Diel and Lunar Variations in Larval Fish Supply in Malindi Marine Park, Kenya

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Abstract — Larval fish supply to reefs influences the structure of adult populations and their response to exploitation. Despite this, few studies have examined patterns of larval fish supply to reefs in the Western Indian Ocean. The temporal variability in fish larval occurrence was thus studied in Malindi Marine Park, Kenya, to assess diel and lunar patterns of larval replenishment. Monthly and 24-hour sampling for fish larvae were undertaken between March 2005 and March 2007. Replicate samples were obtained by towing a 2 m long plankton net (500 μm mesh size, 0.2 m² mouth area) for six minutes within the park. Larval abundance (larvae.100 m⁻³ ± SE) in the park was significantly higher during spring tides (951± 408) than neap tides (394 ± 260). Nocturnal larval abundance was 13-fold greater than daytime concentrations, regardless of tidal regime. The dominant fish families in the larval pool were Engraulidae, Labridae, Blenniidae and Gobiidae. Spectral time-series analysis revealed that larval fish supply occurred in a 30-day cyclical pattern associated with the new moon and was synchronised in the long-term with the northeast monsoon season.

INTRODUCTION

Elucidation of the patterns and processes associated with the supply of fish larvae to habitats is critical to understanding the replenishment and structure of their fish populations (D'Alessandro *et al.*, 2007). Larval supply to habitats is affected by stochastic factors such as chemical, physical and biological oceanographic conditions during planktonic phases (Richards & Lindman, 1987; Kaunda–Arara *et al.*, 2009), and by more deterministic factors such as spawning regimes and seasonal cues (Johannes, 1978; Valles *et al.*, 2001). It is unlikely that biological or physical factors

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will exclusively control variability in the larval supply to reefs. However, larvae have been reported to frequently settle on a cyclical basis, correlated with short-term factors such as lunar cycles or tidal amplitude (Johannes, 1978; Taylor, 1984; