

Patterns of migration between feeding and spawning sites in a coral reef surgeonfish

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Abstract Many coral reef fishes exhibit regular localised migrations between feeding and spawning areas, but the factors affecting these migration patterns, such as the distance, frequency and spawning site fidelity are poorly understood. The aim of this study was to investigate the patterns of migration to spawning sites of the surgeonfish, *Ctenochaetus striatus* (Acanthuridae). We explored relationships amongst an individual's size and sex, the distance and frequency it migrated from its feeding area to spawning sites, fidelity to particular spawning sites and the number of individuals that aggregated to spawn. In order to achieve this, 406 *C. striatus* were captured and tagged on inshore reefs in Kimbe Bay (5°30'S 150°6'E), New Britain, Papua New Guinea. Tagged individuals were consistently observed within spatially discrete but overlapping feeding areas (maximum diameter averaging <13 m). The mean distance migrated was 58 m (ranging from 2 to 291 m). No tagged individuals were witnessed spawning at more than one site. Whilst most individuals ($n = 88$) migrated to the spawning site that was closest to their feeding areas, those that migrated to sites further away ($n = 9$) always spawned at sites where the number of conspecifics aggregating was larger. Neither the size nor the sex of individuals limited migration distance. However, males migrated significantly

more frequently than females (on average once every 2 days vs. once every 3 days), and migration frequency was positively correlated with size in females. Migration distance did not affect the frequency with which individuals spawned. Whether patterns of migration are determined by cost-benefit optimisation, tradition, or an alternative mechanism is unknown.

Keywords Spawning site · Coral reef fish · Migration · Tagging · Feeding area · Fish aggregation

Introduction

Coral reef fishes are typically site-attached, with reef fishes of all sizes being observed foraging within restricted home ranges (Sale 1998; Chapman and Kramer 2000; Meyer and Holland 2005; Jones 2007; Pina-Amargós and González-Sansón 2009; Muñoz et al. 2010). However, reef fishes can relocate to new home ranges (Chateau and Wantiez 2009; Meyer et al. 2010) and an association with particular foraging home ranges is often also associated with localised migrations between sites used for different vital functions (Zeller 1997; Chapman and Kramer 2000; Chateau and Wantiez 2007). Many fishes migrate from feeding sites to specific sleeping or resting shelter sites (Hobson 1973; Montgomery et al. 1989; Meyer et al. 2000; Sluka 2000; Eristhee and Oxenford 2001). The most impressive movements in adult reef fishes are undertaken by those that are known to migrate from feeding home ranges to form spawning aggregations (Domeier and Colin 1997; Claydon 2004; SCRFA Global Database 2011). Whilst the scale of these movements is not well documented, migrations to spawning sites have been recorded ranging from 100 s of m (e.g. *Acanthurus* spp., Robertson 1983; Colin and Clavijo

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1988) to 10 s of km (e.g. *Epinephelus* spp., Colin 1992; Bolden 2000; Nemeth et al. 2007). These shorter migrations often lead to aggregations that are formed daily over prolonged spawning seasons and are referred to as resident spawning aggregations as opposed to the transient aggregations that are formed following larger migrations and typically occur monthly over shorter seasons (Domeier and Colin 1997).

A considerable number of reef fishes have been documented as migrating to spawn in aggregations (Domeier and Colin 1997; Claydon 2004; SCRFA Global Database 2011). However, most research has concentrated on the aggregations themselves rather than migrations to them. Consequently, for many 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 sites (Myrberg et al. 1988; Shibuno et al. 1993; Warner 1995; Zeller 1998; Bolden 2000; Nemeth et al. 2007). Consequently, the factors affecting spawning migration patterns such as the distance migrated, frequency of migration and spawning site fidelity are poorly understood.

Migration incurs increasing costs with distance through: (1) greater energetic expense; (2) less time spent feeding in preferred areas; (3) greater exposure to predators because of the conspicuous nature of movement and of reduced familiarity with shelter outside of home ranges (Chapman and Kramer 2000); and, (4) fewer resources that can be dedicated to growth and/or gametogenesis. An individual's size and sex are predicted to influence the relative magnitude of these costs because the risk of predation and the proportional cost of movement decrease with increasing size (Roff 1991; Domeier and Colin 1997), because smaller individuals dedicate more energy to growth, and because spermatogenesis is less costly than oogenesis (Schärer and Robertson 1999). Therefore, individuals can be expected to minimise costs by migrating to the closest spawning site and having strong fidelity to this site. It can also be predicted that individuals migrating shorter distances will migrate more frequently than those migrating further away. In addition, larger individuals and males should be able to migrate further (as documented for larger individuals of a tropical wrasse, Shibuno et al. 1993) and more frequently than smaller individuals and females.

An individual's choice of spawning site may also be influenced by the number of conspecifics that aggregate to spawn at different sites. It has been proposed that spawning in aggregations is intrinsically beneficial (see review in Claydon 2004), increasing an individual's range of potential mates, and reducing predation on eggs and spawning adults by overwhelming predators with prey (Johannes 1978;

Thresher 1984). These hypothetical 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 sites where a greater number of conspecifics gather to spawn.

The aim of this study was to test predictions concerning the choice of spawning sites and the distance and frequency of spawning migrations in the lined bristletooth surgeonfish *Ctenochaetus striatus* (Acanthuridae) to sites within reefs in Kimbe Bay, Papua New Guinea. In this location, spawning occurs in the afternoon, year-round, and with no apparent lunar periodicity and multiple resident spawning aggregation sites are found within reefs (Claydon 2005). The frequency of spawning in time and space makes *C. striatus* a suitable model species to explore the relationships between an individual's size, sex, the distance it migrates to spawning sites, the frequency of migration and the size of the conspecific aggregations formed. The following specific hypotheses were tested: (1) most individuals should migrate to the nearest spawning site and exhibit strong fidelity to that site; (2) longer migrations should be associated with sites where larger aggregations of conspecifics form; (3) males and larger individuals can migrate further than females and smaller individuals; and, (4) individuals should migrate more frequently if they are males, if they are large and if they migrate shorter distances.

Methods

Study sites and species

This study was conducted on the inshore reefs accessible from the Mahonia na Dari Research and Conservation Centre, Kimbe Bay (5°30'S 150°6'E), New Britain, Papua New Guinea (Fig. 1). The study reefs of Hanging Gardens, Kume and Maya's are all steep-walled platform reefs separated from other reefs by depths of over 50 m and within 1 km of shore.

The focus species of this study was the lined bristletooth surgeonfish, *Ctenochaetus striatus*. *C. striatus* is an abundant reef fish found throughout the Indo-Pacific (Trip et al. 2008). It is a detritivore (Robertson and Gaines 1986; Choat et al. 2002) that forages during the day within home ranges at the outer edges of reefs (Montgomery et al. 1989). Feeding areas are <40 m² (Robertson and Gaines 1986; Krone et al. 2008) and shelter sites are found within 5 m (Montgomery et al. 1989). In Kimbe Bay, *C. striatus* has an estimated maximum age of 28 years (Trip et al. 2008). However, because growth asymptotes after 5 years (Trip et al. 2008), size is a poor indicator of age in all but the smallest individuals. Maturity is reached at 2 years

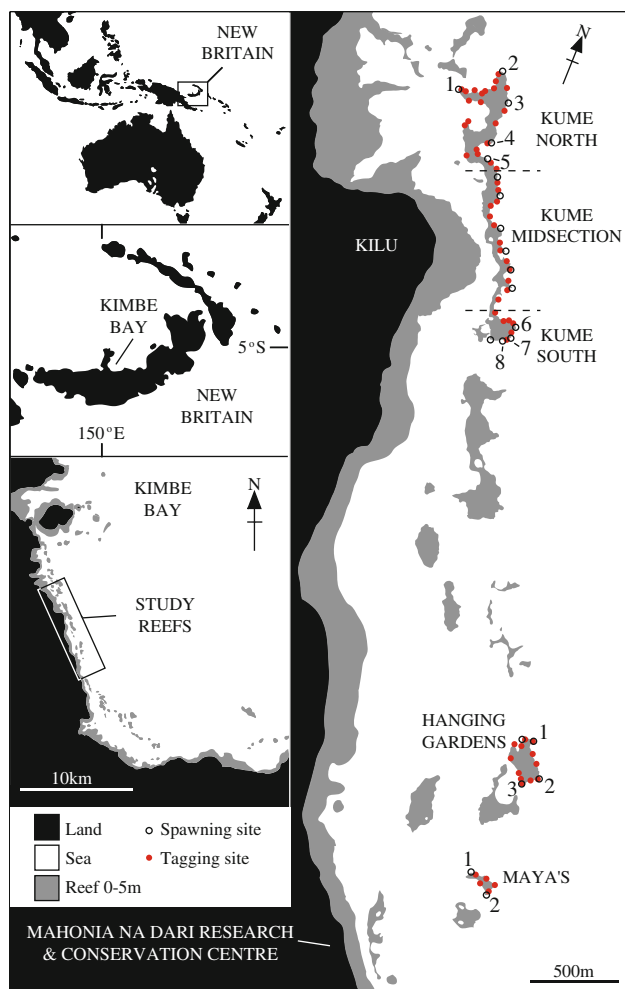


Fig. 1 Study reefs of Kume, Hanging Gardens and Maya's accessed from the Mahonia na Dari Research and Conservation Centre, Kimbe Bay, New Britain, Papua New Guinea. Circles indicate spawning sites of *C. striatus* identified by Claydon (2005). Numbers correspond to spawning sites sampled in the present study. Red dots indicate tagging sites

