Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns

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Spawning sites used by one or more species were located by intensively searching nearshore coral reefs of Kimbe Bay (New Britain, Papua New Guinea). Once identified, the spawning sites were surveyed repeatedly within fixed 5 m radius circular areas, for > 2000 h of observations ranging from before dawn to after dusk spanning 190 days between July 2001 and May 2004. A total of 38 spawning sites were identified on the seven study reefs distributed at an average of one site every 60 m of reef edge. Pelagic spawning was observed in 41 fish species from six families. On three intensively studied reefs, all 17 spawning sites identified were used by at least three species, with a maximum of 30 different species observed spawning at a single site. Spawning was observed during every month of the study, on all days of the lunar month, at all states of the tide and at most hours of the day studied. Nevertheless, the majority of species were observed spawning on proportionately more days from December to April, on more days around the new moon and in association with higher tides. The strongest temporal association, however, was with species-specific diel spawning times spanning < 3 h for most species. While dawn spawning, afternoon spawning and dusk spawning species were differentiated, the time of spawning for the striated surgeonfish *Ctenochaetus striatus* also differed significantly among sites. The large number of species spawning at the same restricted locations during predictable times suggests that these sites are extremely important on this low-latitude coral reef.

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Key words: pelagic spawning; periodicity; resident; spatial distribution; spawning aggregation; transient.

INTRODUCTION

The ability of fishes to synchronize migration to specific sites for reproduction is well documented for numerous marine, freshwater and estuarine species. It is a defining characteristic of anadromous and catadromous fishes that migrate between freshwater and marine environments for breeding (Gross *et al.*, 1988; Dodson, 1997). Among coral reef fishes, migration to spawning sites has been recognized in over 100 species from at least 18 families. Most migrating species are those that spawn pelagic eggs and they are commonly, but not exclusively, the larger-bodied species (Domeier &

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Colin, 1997; Claydon, 2004; SCRFA, 2012). Migration distances vary from just a few metres [*e.g.* the blue green damselfish *Chromis viridis* (Cuvier 1830) (Lewis, 1997)] to over 100 km [*e.g.* Nassau grouper *Epinephelus striatus* (Bloch 1792) (Carter *et al.*, 1994; Bolden, 2000)]. The timing of migrations may be daily [*e.g.* bluehead wrasse *Thalassoma bifasciatum* (Bloch 1791) (Warner, 1995)], semi-lunar [*e.g.* yellowmargin triggerfish *Pseudobalistes flavimarginatus* (Rüppell 1829) (Gladstone, 1994)], lunar [*e.g.* brown-marbled grouper *Epinephelus fuscoguttatus* (Forsskål 1775) (Robinson *et al.*, 2008)], year-round [*e.g.* convict surgeonfish *Acanthurus triostegus* (L. 1758) (Craig, 1998)] or within restricted seasons (*e.g. E. striatus*; Colin, 1992). Despite this wide variety in behaviour, there is increasing evidence that different species of pelagic spawners can migrate to the same spawning sites (Lobel & Neudecker, 1985; Moyer, 1989; Colin & Bell, 1991; Craig, 1998; Johannes *et al.*, 1999; Sancho *et al.*, 2000; Heyman *et al.*, 2001; Whaylen *et al.*, 2004; Colin, 2010). The spatial and temporal dynamics of multispecies spawning sites and the reasons that they form, however, are poorly understood.

Having migrated to a spawning site, the number of conspecifics gathered can range from a single pair [*e.g.* melon butterflyfish *Chaetodon trifasciatus* (Park 1797) (Yabuta, 1997)] to over 100 000 [*e.g. E. striatus* (Smith, 1972)]. When individuals are congregated at spawning sites in groups that are more dense and larger than at non-spawning times, they are said to form spawning aggregations (Domeier & Colin, 1997; Claydon, 2004; Domeier, 2012). When migrations do not culminate in such groups, the individuals concerned are referred to as simple migratory spawners (Domeier & Colin, 1997). Practical thresholds have been proposed and widely accepted (Domeier & Colin, 1997; Domeier, 2012) but because behaviours are related and overlapping, distinguishing spawning aggregations from groups of simple migratory spawners can be ambiguous (see Fig. 1). In addition, while research has focused mainly on spawning aggregations, comparatively little is known about simple migratory spawning reef fishes.

For species forming spawning aggregations, two different types have been distinguished, depending on the origin of the individuals (Domeier & Colin 1997; Nemeth,
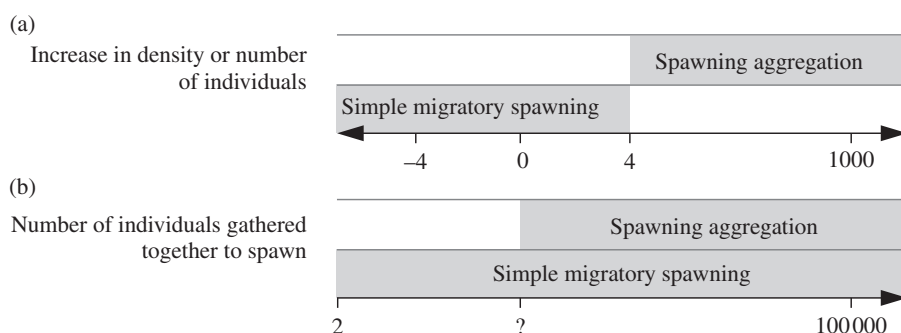

FIG. 1. Characteristics of spawning aggregations *v.* simple migratory spawning along gradients of (a) increase in density or number of individuals compared to non-spawning times (note that this increase can be negative) and (b) the number of individuals gathered together to spawn, the lower limit of which remains undefined or ambiguous for spawning aggregations. Note that scales are not linear. ?, undefined value. Definitions follow Domeier & Colin (1997) and Domeier (2012).
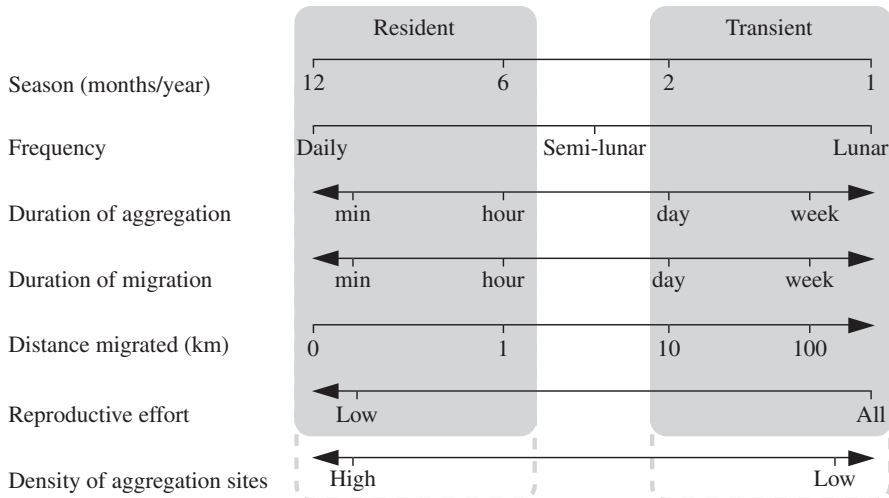
FIG. 2. Characteristics of resident *v.* transient spawning aggregations. Season displays the number of months in a year in which spawning aggregations are formed; frequency displays the periodicity of spawning aggregation formation within a lunar month (daily, semi-lunar and lunar); duration of aggregation shows how long an aggregation remains together once it is formed; duration of migration is the length of time it takes an individual to migrate to a spawning aggregation; distance migrated is the distance an individual migrates beyond its home range; reproductive effort is the proportion of an individual's annual reproductive effort that is expended during one aggregation. Note that scales are not linear. Definitions follow Domeier & Colin (1997) and Domeier (2012).

2009; Domeier, 2012): resident spawning aggregations draw individuals to a site within or nearby their adult home range. They usually (1) occur at a specific time of day over numerous days, (2) last only a few hours or less, (3) occur daily over an often lengthy reproductive period of the year and (4) can occur year-round. A single day of spawning for an individual participating in a resident spawning aggregation represents a small fraction of that individual's annual reproductive effort. By contrast, transient spawning aggregations draw individuals to a site well outside their typical adult home range. Transient spawning aggregations often (1) occur during a very specific portion of one or two months of the year, (2) persist for a period of days or at most a few weeks and (3) do not occur year-round. A single transient spawning aggregation may represent the total annual reproductive effort for participating individuals.

Although the terms resident and transient spawning aggregations were coined to demonstrate a dichotomy in spawning aggregation behaviour, it is becoming increasingly recognized that they represent different ends along multi-factorial continua (Claydon, 2004; Choat, 2012; Sadovy de Mitcheson, 2012; see Fig. 2). In addition, the same terms could also be used to distinguish between different kinds of simple migratory spawners. As such, transient or resident migratory spawners are groups that include both those that form spawning aggregations and those that do not. Albeit loosely related to migration distance, an additional scale along which migratory spawners can be distinguished is the number of spawning sites per unit area of habitat (Fig. 2). Such metrics are rare, however, which is surprising given the potential importance to commercially targeted species.

For many species of reef fishes, migration distances may be constrained to individual reefs that are isolated by a combination of inhospitable depth, habitat and distance (Chapman & Kramer, 1999) or because a species' size and trophic ecology restrict such movements (Choat, 2012). Thus, with nowhere else to go, spawning sites for these more typically resident migratory spawners should be found on all reefs where such species are present, but this assumption has never been tested. Spawning sites of transient migratory spawners are not precluded from any reef, but their distribution is likely to be more widespread.

There is increasing evidence of the use of the same spawning site by multiple species of reef fish, both sequentially and simultaneously, for both resident and transient spawners (Lobel & Neudecker, 1985; Moyer, 1989; Colin & Bell, 1991; Craig, 1998; Johannes *et al.*, 1999; Sancho *et al.*, 2000; Heyman *et al.*, 2001; Whaylen *et al.*, 2004; Colin, 2010). These sites may be preferential locations from which to spawn because they have characteristics that increase survival of offspring and adults (Robertson & Hoffman, 1977; Johannes, 1978; Lobel, 1978; Barlow, 1981; Shapiro *et al.*, 1988). Alternatively, synchronizing egg release at one location may swamp egg predators (Johannes, 1978). While many of the advantages of spawning synchronously may apply both within and among species, the species migrating to the same spawning sites and the characteristics of these sites are poorly understood for most geographic locations (Johannes, 1978; Koenig *et al.*, 2000; Claro & Lindeman, 2003; Whaylen *et al.*, 2004; Heyman & Kjerfve, 2008; Kobara & Heyman, 2010*a*; Schärer *et al.*, 2010). In addition, most research on spawning sites has focused on a single species, often at a single site [with notable exceptions: Sancho *et al.* (2000) and Claro & Lindeman (2003)]. Few studies have addressed the distribution of multiple spawning sites for single species across a reef system and no systematic effort has been made to assess the spatial and temporal congruency of spawning activities for all migrating species occupying the same reef.

Temporal patterns of spawning can differ substantially within and between species at different locations (SCRFA, 2012). Among reef fishes in general, spawning seasons have been linked (both separately and in combination) to temperature, winds, currents and rainfall (Johannes, 1978; Robertson, 1991*a*; Colin, 1992; Tucker *et al.*, 1993). Where annual variability in these factors is negligible, and for species with physiologies and life histories that permit (Robertson, 1991*b*; Choat, 2012), spawning is expected to occur year-round. Such locations are more likely to be found at lower latitudes and longer seasons are more characteristic of resident spawners. Although transient spawners in general may be less physiologically capable of migrating and spawning year-round (Choat, 2012), at low latitudes, the more typically transient spawning squaretailed coralgrouper *Plectropomus areolatus* (Rüppell 1830) and brown-marbled grouper *E. fuscoguttatus* (Forsskål 1775) form spawning aggregations every month, but less frequently at higher latitudes (SCRFA, 2012). Whether spawning corresponds to a tidal or diel pattern can also vary with location. For example, pelagic spawning species may be synchronized with tidal cycles where tidal amplitudes are high and tidal currents are predictable, but at other locations spawn at specific times of the day (Colin & Bell, 1991; Appeldoorn *et al.*, 1994; Domeier & Colin, 1997). Lunar periodicity can also differ depending on the location: the camouflage grouper *Epinephelus polyphekadion* (Bleeker 1849) spawns near the full moon in some locations, but new moon in others (Rhodes, 2012). Although lunar patterns are perhaps the least well-studied

aspects of spawning periodicity, such differences within species appear to be uncommon.

The purpose of this study was to investigate the spatial and temporal characteristics of the use of spawning sites by migratory spawners across a wide range of reef fish taxa in a low-latitude coral reef habitat (Kimbe Bay, Papua New Guinea). This study focused on pelagic spawners because they constitute the majority of fishes known to undertake spawning migrations and included both simple migratory spawners and those that form spawning aggregations. This multispecies approach was complemented by focusing on a single species, the striated surgeonfish *Ctenochaetus striatus* (Quoy & Gaimard 1825), to explore spawning site use over a more extensive area of reefs. The study location lacks distinct climatic seasons; tides and currents are limited and the matrix of reefs are separated by depths > 50 m. Accordingly, the following specific predictions were tested: (1) spawning sites should occur on each reef, (2) spawning sites should be used by multiple species, (3) spawning should occur all year-round and (4) species should spawn at specific times of day rather than states of the tide. No general predictions were made for lunar patterns of spawning as they were expected to vary between species.

MATERIALS AND METHODS

This study was conducted on the inshore reefs of Kimbe Bay (5° 30′ S; 150° 6′ E), New Britain, Papua New Guinea (Fig. 3). The study reefs are steep-walled platform reefs separated by depths of over 50 m and within 1 km of shore. The tidal characteristics of Kimbe Bay are complicated and are composed of a series of days of diurnal tides followed by a series of days of mixed tides. The tidal range in this area is small, being only *c*. 1 m. Study reefs, however, become exposed at an extreme low tide. Currents are predominantly weak with no predictable inflow or outflow related to specific tides (Claydon, 2005). In addition, at this low latitude, among days of sampling, the time of sunrise or sunset differed by < 15 min, and thus, time of spawning was not adjusted for day length.

LOCATING SPAWNING SITES

Spawning sites of all species were searched intensively on the reefs of Hanging Gardens, Maya's and Limuka. All reefs were divided into sections of reef edge small enough to sample in their entirety at least once every 30 min by snorkelling. An observer searched within a single section repeatedly over a day, and each section was sampled for a minimum of 5 days. The species, number of individuals gathered to spawn and time and location of spawning were recorded. Numbers of individuals ≤ 20 could be counted accurately, but blocking, a commonly used technique to estimate the size of flocks of birds (Bibby *et al.*, 2000; Gregory *et al.*, 2004), was used to estimate > 20 individuals. As such, estimates in the ranges of 21–60, 61–100, 101–500 and >500 were to the nearest 5, 10, 50 and 100 individuals, respectively. Location of spawning was documented in relation to markers placed at 20 m intervals around the reef edge (Claydon *et al.*, 2012).

In order to explore the distribution of spawning sites over an additional larger expanse of contiguous reef, it was necessary to focus on a single-model species, *C. striatus*. As such, spawning sites of *C. striatus* were intensively sought on the seaward-facing edge of Kume, a > 3 km stretch of reef. The protocol described above was followed except that sightings of other species using spawning sites were opportunistic. *Ctenochaetus striatus* was chosen because it spawns in a conspicuous manner often in large aggregations, and thus locating spawning sites of this species was comparatively easy.

Opportunistic observations were also made on Gava Gava, Luba Luba and Madaro where locations were estimated from landmarks and aerial photographs. The sites of aggregations of
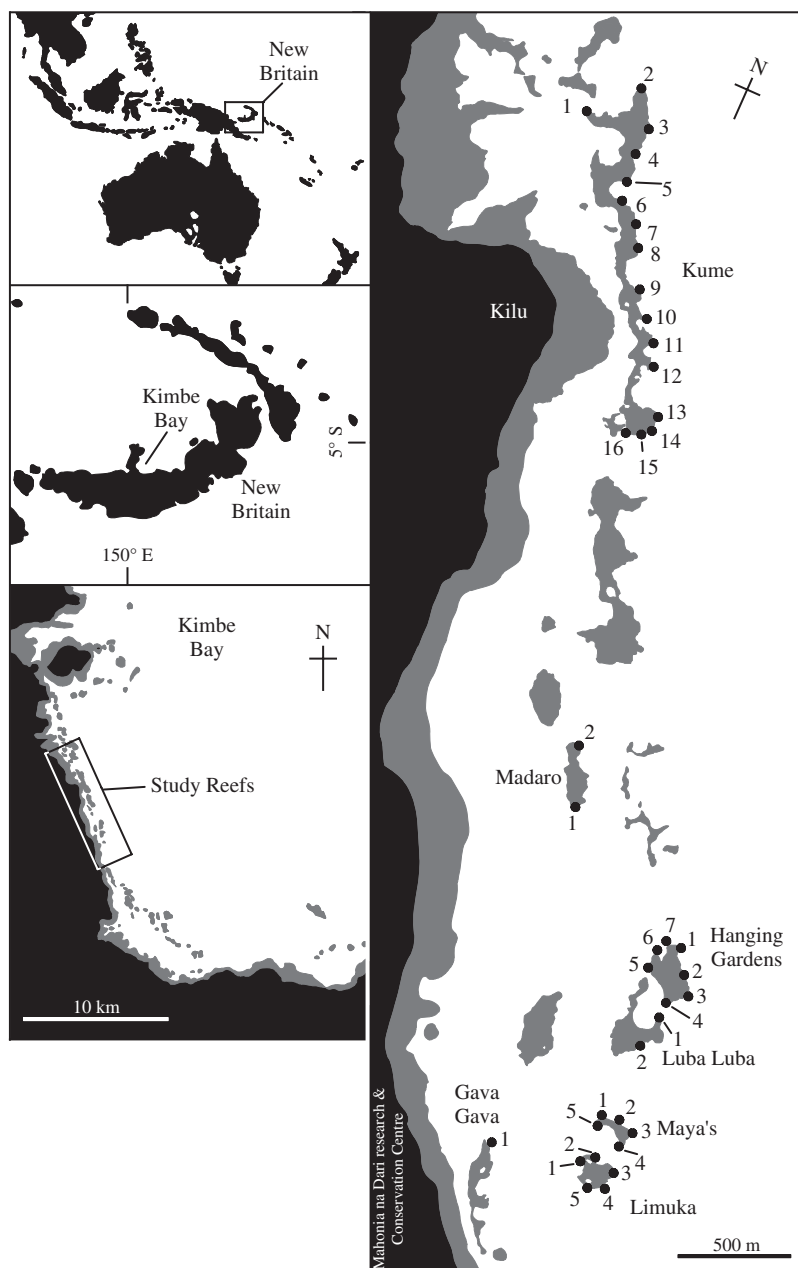
FIG. 3. Study reefs and spawning sites found in Kimbe Bay, West New Britain Province and Papua New Guinea (5° 30′ S; 150° 6′ E). ■, land; □, Reef 0–5 m; ▨, sea; ●, spawning site; MND, Mahonia na Dari Research and Conservation Centre.

spawning fishes were not deemed to be sensitive information because the species concerned are neither of conservation concern nor the targets of commercial fisheries.

MULTISPECIES USE OF SITES AND PERIODICITY

Once spawning sites had been identified, sampling effort focused on Hanging Gardens, Limuka and Maya's in order to investigate (1) the extent to which spawning sites were used by multiple species, (2) the number of conspecifics gathered to spawn at sites and (3) possible seasonal, lunar, diel and tidal rhythms to spawning. Spawning sites were on average 60 m from one another, but < 30 m apart in some locations. Thus, fish assemblages at spawning sites were sampled in circular areas of 5 m radius, a size considered to be large enough to accurately represent spawning activities, yet discrete enough to avoid overlapping with adjacent sites. The sampling areas were positioned in the assumed centres of spawning activity (as determined by preliminary observations) at each site. While many species form mobile spawning pairs or groups, the spawning and courtship of most species were adequately contained within the 5 m radii.

The days upon which reefs were sampled were randomized except when confounded by logistical considerations. Within a day, all spawning sites on the reef studied were monitored sequentially by moving around the reef from site to site such that on average every spawning site was sampled at least once every 15 min. The fish assemblage was recorded at each site and any pelagic spawning or courtship was documented. In order to increase observations of spawning, any species displaying courtship behaviours were observed for an additional 10 min or until spawning was documented. Numbers of individuals were estimated as described previously.

Pelagic spawning was verified by observing the release of gametes. The types of pelagic spawning observed were recorded as (1) pair spawning where a single male courts and spawns with a single female, (2) streak spawning where one or more additional males rush to add sperm to a pair spawn and (3) group spawning where >2 individuals court and spawn together (Domeier & Colin, 1997). Migration to spawning sites was established indirectly by the presence of individuals within sampling areas during courtship and spawning, but their absence at other times. Thus, it was not possible to estimate migration distances. Observers remained outside the 5 m radii and their presence did not appear to affect fishes' behaviours.

In order to establish possible seasonal, lunar, diel and tidal rhythms of spawning, over 2000 h of observations on 190 days between July 2001 and May 2004, with 12, 67, 105 and 6 days sampled in 2001, 2002, 2003 and 2004, respectively. Sampling was balanced across lunar days, tide phases and tide heights, but not across months, with no observations in January, June or August of any year (see Fig. 4), and not across times of the day (see Fig. 5): for logistical and safety reasons, early morning observations were only undertaken during periods of high tide. Therefore, for species seen spawning exclusively in the morning, only diel patterns of spawning were assessed. Tidal data were obtained under licence from Seafarer Tides (Australian National Tide Tables; www.bom.gov.au/oceanography/projects/ntc/ntc.shtml).

Following Domeier (2012), in order to determine whether spawning events in the current study could be considered to be spawning aggregations, it was necessary to assess whether densities during spawning were at least four times greater than the species' densities at non-spawning times (background densities). Spawning densities were calculated from the numbers of individuals observed in the 5 m radii areas. Species' background densities were estimated from randomly placed 50 × 4 m visual transects at 0, 2, 6 and 10 m depths used in a monitoring programme of Kimbe Bay's inshore reefs (Jones, 2004). Between 2001 and 2004, 128 surveys were conducted at each depth. For each species, only depth strata representative of the species' range were used to calculate background densities.

STATISTICAL ANALYSES

Patterns of spawning v. sampling effort

Spawning in association with seasonal, lunar and tidal patterns was assessed for the 13 species most commonly observed spawning. Diel patterns were assessed for 17 species, as this included
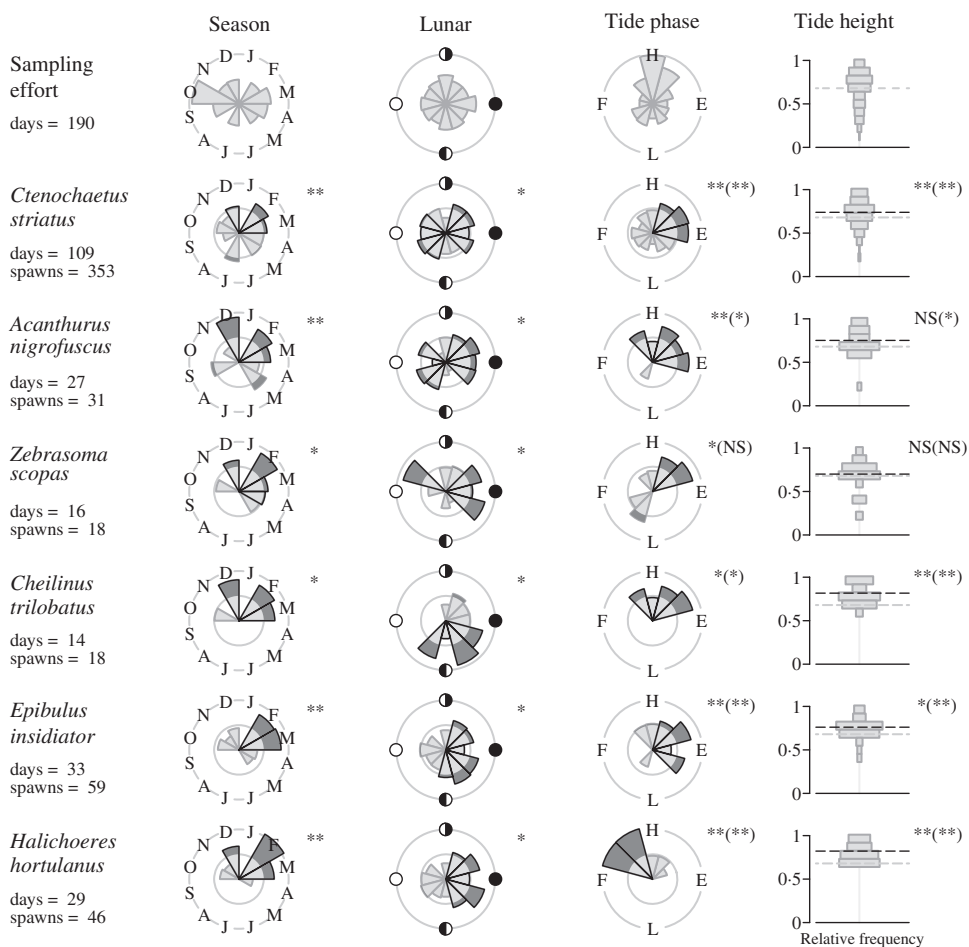
FIG. 4. Seasonal, lunar and tidal periodicity of spawning activity by species. For sampling effort, the areas of segments in rose diagrams are proportional to the number of days in a month, days within a lunar period or occasions that a particular tidal phase was sampled. For species rose diagrams, the segments have areas proportional to the number of spawns observed (n_{obs}) divided by the number of spawns expected from sampling effort (n_{exp}). The inner grey circles indicate where $n_{obs} = n_{exp}$. Where $n_{obs} = n_{exp}$, the portions extending beyond the inner circles are in ☐. Black outlines to segments indicate a continuous period of significantly more spawning than expected; each rose diagram can have one or two such periods. All rose diagrams run clockwise. Lunar phases: ○, full moon; ●, new moon, ◑, first quarter; and ◐, last lunar quarter. Tidal phase represents position along sinusoidal wave from high tide (H) to low tide (L); E, ebb tide; F, flood tide. Tidal height: horizontal bars represent relative frequency of observations during different ranges of tidal height from 0 to 1 m. --- , mean tidal height during sampling; --- , the mean height of the tide during which spawning was observed for the species in question. Results of Williams-corrected G-tests assessing frequency of observations against those predicted by total sampling effort are indicated as *P < 0·05; **P < 0·01; NS, not significantly different (P > 0·05). For tide height, results are from one-tailed Mann–Whitney U-tests assessing if median height is greater than that predicted by total sampling effort. Results in parentheses indicate the results of tests performed against frequencies or tidal height predicted from sampling effort during species' diel spawning interval.
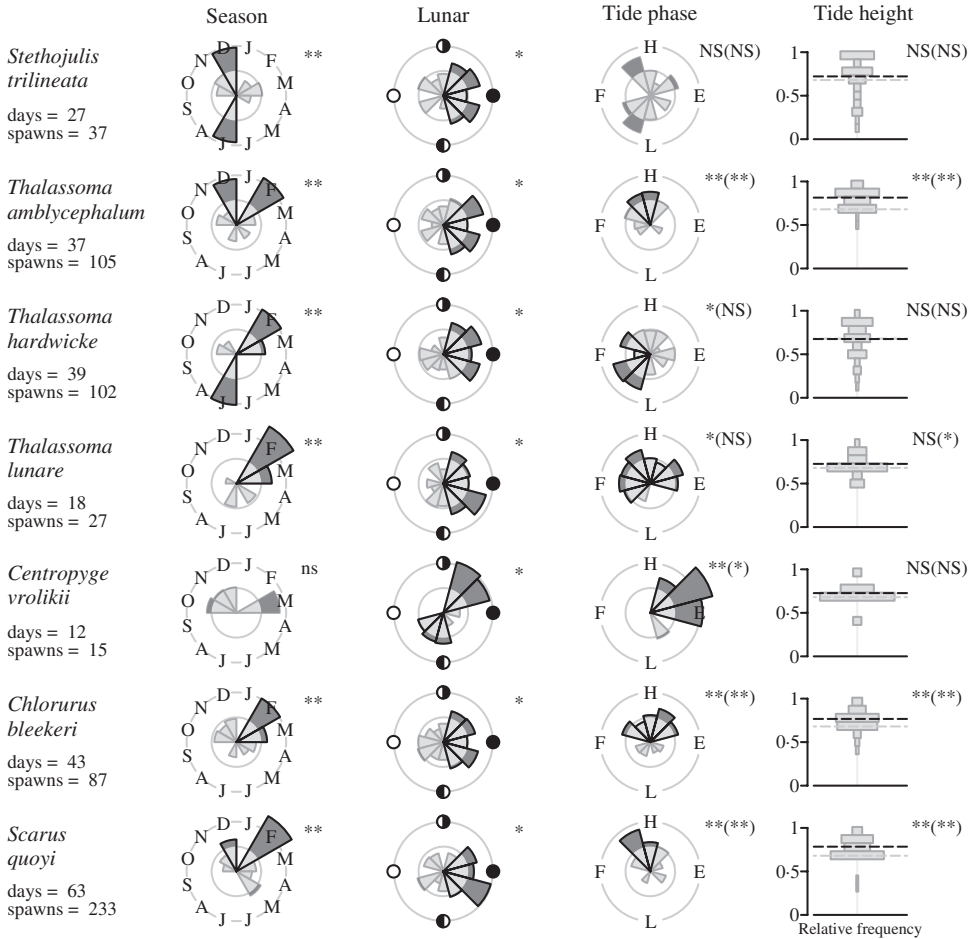
FIG. 4. continued.

an additional four dawn-spawning species excluded from other analyses. Seasonal periodicity was tested using G-tests to establish whether the observed frequencies of spawning on different months differed significantly ($P < 0.05$) from that predicted by the frequency of sampling during those months and whether any differences corresponded to increased spawning during defined seasons (*i.e.* continuous periods of 1–11 months of significantly greater than expected spawning activity). Data were pooled where appropriate; a Williams correction was employed; and where frequencies were too low a Fisher's exact test was used (Sokal & Rohlf, 1995). Lunar and diel periodicity were tested in a similar manner using frequency of spawning observations during days of the lunar month and hours of the day, respectively. The patterns of species' spawning with reference to tidal phase and tidal height were also tested. Tidal phase was determined along a sinusoidal wave from high to low tide. Using Williams-corrected G-tests, the frequency of spawning in association with tidal phases was tested against the frequency predicted by total sampling effort and separate tests were performed against the frequency predicted during the species-specific diel spawning periods observed. Tidal height data were not normally distributed and thus one-tailed Mann–Whitney *U*-tests were used to test whether the median tidal heights during spawning differed from (1) the median tidal height during all hours of sampling and (2) the median tidal height during species-specific diel spawning periods on days of sampling.

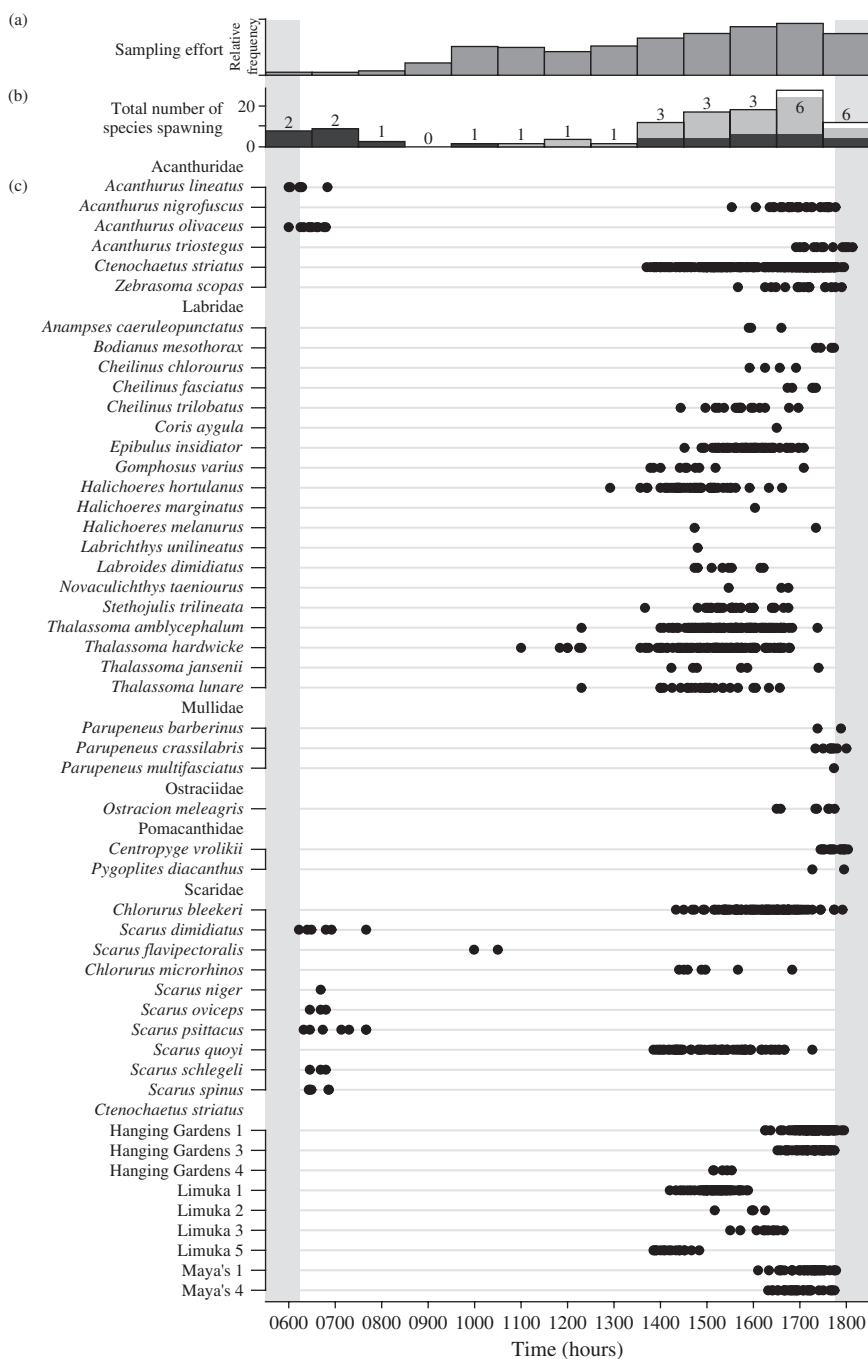FIG. 5. (a) Histogram displays relative frequency of sampling during time periods. (b) Total number of species spawning during time periods separated into herbivores (■), carnivores (■) and omnivores (□), with number of families indicated by numbers. (c) Diel spawning times of species and times of spawning at different sites for *Ctenochaetus striatus*. ●, an observed spawning event. Grey areas, dawn and dusk.

Inter and intraspecific analyses

Post hoc pair-wise comparisons using Holm's sequential Bonferroni procedure were used to assess differences in seasonal, lunar, diel and tidal (phase and height) patterns of spawning between species, families and trophic levels. Williams-corrected G-tests (substituted with Fisher's exact tests when frequencies were low) were used for seasonal, lunar and tidal phase data and Wilcoxon tests were used to assess differences between species in times of the day and tidal heights when spawning was observed. The times of day ranged from dawn to dusk (spanning *c*. 12 h) and thus were not treated as circular data.

A two-way ANOVA was performed to test whether the spawning times of *C. striatus* differed between Hanging Gardens, Limuka and Maya's reefs and whether spawning times within reefs differed among different sites. Sufficient data were not available for other species. Because days upon which reefs were sampled were randomized and all sites within a reef were monitored on the same day, any differences in spawning times between reefs and among sites within reefs could not be attributable to an artefact of sampling. Data were tested for normality and homogeneity of variances.

All statistical analyses were performed using R (R Core Development Team; www.r-project. org). Data were pooled across years, months, lunar days and tidal phases where appropriate.

RESULTS

DISTRIBUTION OF SPAWNING SITES

Thirty-eight different spawning sites were identified, with at least one found on every reef (Fig. 3 and Table I). On Hanging Gardens, Limuka and Maya's, spawning sites were found distributed at an average of one per 60 m of reef edge. *Ctenochaetus striatus* were found spawning in aggregations at 29 different sites with at least one site found on every reef studied. On the reefs for which *C. striatus* was intensively searched (Kume, Hanging Gardens, Limuka and Maya's), the distribution of *C. striatus* spawning sites averaged at least one site per 200 m of reef edge.

SPECIES SPAWNING AT SITES

Pelagic spawning was observed in 41 species from six families (Table I). Spawning for 39 of these species involved migration of individuals to spawning sites. Only the pearlscale angelfish *Centropyge vrolikii* (Bleeker 1853) and the bluestreak cleaner wrasse *Labroides dimidiatus* (Valenciennes 1839) did not migrate from outside the 5 m radius sampling areas to spawn.

Throughout the reefs studied, 28 of 38 spawning sites were used by more than one species (Table I). On the intensively studied reefs of Hanging Gardens, Limuka and Maya's, at least three species were observed spawning at every site. Hanging Gardens sites 1 and 3 had 25 and 30 species spawning, respectively. While a number of species spawned on the same days within a site (at both overlapping and different times of day), these values represent total number of species that had been observed spawning at a site by the end of the study.

SIZE OF SPAWNING GROUPS

Between all species observed, the maximum number of individuals gathered to spawn (*i.e.* the number of conspecifics gathered to spawn at a site) ranged from two to 2000 individuals (see Table I). Within species, the maximum number of individuals gathered

TABLE I. Species observed spawning pelagically on study reefs. Numbers in species rows indicate maximum number of conspecifics observed gathering to spawn at that site. Numbers in bold indicate densities at least four times greater than background

Reef	Hanging gardens							Maya's					Limuka					Madaro		Spawning mode
Species / Site	1	2	3	4	5	6	7	1	2	3	4	5	1	2	3	4	5	1	2	
Acanthuridae																				
Acanthurus lineatus	–	–	**200**	–	–	–	–	–	–	–	**150**	–	–	–	–	**150**	–	–	–	G
Acanthurus nigrofuscus	6	–	**5**	–	–	–	–	**12**	–	–	**5**	–	–	**10**	–	**7**	–	–	–	G
Acanthurus olivaceus	–	–	**4**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Acanthurus triostegus	–	–	**40**	–	–	–	–	–	–	–	–	–	–	–	–	**4**	–	–	–	G
Ctenochaetus striatus	**700**	–	**450**	**400**	–	**60**	**400**	**400**	–	–	**300**	–	**250**	**200**	**500**	–	**1000**	**1500**	**50**	G
Zebrasoma scopas	**5**	–	3	–	–	**10**	–	–	–	3	**5**	–	3	–	3	–	**5**	–	–	P
Labridae																				
Anampses caeruleopunctatus	**2**	–	–	–	–	–	–	–	–	**3**	–	–	–	–	–	–	–	–	–	P
Bodianus mesothorax	**4**	–	2	–	–	–	–	**2**	–	–	–	–	–	–	–	–	–	–	–	P
Cheilinus chlorourus	**2**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Cheilinus fasciatus	**3**	–	7	–	–	**3**	–	–	–	–	–	2	–	–	–	–	–	–	–	P
Cheilinus trilobatus	**4**	–	9	–	–	–	–	–	**2**	**3**	–	–	–	–	–	–	–	–	–	P
Coris aygula	–	–	–	–	–	–	–	–	–	–	**3**	–	–	–	–	–	–	–	–	P
Epibulus insidiator	**10**	–	25	–	–	–	–	–	–	–	–	–	–	–	**2**	–	–	–	–	P,S
Gomphosus varius	7	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Halichoeres hortulanus	**5**	**8**	7	–	–	–	**3**	**3**	**3**	4	–	**3**	**5**	**5**	–	–	**3**	**12**	–	P
Halichoeres marginatus	**2**	–	–	–	–	–	–	–	–	–	**3**	**2**	–	–	–	–	–	–	–	P
Halichoeres melanurus	**2**	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	P
Labrichthys unilineatus	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Labroides dimidiatus	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Novaculichthys taeniourus	–	–	–	**3**	**2**	–	–	–	–	–	–	–	–	–	–	–	**4**	–	–	P
Stethojulis trilineata	**50**	**8**	**12**	**40**	–	–	**80**	–	–	3	–	–	–	–	4	–	–	–	–	G,P

Table I. continued

Species	Hanging gardens							Maya's					Limuka					Madaro		Spawning mode
Reef Site	1	2	3	4	5	6	7	1	2	3	4	5	1	2	3	4	5	1	2	
Thalassoma amblycephalum	**100**	–	**300**	–	–	–	–	–	–	**10**	**60**	–	–	–	–	–	–	–	–	G,P,S
Thalassoma hardwicke	**250**	16	**200**	–	–	–	**1000**	20	**60**	10	20	5	–	–	50	–	9	–	–	G,P,S
Thalassoma jansenii	**4**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P,S
Thalassoma lunare	**80**	–	**100**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	G,P,S
Mullidae																				
Parupeneus barberinus	–	–	**4**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Parupeneus bifasciatus	**10**	–	**10**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P,S
Parupeneus multifasciatus	–	–	–	–	–	–	**6**	–	–	–	–	–	–	–	–	–	–	–	–	P
Ostraciidae																				
Ostracion meleagris	**2**	–	**3**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Pomacanthidae																				
Centropyge vrolikii	**2**	2	**2**	–	2	2	2	2	–	–	–	2	–	–	–	–	–	–	–	P
Pygoplites diacanthus	–	–	**4**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scaridae																				
Chlorurus bleekeri	**7**	–	**20**	–	–	–	**7**	**3**	**3**	**3**	**3**	–	**3**	–	–	–	**3**	–	–	P,S
Scarus dimidiatus	–	–	**100**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P,G
Scarus flavipectoralis	–	–	–	–	**8**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus microrhinos	**4**	–	**5**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus niger	–	–	**5**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus oviceps	–	–	**5**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus psittacus	–	–	**45**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus quoyi	**30**	–	**17**	–	–	–	**3**	–	–	–	–	–	>3[a]	–	>3[a]	–	>3[a]	–	–	G,P

TABLE I. continued

Species	Hanging gardens 1	2	3	4	5	6	Maya's 7	8	9	10	11	12	13	14	15	16	Limuka 1	2	3	4	5	Madaro 1	2	Spawning mode
Scarus schlegeli	–	–	**8**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Scarus spinus	–	–	**10**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Total species at site	25	4	30	4	3	3	7	8	4	8	10	5	–	5	3	6	3	7	2	1				

Species	Reef Site — Kume 1	2	3	4	5	6	7	Gava Gava 1	Luba Luba 1	2	Spawning mode
Acanthuridae											
Acanthurus nigrofuscus	–	8	–	–	–	7	–	–	–	–	G
Acanthurus triostegus	100	2000	350	–	600	200	30	250	300	30	G
Ctenochaetus striatus	–	–	–	–	–	200	–	200	–	–	G
Zebrasoma scopas	–	–	–	20	9	–	–	2	–	–	P
Labridae											
Cheilinus trilobatus	–	–	–	–	–	–	–	4	–	–	P
Halichoeres hortulanus	–	6	–	–	–	–	3	4	4	–	P
Novaculichthys taeniourus	3	–	–	–	–	–	–	–	–	–	P
Stethojulis trilineata	8	–	10	–	–	–	10	–	5	–	G,P
Thalassoma amblycephalum	–	1000	350	–	–	40	200	100	–	30	G,P,S
Thalassoma hardwicke	–	–	–	–	–	–	–	–	–	200	G,P,S
Thalassoma jansenii	4	–	–	–	–	–	–	–	–	–	P,S
Scaridae											
Chlororus bleekeri	–	–	–	–	5	–	–	–	–	–	P,S
Scarus quoyi	–	–	–	–	–	–	30	–	10	–	P
Total species at site	6	3	1	3	3	1	5	5	1	1	6	4	4	4	2	1	1	1	2

[a] Individuals moved quickly up and down the reef wall, in and out of sight, preventing more accurate estimates.
G, group spawning; P, pair spawning; S, streaking.

to spawn varied widely between sites, being most pronounced for *C. striatus* (seven to 2000), sixbar wrasse *Thalassoma hardwicke* (Bennett 1830) (five to 1000), bluntheaded wrasse *Thalassoma amblycephalum* (Bleeker 1856) (10–1000) and lined surgeonfish *Acanthurus lineatus* (L. 1758) (three to 350; see Fig. 6). In addition, within sites, the maximum number of individuals gathered to spawn also differed substantially within species on different days of spawning, ranging from seven to 700 for *C. striatus*, five to 200 for *T. hardwicke* and three to 200 for *A. lineatus* (Fig. 6). In general, the number of conspecifics gathered at a spawning site was low: for 27 species, the maximum size of aggregations was 10 individuals or less; for 18 species, on certain days and at certain sites, only a solitary spawning pair was observed; four of these species [*C. vrolikii*, floral wrasse *Cheilinus chlorourus* (Bloch 1791), tubelip wrasse *Labrichthys unilineatus* (Guichenot 1847) and *L. dimidiatus*] were found exclusively as solitary pairs at spawning sites.

Spawning densities were four times greater than background densities for all except four species (the tail-spot wrasse *Halichoeres melanurus* (Bleeker 1851), *L. unilineatus*, *L. dimidiatus* and *C. vrolikii*; Fig. 6 and Table I). Because of the range in number of conspecifics gathered to spawn, for seven species [*A. lineatus*, *C. striatus*, twotone tang *Zebrasoma scopas* (Cuvier 1829), three-lined rainbowfish *Stethojulis trilineata* (Bloch & Schneider 1801), *T. hardwicke*, moon wrasse *Thalassoma lunare* (L. 1758) and Bleeker's parrotfish *Chlorurus bleekeri* (de Beaufort 1940)], some spawning events were in densities greater than this threshold and others were not. This varied both among spawning sites and on different days within the same spawning site.

PERIODICITY

Seasonal

Spawning was observed throughout the study period. *Ctenochaetus striatus* spawned on all months studied (Fig. 4). *Chlorurus bleekeri* spawned on all but one month studied. Five species [*Z. scopas*, sling-jaw wrasse *Epibulus insidiator* (Pallas 1770), *S. trilineata*, *T. hardwicke* and Quoy's parrotfish *Scarus quoyi* (Valenciennes 1840)] spawned on all but two months. Absence of spawning observations during certain months of the year may be attributable to the limited number of days upon which spawning was observed, with a significant positive linear regression between the number of months in which a species was observed spawning and number of days spawning was observed ($r^2 = 0.60$; $P < 0.01$; day values were square root transformed). The frequency with which species were observed spawning on separate months of the year, however, differed significantly from sampling effort for all species analysed except *C. vrolikii* (Fig. 4). For 10 species, this corresponded to distinct seasons of greater than expected spawning activity (as determined by number of days during which a species was observed spawning), falling between December and April: spanning this entire period for *Z. scopas*; December to March for *C. striatus*, the brown surgeonfish *Acanthurus nigrofuscus* (Forsskål 1775), the tripletail wrasse *Cheilinus trilobatus* (Lacépède 1801) and the checkerboard wrasse *Halichoeres hortulanus* (Lacépède 1801); December to February for *S. quoyi* and *T. amblycephalum*; February to March for *E. insidiator*, *T. lunare* and *C. bleekeri*. Two species appeared to have two seasonal peaks in spawning activity: *S. trilineata* and *T. hardwicke* both spawned on significantly more days in July than predicted by sampling effort, with the former also spawning
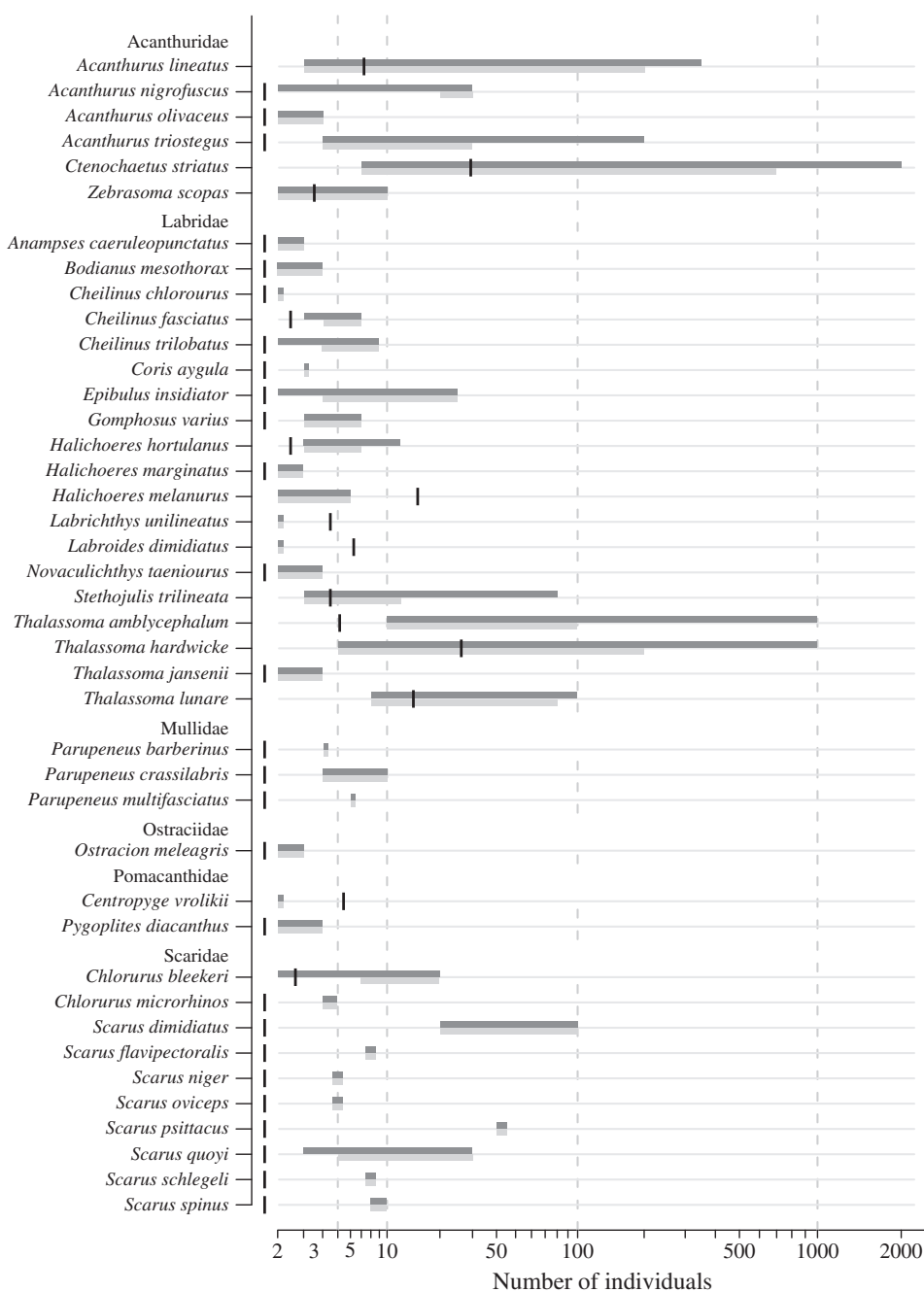
Fig. 6. Number of conspecifics gathered to spawn by species. Values indicate maximum number of conspecifics gathered to spawn at a site on a single day. ▬, the range for all sites combined; ▬, the greatest range observed within a single site. Days when a species was not observed spawning were not included. ⎸, the threshold number of individuals representing densities four times greater than background densities. Lines at < 2 are in the range of 0 to < 2 individuals rather than displaying exact values.

on more days in December and the latter in February and March. Interspecifically, however, the frequency with which spawning occurred on different months of the year only differed significantly between *C. striatus* and *T. amblycephalum* (pair-wise comparisons using Holm's sequential Bonferroni procedure, $P < 0.05$).

Lunar

All species analysed were observed spawning during all four lunar quarters except for *C. trilobatus*, which was not observed spawning over the full moon period. All 13 species displayed patterns of spawning over the lunar month that differed significantly from sampling effort (Fig. 4). The majority of species ($n = 9$) spawned on more days around the new moon period. Four species displayed semi-lunar patterns, with the three Acanthuridae spawning on more days in both the new and full moon periods and *C. vrolikii* spawning more between the last quarter and new moon and between the first quarter and full moon. Lunar periodicity, however, did not differ significantly between species (pair-wise comparisons using Holm's sequential Bonferroni procedure, $P > 0.05$).

Tidal

Only *S. trilineata* did not spawn significantly more often around a tidal phase or combination of adjacent tidal phases than predicted by sampling effort (Fig. 4). *Thalassoma amblycephalum*, *C. bleekeri* and *S. quoyi* spawned significantly more around high tide; *C. striatus*, *A. nigrofuscus*, *Z. scopas*, *C. trilobatus*, *C. vrolikii* and *E. insidiator* around high and ebb tide; *T. hardwicke* around flood tide; *H. hortulanus* between flood and high tide; *T. lunare* spawned more around flood, high and ebb tide. For all these species except *T. hardwicke*, *T. lunare* and *Z. scopas*, spawning also differed significantly from sampling effort within their species-specific diel spawning intervals. Although spawning was predominantly concentrated around higher tidal phases, all species except *C. trilobatus* and *H. hortulanus* were also observed spawning at tidal phases on the lower half of the sinusoidal wave from between ebb and flood tide spanning low tide.

There were relatively few significant interspecific differences in the frequencies of spawning with relation to tidal phases (Table II). Differences observed did not fall consistently along familial or trophic divisions. The most distinct patterns were shown by *T. amblycephalum* and *T. hardwicke*, each of which differed significantly from eight other species.

A general tendency to spawn at higher tidal heights was also displayed (Fig. 4). Seven species spawned on tides significantly higher than those predicted by total sampling effort and by sampling effort during species-specific spawning intervals (one-tailed Mann–Whitney U-tests; $P < 0.05$). Two species (*A. nigrofuscus* and *T. lunare*) spawned at significantly higher tides than predicted by their species-specific spawning intervals, but not when compared to total sampling effort. Four species (*Z. scopas*, *S. trilineata*, *T. hardwicke* and *C. vrolikii*) did not spawn at significantly higher tides than both levels of sampling effort. Nine of the 13 species analysed spawned at lower tides (*i.e.* tides in the lower half of the tidal range), with *S. trilineata* and *T. hardwicke* also spawning on the lowest tides observed during the study. Pair-wise comparisons revealed that the height of the tide during spawning did not differ significantly between all but three pairs of species: *C. striatus* spawned at higher tides than *T. amblycephalum*, and *T. hardwicke* spawned at lower tides than both *T. amblycephalum*

TABLE II. Tide phase spawning periodicity: interspecific pair-wise comparisons using Holm's sequential Bonferroni procedure. Species are listed in ascending order of trophic level (values from Froese & Pauly, 2011) and grouped in families

		Scaridae		Acanthuridae			Pomacanthidae	Labridae						
Trophic level		Cb	Sq	An	Cs	Zs	Cv	Ta	St	Hh	Ct	Tl	Th	Ei
Herbivore and Detritivore														
2·0	*Chlorurus bleekeri*		NS	NS	NS	NS	*	NS	NS	NS	NS	NS	*	NS
2·0	*Scarus quoyi*			NS	*	NS	*	NS	*	NS	NS	NS	**	*
2·0	*Acanthurus nigrofuscus*				NS	NS	NS	*	NS	NS	NS	NS	*	NS
2·0	*Ctenochaetus striatus*					NS	NS	**	NS	*	NS	NS	***	NS
2·0	*Zebrasoma scopas*						NS	*	NS	NS	NS	NS	NS	NS
Omnivore														
2·8	*Centropyge vrolikii*							**	NS	*	NS	NS	**	NS
Carnivore														
3·1	*Thalassoma amblycephalum*								**	NS	NS	*	**	**
3·2	*Stethojulis trilineata*									NS	NS	NS	NS	NS
3·4	*Halichoeres hortulanus*										NS	NS	*	*
3·5	*Cheilinus trilobatus*											NS	NS	NS
3·5	*Thalassoma lunare*												NS	NS
3·6	*Thalassoma hardwicke*													**
3·8	*Epibulus insidiator*													

Cb, *Chlorurus bleekeri*; Sq, *Scarus quoyi*; An, *Acanthurus nigrofuscus*; Cs, *Ctenochaetus striatus*; Zs, *Zebrasoma scopas*; Cv, *Centropyge vrolikii*; Ta, *Thalassoma amblycephalum*; St, *Stethojulis trilineata*; Hh, *Halichoeres hortulanus*; Ct, *Cheilinus trilobatus*; Tl, *Thalassoma lunare*; Th, *Thalassoma hardwicke*; Ei, *Epibulus insidiator*.

