closest to their mean home range and those migrating to sites further away. (b) The mean sizes of tagged males and females seen spawning and those resighted on more than 3 days but never seen spawning.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

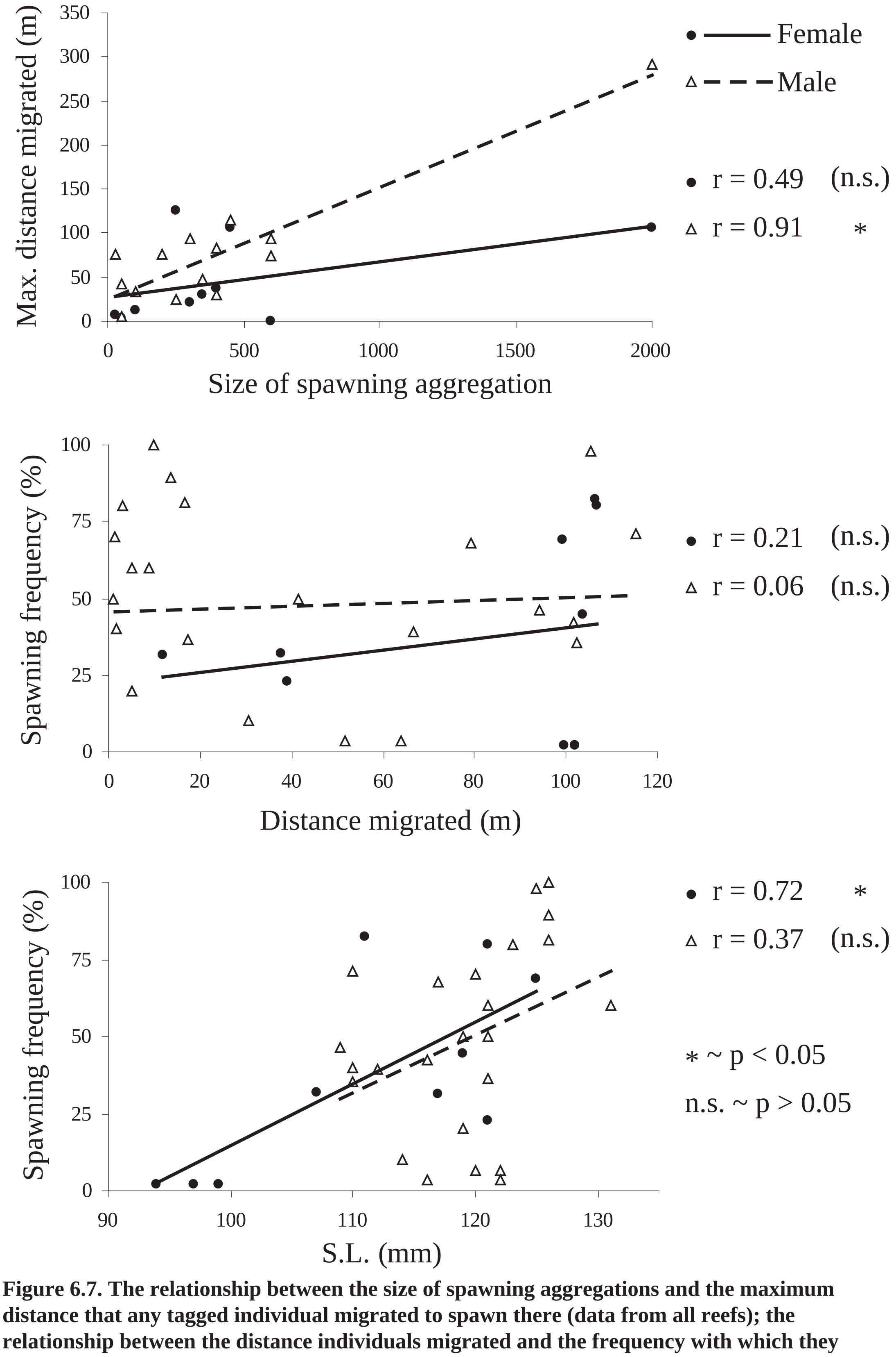

Figure 6.7. The relationship between the size of spawning aggregations and the maximum distance that any tagged individual migrated to spawn there (data from all reefs); the relationship between the distance individuals migrated and the frequency with which they migrated to spawn in aggregation (data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

6.4 Discussion

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

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

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

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

6.4.1 Non-reproductive individuals:

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

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

6.4.2 Cost-benefit optimisation vs. tradition:

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

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

6.4.3 Metapopulations

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

6.5 Conclusion:

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

CHAPTER 7: GENERAL DISCUSSION

7.1 Synthesis of results:

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

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

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

7.2 Adaptation in spawning aggregation formation:

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

7.2.1 Resource assessment

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

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

7.2.2 Behavioural "rules of thumb"

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

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

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

7.3 Future research

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

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

APPENDICES

Appendix 1: Publications arising from PhD project:

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

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