(Choat and Robertson 2002), which corresponds to between 90 and 140 mm fork length in Kimbe Bay (Trip et al. 2008). Adults of this species migrate to spawning sites in the afternoon to reproduce (Robertson 1983; Myrberg et al. 1988). In Kimbe Bay, spawning occurs within site-specific 2 h periods (ranging from 1330 to 1800 h), year-round, and with no apparent lunar periodicity and multiple spawning sites are found within reefs (Claydon 2005).

The location of spawning sites on the study reefs had been identified previously, with 4, 15 and 2 sites on Hanging Gardens, Kume and Maya's, respectively (Fig. 1; Claydon 2005). For the purposes of this study, a spawning site of *C. striatus* is defined as a site where a temporary aggregation of at least 20 conspecifics was observed gathering to spawn in a manner consistent with spawning



Fig. 2 *Ctenochaetus striatus*. Individual tagged with beads attached at three loci through the musculature along the dorsal fin margin

of this species described by Randall (1961). In over 1,000 h of observations undertaken over 3 years, *C. striatus* was never observed spawning outside of aggregations on any of the inshore reefs of Kimbe Bay and currents did not appear to influence spawning (Claydon 2005).

Tagging

In August 2003, 406 *C. striatus* individuals were tagged on the study reefs (59 on Hanging Gardens, 43 on Maya's and 94, 58 and 152 on the north, south and mid sections of Kume, respectively) so that their patterns of movement from feeding areas to spawning sites could be observed. Fish were caught in fence nets, sexed by stripping gametes, measured (standard length, SL) and tagged with brightly coloured beads (approximately 2 mm in diameter) on nylon monofilament line (0.2 mm). Similar tagging techniques have been used in a number of studies (Greenberg and Holtzman 1987; Langley and Driscoll 1989; Chapman and Bevan 1990; Verweij and Nagelkerken 2007; Verweij et al. 2007). Each tagged individual was identifiable by a unique tag code that combined different coloured beads at three loci on the dorsal region (Fig. 2). Where possible, fish were caught from locations with a representative range of distances from spawning 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. Fish were caught and tagged at 57 locations around the 3 study reefs (Fig. 1). Tagged individuals were released at their sites of capture.

Sex determination

The 406 *C. striatus* tagged ranged in size from 94 to 150 mm SL. Individuals were sexed by stripping gametes by hand, applying pressure to the abdomen as per Casselman (1974), a technique used to sex another species of surgeonfish (Kiflawi and Mazeroll 2006). Stripping

released gametes from 62% of fish caught and 98% of these released sperm. Whilst only four 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 tagged. Spawning was also observed by 29 individuals that did not release gametes during stripping. The females that released eggs during stripping were caught exclusively whilst aggregating to spawn or whilst migrating to spawning sites. 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. Hereafter, tagged *C. striatus* confirmed as females (by releasing eggs) and those presumed to be females are collectively referred to as females. Stripping could not be relied upon to sex individuals that bore deep marks on the abdomen indicating heavy entanglement in the net. These individuals could have released all available gametes as a result of excessive pressure from the net and thus released no gametes when stripped. Sex was left undetermined for such individuals.

Sampling strategy

Surveys to locate tagged individuals were made on 49 days on Hanging Gardens, 22 days on Kume, and 11 days on Maya's, between September 2003 and February 2004. Greatest effort was concentrated on Hanging Gardens in order to establish frequency of migration to spawning sites. The relatively low effort on Maya's reflected the small reef area and did not adversely affect the proportion of tagged individuals observed at liberty nor the proportion observed at spawning sites. Effort to locate tagged fish was focussed on two time periods: (1) times in the mid to late morning (900–1145 h) when individuals were expected to be found in feeding areas and not spawning or migrating to spawning sites, and (2) times of spawning (1330–1800 h). This diel cycle was verified in Kimbe Bay prior to the study (Claydon 2005). Because *C. striatus* has been documented spawning year-round and at all states of the lunar month in Kimbe Bay (Claydon 2005), days upon which observations were made were not predicted to influence results and thus chosen haphazardly.