$*P < 0.05$; $**P < 0.01$; NS, $P > 0.05$.

and *H. hortulanus*. The largest difference in mean tidal heights during spawning, however, was <15 cm.

Diel

Spawning was observed at all hours of the day studied except between 0800 and 0900 hours. The time of day that individuals spawned varied considerably between species, ranging from dawn to dusk. The number of species spawning was reduced during the late morning and early afternoon (see Fig. 5). All species' diel spawning intervals were restricted with the majority of species (31 of 41) spawning exclusively in the period from early afternoon to dusk (Fig. 5). Eight species, however, were observed spawning exclusively within a 2 h period of dawn. The hours during which spawning was observed differed significantly from the frequencies predicted by sampling effort for all 17 species analysed: the 13 species included in seasonal, lunar and tidal analyses, plus an additional four dawn-spawning species: *A. lineatus*, orangespot surgeonfish *Acanthurus olivaceus* (Bloch & Schneider 1801), yellowbarred parrotfish *Scarus dimidiatus* (Bleeker 1859) and common parrotfish *Scarus psittacus* (Forsskål 1775).

Patterns of spawning with families and trophic groups were mixed (Fig. 5 and Table III). Mullidae, Ostraciidae and Pomacanthidae spawned exclusively within one and a half hours of dusk, with the omnivorous *C. vrolikii* (the only species analysed within this group), spawning significantly later than all other species analysed (Table III). Except for a few late morning observations for *T. hardwicke*, Labridae spawned in the afternoon largely avoiding dusk, with considerable overlap among species. Spawning times of all Labridae analysed differed significantly from all Acanthuridae and from the majority of Scaridae, with the last two families mostly spawning in the early morning or late afternoon. This division also represents carnivores (Labridae) *v.* herbivores (Acanthuridae and Scaridae). Most herbivores spawned at significantly different times from one another. Spawning times did not differ within two clusters of herbivores: those spawning in the early morning (*A. lineatus*, *A. olivaceus*, *S. dimidiatus* and *S. psittacus*) and among Acanthuridae spawning later in the afternoon (*A. nigrofuscus*, *C. striatus* and *Z. scopas*).

Ctenochaetus striatus was observed spawning at a range of times in a 4·5 h period in the afternoon (Fig. 5). The time of spawning differed significantly between reefs ($F_{2,295} = 1035·7$, $P < 0·05$) and also differed significantly among sites within reefs ($F_{3,295} = 27·2$, $P < 0·05$) (Fig. 5). Within sites, *C. striatus* spawned within discrete fixed diel intervals of < 2 h.

DISCUSSION

A large number of fish species in Kimbe Bay appear to migrate to spawn at predictable places and times on the inshore reefs. Spawning sites were found on all reefs studied with 38 sites identified distributed at an average of one site every 60 m of reef edge. Forty-one pelagic spawning species from six families were observed using these locations. All but the two smallest of these species appeared to migrate to spawn from outside the 5 m radius sample areas, and the majority of spawning sites were used by multiple species. The number of conspecifics at spawning sites ranged from two to 2000. Spawning was observed during every month of the study, on all days of the lunar month, at all states of the tide and at all hours of the day studied except between

TABLE III. Diel spawning periodicity: interspecific pair-wise comparisons using Holm's sequential Bonferroni procedure. Species are listed in ascending order of trophic level (values from Froese & Pauly, 2011) and grouped by family

		Scaridae				Acanthuridae					Pomacanthidae	Labridae						
Trophic level		Sd	Sp	Cb	Sq	An	Cs	Zs	Al	Ao	Cv	Ta	St	Hh	Ct	Tl	Th	Ei
Herbivore and Detritivore																		
2·0	*Scarus dimidiatus*		NS	**	**	*	**	*	NS	NS	*	**	*	**	*	*	*	*
2·0	*Scarus psittacus*			**	**	**	**	*	NS	NS	**	**	**	**	*	**	**	**
2·0	*Chlorurus bleekeri*				**	**	**	**	**	**	**	NS	**	**	NS	**	**	*
2·0	*Scarus quoyi*					**	NS	NS	**	**	***	NS	***	NS	NS	NS	NS	NS
2·0	*Acanthurus nigrofuscus*						NS	NS	*	**	***	***	***	***	*	***	***	**
2·0	*Ctenochaetus striatus*							NS	**	**	***	***	**	***	**	***	**	**
2·0	*Zebrasoma scopas*								*	NS	***	***	*	***	*	*	*	*
2·0	*Acanthurus lineatus*									NS	*	**	**	**	**	**	**	**
2·2	*Acanthurus olivaceus*										**	**	**	**	**	**	**	**
Omnivore																		
2·8	*Centropyge vrolikii*											**	NS	**	NS	*	NS	NS
Carnivore																		
3·1	*Thalassoma amblycephalum*												NS	**	NS	*	NS	NS
3·2	*Stethojulis trilineata*													**	**	*	*	**
3·4	*Halichoeres hortulanus*														**	NS	*	**
3·5	*Chelinus trilobatus*															*	NS	NS
3·5	*Thalassoma lunare*																NS	**
3·6	*Thalassoma hardwicke*																	**
3·8	*Epibulus insidiator*																	

Sd, *Scarus dimidiatus*; Sp, *Scarus psittacus*; Cb, *Chlorurus bleekeri*; Sq, *Scarus quoyi*; An, *Acanthurus nigrofuscus*; Cs, *Ctenochaetus striatus*; Zs, *Zebrasoma scopas*; Al, *Acanthurus lineatus*; Ao, *Acanthurus olivaceus*; Cv, *Centropyge vrolikii*; Ta, *Thalassoma amblycephalum*; St, *Stethojulis trilineata*; Hh, *Halichoeres hortulanus*; Ct, *Chelinus trilobatus*; Tl, *Thalassoma lunare*; Th, *Thalassoma hardwicke*; Ei, *Epibulus insidiator*.

$*P < 0.05$; $**P < 0.01$; NS, $P > 0.05$.

0800 and 0900 hours. Nevertheless, the majority of species were observed spawning on proportionately more days between December and April, on more days around the new moon and in association with higher tides. The strongest temporal association was with species-specific diel spawning times spanning < 3 h for most species, 75% of which spawned between mid-afternoon and dusk. Migrations on the study reefs have only been measured for *C. striatus*, averaging < 60 m and with individuals spawning exclusively within home reefs (Claydon *et al.*, 2012). With spawning sites available and deep boundaries between reefs, it is also likely that most other species in this study spawn within home reefs and are therefore restricted to migrations < 2 km. Thus, these migratory spawners displayed behaviours at the resident end of the behavioural continua: presumed short migrations to sites where they do not remain for more than a few hours and spawning over long seasons and throughout the lunar month (see Fig. 2).

The use of spawning sites by multispecies was a common phenomenon occurring within relatively small discrete areas: all 17 spawning sites on the intensively studied reefs were used by a minimum of three species, with up to 30 species observed spawning (at mostly different times) within the same circular area of 5 m radius. Spawning of multiple species within a single site has been documented elsewhere, being commonly observed for transient species of conservation and management concern (Heyman *et al.*, 2001; Claro & Lindeman, 2003; Whaylen *et al.*, 2004; Sadovy, 2005; Kobara & Heyman, 2010*b*), and for resident spawners (Randall & Randall, 1963; Colin & Clavijo, 1988; Moyer, 1989; Colin & Bell, 1991; Colin, 1996; Sancho *et al.*, 2000). Furthermore, the same site can also be used by both resident and transient spawners (Johannes *et al.*, 1999; Heyman & Kjerfve, 2008). Compared to the current study, a similar or even greater diversity of spawners has been documented at the same site (Colin & Bell, 1991; Johannes *et al.*, 1999). It has not been possible, however, to assess how well these observations represent spawning sites in general: studies have usually focused on previously identified sites of varying, but substantially larger dimensions, and the spatial arrangement of similar sites within adjacent reefs has not been addressed. In Kimbe Bay, use of spatially discrete sites by multispecies appears to be ubiquitous, and there is a great abundance of these sites distributed over relatively small areas of reef.

Pelagic spawning reef fishes are widely believed to optimize the survival of their offspring by releasing eggs at sites and times that (1) have limited predator densities (Shapiro *et al.*, 1988), (2) coincide with currents that limit the time eggs are exposed to predators (Randall & Randall, 1963; Johannes, 1978; Lobel, 1978) or (3) enhance the future settlement of larvae onto reefs (Lobel, 1978; Barlow, 1981; Lobel & Robinson, 1988). Superficially, the use of the same spawning sites by multiple species appears to support the notion that the sites in question are intrinsically more beneficial locations from which to spawn than alternative areas of reef.