At non-spawning times, all areas of Hanging Gardens and Maya's were searched for tagged fish. However, only the north and south ends of Kume were searched. The locations of all tagged individuals observed were recorded along with their tag codes. Although multiple sightings of tagged individuals were made within their feeding areas, home ranges per se were not established. Following the

activities of tagged individuals within feeding areas over prolonged periods of time was prohibitively time-consuming. It was more productive to swim around the reef recording the positions of all tagged fish, instead. By repeating this process over a number of days, it was possible to establish a record of positions for each individual and calculate mean locations within their feeding areas.

During spawning times, observations were made exclusively at spawning sites 1, 2, 3, 4 and 5 at the north end of Kume, and sites 6, 7 and 8 at the south end of Kume, sites 1, 2 and 3 on Hanging Gardens and both spawning sites (1 and 2) on Maya's. The location and tag codes were recorded of all tagged individuals observed within these sites. These data were used to assess spawning site fidelity, and migration distance from feeding areas. Migration distance was calculated as the straight line distance from an individual's mean location within its feeding area to its mean location at the spawning site within which it was observed. The number of conspecifics aggregated to spawn was also recorded.

Although 152 individuals were caught and tagged from the midsection of Kume, further observations were not made within this 1 km stretch of reef. However, these individuals were useful in determining whether migrations were occurring beyond the scale of the areas surveyed. If individuals tagged from the midsection of Kume were observed spawning at sites surveyed at the north or south of the reef, then these data would assist in establishing the upper limits for the migration of *C. striatus* on the study reefs. Migration distances for these individuals could be estimated from the coordinates of their tagging sites and where they were observed at the spawning sites.

x - y Coordinates of tagged fish

The location of tagged individuals was determined with reference to highly visible numbered markers deployed at intervals of 20 m 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 (distance east and 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 possible to determine the x - y coordinates of any tagged individuals observed by measuring their distances and bearings from the closest marker. This technique was favoured over a GPS-based system because the location of individuals could be consistently calculated to a resolution of <1 m. The arithmetic means of x and y values were used to estimate x - y coordinates representing an individual's mean location within its feeding area and within a spawning site.

Statistical analyses

A Kolmogorov–Smirnov two-sample test was used to investigate whether the size frequency distribution of males differed significantly to that of females. A Fisher’s Exact test assessed whether males and females differed in the proportion of individuals that migrated to spawning sites closest to their feeding areas versus those that migrated to sites further away. A one-tailed Welch’s two-sample *t* test was used to determine whether individuals migrating the furthest distances (>75% of maximum migration distance recorded) were larger than those migrating shorter distances. Student’s *t* tests assessed differences between: (1) the size of individuals migrating to the closest spawning 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 (1) migration distance between males and females, and (2) the size of tagged individuals seen at spawning sites with the size of tagged individuals observed on more than 3 days but never seen at spawning sites. For the latter, separate Mann–Whitney *U* tests were performed for males and females.

A Spearman rank correlation was performed to assess the relationship between the distance individuals migrated to spawning sites and the size of the conspecific aggregations formed. Pearson product-moment correlation coefficients were calculated to investigate associations between: (1) migration distance and size of individuals, (2) individuals’ migration frequencies and their migration distances, and (3) individuals’ migration frequencies and their body sizes. Correlation analyses did not include individuals that were not observed migrating. Males and females were treated separately in all correlations. All statistical procedures followed Sokal and Rohlf (1995) and all statistical tests were performed using R (R Development Core Team 2010).

Results

Of the 406 individuals tagged, 235 (58%) were male, 151 (37%) were female and stripping could not be relied upon to sex 20 (5%) individuals. Despite considerable overlap in sizes, males (mean = 122.0 mm SL, SD = 8.6) were significantly bigger than females (mean = 115.2 mm TL, SD = 8.7; Kolmogorov–Smirnov two-sample test: $D_{(235,151)} = 0.336$, $P < 0.05$; Fig. 3). On Hanging Gardens, 81% of tagged individuals were observed at liberty, with 72% on Maya’s, 69% on the north section of Kume and 81% from the south section of the reef. During non-spawning times, tagged individuals were consistently observed within overlapping but spatially discrete feeding

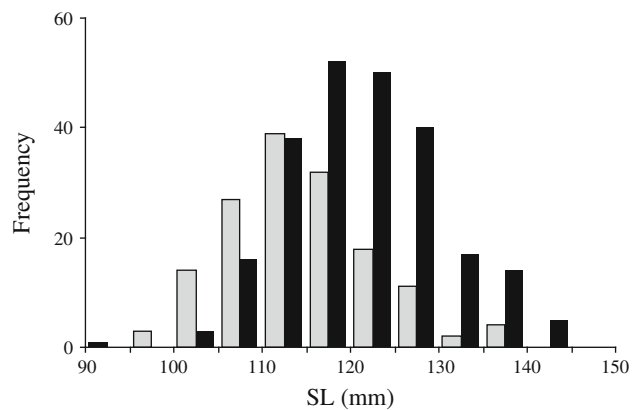


Fig. 3 Size frequency distribution of tagged individuals. Grey bars are female; black bars are male. Males were significantly larger than females (see text for details)

Table 1 Number of tagged individuals that migrated to spawning sites

| Reef | Hanging Gardens | | | Kume | | | | | | | | Maya’s | |
|---------------|-----------------|----|----|------|----|---|---|---|----|---|---|--------|---|
| | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 1 | 2 |
| Spawning site | | | | | | | | | | | | | |
| <i>n</i> | 7 | 11 | 14 | 3 | 12 | 4 | 4 | 2 | 10 | 3 | 4 | 15 | 8 |

areas (mean maximum diameter of <13 m). Of these, 97 individuals were observed at spawning sites (Table 1) on a total of 549 occasions and migrated a mean distance of 58 m, ranging from those with feeding areas overlapping the site in which they spawned to those migrating up to 291 m (Fig. 4). Migration was not a conspicuous activity. Individuals migrated in small (<20 individuals), loose groups. Intermittent, feeding was observed both during migrations and whilst at spawning sites.

Spawning site choice and fidelity

The distance an individual migrated was determined largely by the location of its feeding site and the location of the nearest spawning site (Fig. 4): whilst feeding sites overlapped between individuals migrating to different spawning sites, over 90% of individuals migrated to the spawning sites closest to their mean coordinates within feeding areas. No individuals tagged in the midsection of Kume were observed at spawning sites monitored to the north or south of the reef. An individual’s spawning site fidelity was absolute. None of the 65 tagged individuals seen spawning on multiple occasions spawned at more than one site over the study period.

Fig. 4 Tagged individuals in their feeding areas on Hanging Gardens, Kume and Maya's reefs. Each dot represents a single sighting of a tagged individual within its feeding area. Only tagged individuals that were also observed at spawning sites are plotted. Colours indicate which spawning site these individuals migrate to and correspond to the coloured dot in parentheses by the spawning site label. The numbers in parentheses indicate the maximum number of individuals estimated aggregating at the spawning site

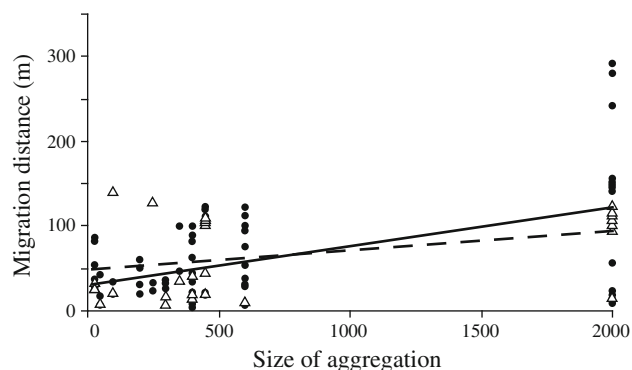
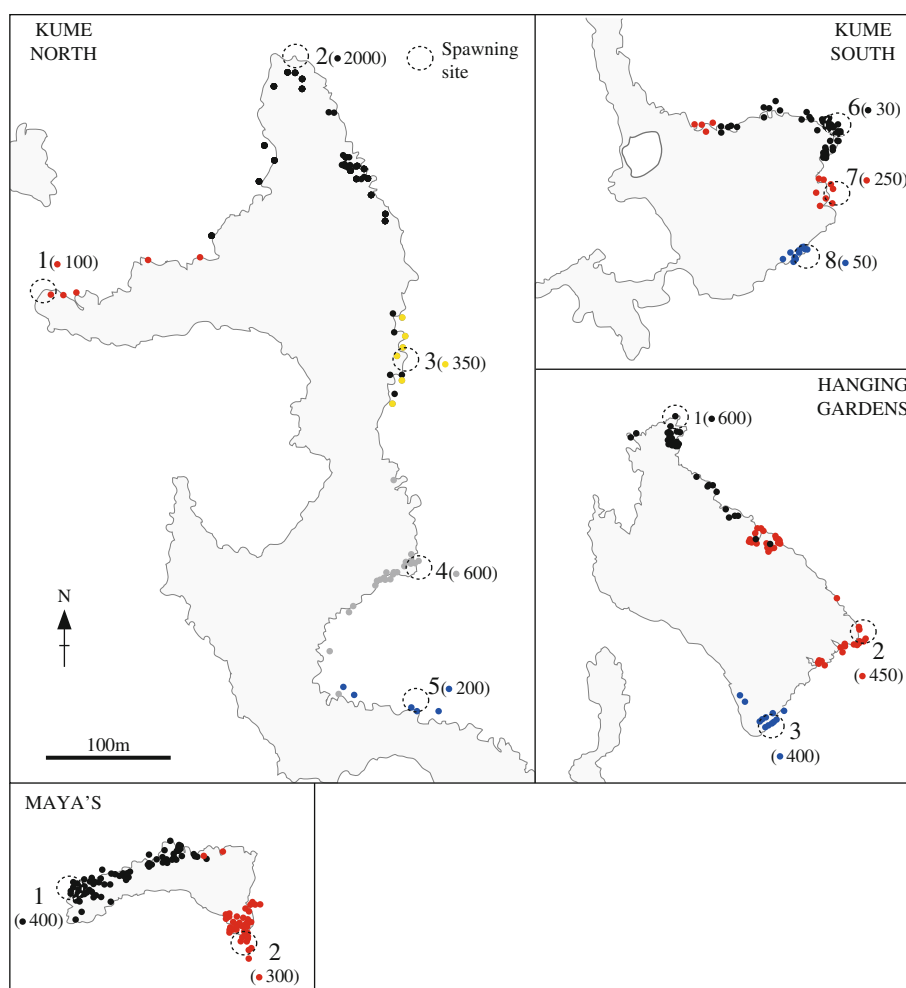