Because the majority of sampling occurred in 2003 and no observations were made in January, June or August of any year, conclusions about seasonality should be considered tentatively. All species in this study appear to have long or unrestricted spawning seasons. This concurs with records of multi-familial year-round recruitment in Kimbe Bay, which was attributed to the low latitude location and lack of clear climatic differences throughout the year (Srinivasan & Jones, 2006), with water temperature varying on an annual basis by <2° C (Cervino *et al.*, 2006). Nevertheless, most species in this study appeared to spawn more frequently between December and April than during

other times of the year. Similar patterns have been identified from higher latitude reefs where climatic seasons are more pronounced (Randall, 1961; Munro *et al.*, 1973; Walsh, 1987; Colin & Clavijo, 1988; Lobel, 1989; Craig, 1998; Robertson *et al.*, 1999). This has been proposed to correspond to concentrating spawning at environmentally favourable times of the year, but also bet-hedging by spawning at lower intensities outside these periods (Robertson, 1991*a*, *b*). In Kimbe Bay, it is unclear whether December to April represents environmentally more favourable months during which to spawn, but this period does correspond to increased rainfall (Srinivasan & Jones, 2006). As the magnitude of seasonal differences declines with decreasing latitude, it may be expected that proportionally more spawning effort is spread throughout the year compared to the higher concentration of spawning effort within limited months at higher latitudes. Sufficient data are not currently available, however, to identify such latitudinal gradients within species.

The patterns of spawning with moon phase appear to fall along phylogenetic divisions: Larbidae and Scaridae displayed one pulse (predominantly around the new moon) and semi-lunar patterns were displayed by Acanthuridae (around the new and full moon) and by *C. vrolikii* (between the first quarter and full moon and between the last quarter and new moon). Semi-lunar patterns for the same three acanthurids were also observed by Robertson (1983) in Palau. While lunar patterns are well documented in some reef fishes (Oliviera & Sánchez-Vázquez, 2010; Takemura *et al.*, 2010) and are a defining characteristic of transient migratory spawners (Domeier & Colin, 1997; Domeier, 2012), such patterns are less commonly recognized for resident migratory spawners. Nonetheless, this could simply be a reflection of the relatively small amount of data required to identify a pattern involving continuous days of spawning followed by days without spawning during a lunar month (*i.e.* transient) compared to a pattern where spawning is not excluded from any lunar days (*i.e.* resident) but occurs more often at certain phases of the moon, as was demonstrated for all species in this study. Low numbers of observations may explain why no lunar patterns were discerned among a large group of labrids and scarids (including 19 species seen in this study) at sites in Enewetak (Colin & Bell, 1991). While Colin & Bell (1991) and this study used necessarily coarse measures of spawning activity, more pronounced patterns of spawning periodicity may be revealed by measuring spawning intensity [*i.e.* number of spawns at a site per unit time; Ross (1983); Sancho *et al.* (2000)] and gonado-somatic indices (West, 1990; Bushnell *et al.*, 2010; Sheaves & Molony, 2013) as well as looking at the behaviour of individuals (Zeller, 1998; Starr *et al.*, 2007) rather than spawning groups as a whole.

Albeit possibly related to lunar patterns, spawning was observed more often on days when species' diel spawning times coincided with higher tides. This may enhance the survival of eggs through distancing them from reef-based planktivores (Johannes, 1978) and limiting the threat of mechanical damage from being washed onto exposed reefs at lower tides. For all the study species, the strongest temporal association was to the restricted species-specific diel spawning periods themselves, the selective advantage of which remains unclear. Despite spawning within the same limited areas, the time of spawning differed substantially among species, with characteristically dawn spawning, afternoon spawning and dusk spawning species within the same site. Similar patterns have been observed in other locations (Colin, 1982; Thresher, 1984; Moyer, 1989; Sancho *et al.*, 2000) and they appear to be widespread among coral reef fishes (Thresher, 1984), especially in areas with limited tidal activity.

Spawning times may be loosely synchronized with specific environmental variables such as high tides that enhance offspring's survival. The fact that there was a broad range of species-specific diel spawning periods among the 41 study species, however, suggests that diel spawning times *per se* may not have evolved to facilitate this synchrony. The difference in spawning times of *C. striatus* both among reefs and among sites within reefs (some as little as 100 m away from one another) further questions whether this timing is adaptive with regard to environmental variables. Spawning times could reflect a species-specific and site-specific trade-off between the risks of predation on spawning adults and their eggs (Robertson & Hoffman, 1977; Kuwamura, 1981; Sancho *et al.*, 2000; Claydon, 2004), factors not assessed in this study. Alternatively, these times could be adapted around the daily needs of the adults (Robertson, 1991*b*): dawn spawning in *A. lineatus* has been hypothesized to minimize the costs that would be incurred from migrating away from their aggressively defended feeding territories at other times of the day (Robertson, 1983). Currently, too little is known about the biology of other species to match their diel spawning periods in a similar fashion.

The timing and location of spawning could benefit spawners for a different reason. They may serve simply as temporal and spatial cues to synchronize spawning (Lobel, 1978; Colin *et al.*, 1987; Colin & Clavijo, 1988; Colin & Bell, 1991). The sites and times of spawning may be of no intrinsic value beyond their clarity as cues to synchronize spawning behaviour among conspecifics. The timing and location could be maintained through tradition (Warner, 1988; 1990; Brown & Laland, 2003). This fits with the patterns displayed by *C. striatus* on the study reefs: individuals appear to migrate repeatedly to only one spawning site, usually the site closest to their feeding areas (Claydon *et al.*, 2012); thus, adjacent sites are maintained within relative short distances of one another by different groups of individuals and spawning times are specific to each site.

Many of the species in this study formed spawning aggregations, but understanding exactly how many is confounded by the problematic and arbitrary nature of defining spawning aggregations (Domeier & Colin, 1997; Claydon, 2004; Domeier, 2012). Albeit questioned by Claydon (2004), widely accepted definitions require an increase in density or numbers of individuals during spawning compared to non-spawning times, by a factor of four (Domeier, 2012), increased from three in the original definition (Domeier & Colin, 1997). All except four species displayed such increases in densities during spawning, but densities above threshold levels were not observed at all sites on all days. For example, at the same spawning site, *C. striatus* spawned at densities ranging from less than background densities on some days up to levels 100 times greater on others. Within all species, there was no noticeable difference in the dynamics of spawning except for the numbers of individuals that migrated to spawn together.

A further complication to whether spawning groups are categorized as spawning aggregations hinges on the minimum number of individuals required to be considered an aggregation (see Fig. 1). During the course of the study, spawning was observed in densities above threshold levels but in solitary pairs for 12 species or in groups of three for 17 species. Of these species, four also spawned in aggregations of 20 or more individuals. In addition, on different days, but within the same site, the number of individuals gathered ranged from three to 200 for *A. lineatus* and seven to 700 for *C. striatus*. A numerical prerequisite based on the word aggregation may only serve to create an arbitrary distinction that separates ecologically identical phenomena. An

additional consideration is that a number of species in this study may have haremic social structures [*e.g.* regal angelfish *Pygoplites diacanthus* (Boddaert 1772), *C. vrolikii* (Thresher, 1982) and whitespotted boxfish *Ostracion meleagris* Shaw 1796 (Moyer, 1989)]. While this characteristic in itself should not preclude species forming spawning aggregations, it has been assumed that increases in densities above threshold levels do not occur in haremic species during spawning (Colin *et al.*, 2003). Such increases in density were observed for the haremic *O. meleagris* and *P. diacanthus*, albeit representing spawning groups of two to three and three to four individuals, respectively. Conventional definitions would determine that some of these reproductive phenomena are spawning aggregations and others are merely spawning events of simple migratory spawners. Basing such distinctions on arbitrary thresholds of density or numbers of individuals may be useful in contexts of management and conservation where maintaining focus on larger groupings of fishes might be more important (Domeier, 2012). With regard to promoting a better understanding of the spawning ecology of reef fishes, however, distinctions with no ecological basis along continua of density and numbers of individuals may not be helpful and perhaps alternative terminology should be developed.

All migratory pelagic spawners observed in the current study displayed characteristics at the resident end of behavioural continua, probably migrating short distances, spawning frequently, year-round and remaining at spawning sites for only a few hours. The absence of transient behaviours can be explained in several ways: (1) there is a relative paucity of such species on Indo-Pacific reefs (Choat, 2012), (2) resident spawning, by definition, occurs considerably more frequently in space and time, (3) there is a greater likelihood that transient spawners migrate away from the study reefs to spawn and (4) because all observations were made using snorkel between dawn and dusk, sampling would have missed any species spawning at greater depths and any species that spawned at night, characteristics probably more typical of transient migratory spawners. Despite the large number of spawning sites found and large number of species observed spawning pelagically, this study almost certainly under-represents both the number of species migrating to spawning sites and the number of sites used in the study area. The majority of these are also likely to be at the resident end of behavioural continua: > 30 additional migratory pelagic spawning species (from Acanthuridae, Caesionidae, Chaetodontidae, Labridae, Lutjanidae, Scaridae, Scorpaenidae, Serranidae and Zanclidae) have been observed on inshore reefs of Kimbe Bay [data from monitoring surveys in Jones *et al.* (2004); J.A.B. Claydon, pers. obs.] and for those with information available almost 80% display typically resident characteristics (Domeier & Colin, 1997; Claydon, 2004; SCRFA, 2012).

In conclusion, this study demonstrates that migrating to spawn pelagically at well-defined sites is a common phenomenon on the inshore reefs of Kimbe Bay, spatially, temporally and with regard to the number of species involved. Predominantly, sites are used by multiple species. Seasonality may differ and the number of species involved will reflect local diversity, but migration to spawning sites is likely to be a similarly common phenomenon on coral reefs throughout the region.

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