Fig. 5 The relationship between migration distance and number of conspecifics aggregated to spawn. Triangles and dashed line correspond to females; black dots and line correspond to males. Significant correlation for males but not females (see text for details)

Migration distance and number of conspecifics aggregated

The distance that tagged individuals migrated to spawning sites was significantly correlated to the maximum size (number of individuals) of the aggregation for males

($r_s = 0.37$, $P < 0.05$) but not for females ($r_s = 0.34$, $P > 0.05$; Fig. 5). However, for males, this result was heavily dependent on data from the site with the largest aggregation (Kume Site 2, 2,000 individuals); exclusion of this site resulted in a weaker and non-significant correlation ($r_s = 0.28$, $P > 0.05$).

The nine individuals that did not migrate to the spawning site closest to their home ranges all migrated to sites where larger numbers of conspecifics aggregated to spawn. Eight males migrated to the site where the largest aggregation on Kume was formed (Site 2, 2,000 individuals), a journey of up to 203 m further than migrating to the closer aggregation site (Site 3, 350 individuals). Similarly, a female was observed migrating an additional 34 m to the site with the largest aggregation on the southern section of Kume (Site 7, 250 individuals), rather than to a closer site (Site 6, 30 individuals).

Migration distance, sex and size

Of the 97 individuals documented migrating, only 2 males and 1 female migrated >150 m, with migrations of 291,

277 and 241 m, respectively. The median distance migrated was substantially further for females (80 m, ranging from 2 to 241 m) than males (23 m, ranging from 3 to 291 m), but this difference was not significant (Mann–Whitney U test: $U_{(62,30)} = 1,143.5$, $P > 0.05$). The proportion of individuals that migrated to spawning sites further away than their closest sites did not differ significantly between males and females (Fisher's Exact test: $P > 0.05$).

There was no significant correlation between the size (SL) of individuals and the distance they migrated in either males ($r = -0.21$, $P > 0.05$) or females ($r = 0.20$, $P > 0.05$). Individuals migrating to spawning sites closest to their feeding areas did not differ significantly in size from those migrating further (Student's t test: t value = 0.0015, $df = 111$, $P > 0.05$). In addition, the mean size of the three individuals that migrated >220 m (i.e. $>75\%$ of the maximum migration distance recorded) was not significantly larger than the mean size of all other individuals (one-tailed Welch's two-sample t test: $t = 0.511$, $df = 2$, P value > 0.05).

Migration frequency, sex and size

On Hanging Gardens, males migrated significantly more frequently than females (Student's t test: t value = 2.09, $df = 29$, $P < 0.05$) and, on average, more than once every 2 days for males (migrating on a mean of 56% of days, $SD = 29.2$) as opposed to once every 3 days for females ($M = 33\%$ of days, $SD = 29.3$). 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, $r = 0.21$, $P > 0.05$). 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 Fig. 6). However, for females this correlation was not significant if individuals less <100 mm SL were excluded. On Hanging Gardens, 11 tagged individuals were observed on numerous occasions but never seen at spawning sites. For both males and females, there was no significant difference between the size 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, $U_{(10,6)} = 24$, $P > 0.05$).

Discussion

This study confirmed that a number of factors influence migration distance, frequency of spawning and spawning site choice in the focal surgeonfish species. An individual's sex, its size, the distance of its feeding area from spawning sites and the number of conspecifics aggregating all appeared to potentially affect the patterns of migration of

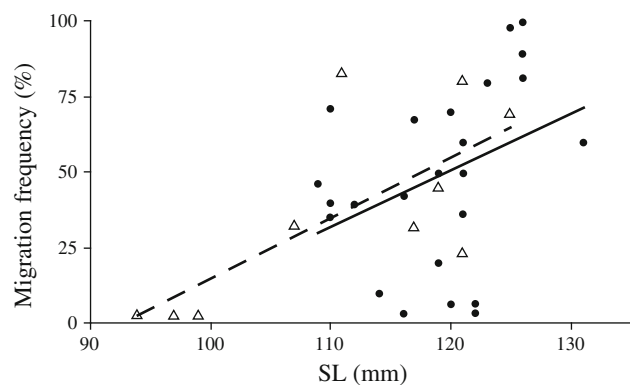


Fig. 6 The relationship between migration frequency and the size of individuals. Triangles and dashed line correspond to females; black dots and line correspond to males. Only individuals observed migrating are included. Significant correlation for females but not males (see text for details)

C. striatus to varying degrees, but not necessarily as predicted.

Spawning site choice and fidelity

Most individuals migrated the shortest distance possible by travelling to the spawning sites closest to their feeding areas. This pattern was also seen for coral trout, *Plectropomus leopardus* (Zeller 1998) and is consistent with minimising the costs of migration. The fidelity displayed by individuals in the present study to a single spawning site has also been documented for other species of surgeonfish (Myrberg et al. 1988) and larger species such as *P. leopardus* (Zeller 1998). However, it is presently not known whether such spawning site fidelity is widespread amongst species forming spawning aggregations and mechanisms other than cost limitation can also explain this behaviour. Individuals may migrate to the first spawning site of which they become aware. There is a higher probability that these sites will be the ones closest to their feeding areas rather than sites further away, and individuals will continue to migrate to the same site because the risks (reduced spawning success and increased predation) of migrating to an alternative site are unknown.

Migration distance and number of conspecifics aggregated

The nine individuals that migrated to spawning sites other than those closest to their feeding areas all migrated to sites where larger conspecific aggregations formed. This supports the notion that the benefits of spawning in aggregations increase with increasing numbers of conspecifics aggregated and that individuals will be prepared to migrate

further to profit from this. Additional support for this prediction came from a significant positive correlation between the distances that males were recorded migrating and the maximum size of the aggregation at that site. However, this relationship can also be explained more simply: on reefs with relatively uniform population densities, larger spawning aggregations will necessarily be comprised of individuals from a larger catchment area and thus mean migration distances will be longer.

Migration distance, sex and size

Sex and size of *C. striatus* did not appear to influence the distance that they were able to migrate. Although the longest migration was undertaken by a male, the median migration distance was higher in females, albeit not significantly and there was no relationship with size. Additionally, the individuals that migrated to sites other than those closest to their feeding areas were no more likely to be males than females and were no larger than those that migrated to the closest spawning sites.

Acanthurus nigrofuscus, a surgeonfish of similar size to *C. striatus*, has been documented migrating up to 1.5 km in the Red Sea (Mazeroll and Montgomery 1998) and although *C. striatus* might be able to migrate as far, such migrations are unnecessary on the study reefs where a spawning site is within 200 m of any location. Thus, the distances migrated (<300 m) may have been too short to incur costs that would preclude females or smaller individuals. In fact, the spatial distribution of spawning sites may be determined partly by having sites spaced close enough to one another so that all adults are able to migrate to a spawning site. However, size was significantly correlated to the distance of migrations to spawning sites in *Halichoeres marginatus* (Labridae), another reef fish of similar size to *C. striatus* and migrating over comparable distances (Shibuno et al. 1993).

Migration frequency, sex and size

Sex and size did influence migration frequency in *C. striatus*. Females migrated less frequently than males, which has also been observed in *Thalassoma bifasciatum* and can be explained by the greater cost of producing eggs compared to sperm (Schärer and Robertson 1999). In addition, migration frequency was correlated with body size in female *C. striatus* which may correspond to smaller females dedicating proportionally more energy to growth and less to oogenesis than larger ones. Similar patterns have been documented in iteroparous fishes from reefs and other environments, where larger females spawn more frequently or over a longer spawning season than smaller ones (DeMartini and Fountain 1981; Parrish et al. 1986;

Marteinsdottir and Thorarinsson 1998; Millan 1999; McBride and Thurman 2003; Claramunt et al. 2007; Nye and Targett 2008). The negligible costs of spermatogenesis may explain why no relationship was observed between body size and migration frequency in male *C. striatus*.

In Kimbe Bay, growth of *C. striatus* asymptotes by 5 years at a relatively wide range of sizes and individuals may live for up to 28 years (Trip et al. 2008). Therefore, migration frequency may be more closely associated with growth rate rather than size. This may explain why the difference in migration frequency was particularly pronounced between small adults (i.e. <100 mm SL) that may still be growing and larger individuals that may have attained or may be close to their asymptotic sizes (Trip et al. 2008).

The distance that *C. striatus* migrated to spawning sites did not influence how frequently they migrated. In *Thalassoma bifasciatum*, the frequency of migrations to spawning sites was also observed to be independent of migration distance (Warner 1995). However, for *T. bifasciatum* the individuals that migrated longer distances fed at higher rates within their home ranges than those that migrated shorter distances to spawn. This suggests that more energy was required to maintain migration frequency with increasing migration distance in *T. bifasciatum*. Unlike *C. striatus*, *T. bifasciatum* was not observed feeding during migrations or whilst at spawning sites, and individuals migrated considerably longer distances than those in the present study (>1,500 m vs. <300 m). Thus, even the longest distances over which *C. striatus* migrated may be too short to influence the frequency of migration to spawning sites, especially whilst feeding is maintained, albeit at a possibly reduced rate. Alternatively, these costs may have been expressed in characteristics not investigated such as reduced batch fecundity and/or growth rates.

Cost-benefit optimisation and tradition

The benefit of spawning at a particular site may not be derived exclusively from the number of conspecifics aggregating. Other potential site-specific benefits include reduced predation on spawning adults and their offspring (Randall and Randall 1963; Johannes 1978; Lobel 1978; Shapiro et al. 1988) and increased survival and recruitment of larvae (Lobel 1978; Barlow 1981; Lobel and Robinson 1988). Whilst these additional benefits may obscure patterns predicted by aggregation size alone, if site choice is determined purely by cost-benefit optimisation, then catchment areas to spawning sites would still be clearly delineated: all individuals with home ranges within a certain radius of a spawning site would migrate to the same location. The length of this radius and the subsequent boundary between the catchment areas of two adjacent

spawning sites would be determined by a trade-off between the costs of migrating to the sites and the site-specific benefits of spawning there. However, where data were available, the degree of overlap between catchment areas of adjacent spawning sites for *C. striatus* suggests that spawning site choice does not reflect such a trade-off.

Warner (1988, 1990) concluded that the location of spawning sites in *T. 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 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 or large groups, as documented for some surgeonfishes (Robertson 1983; Myrberg et al. 1988; Mazeroll and Montgomery 1995, 1998; Kiflawi and Mazeroll 2006) and a wrasse (Warner 1995), all recruits within an area are likely to learn the location of the same spawning site. There is one unambiguous set of social cues that lead to one site with little opportunity for an individual to follow conspecifics migrating to an alternative location. However, on the study reefs, such social cues may be less conspicuous for *C. striatus* which migrated in small, discrete groups. For this species, the site to which an individual migrates may be determined by the subset of neighbours that it follows initially. In such a system, tradition has the potential to maintain differential spawning site use by individuals with overlapping home ranges because they inherit their choices of spawning site as cultural traits from distinct subsets of neighbours.

In conclusion, this study suggests that the spawning site to which a *C. striatus* individual migrates is determined most by the location of an individual's feeding area. Whether site choice is a result of cost-benefit optimisation or another mechanism such as tradition remains unclear. An individual's sex and, to a lesser extent, its size had a greater influence over migration frequency than the distance an individual travelled. However, spawning migrations were likely to have been too short to incur costs substantial enough to affect the patterns of migration in *C. striatus*. Migrating to spawn in aggregations appears to be a crucially important process for many coral reef fishes and this study represents some of the first steps in understanding the patterns of this behaviour.

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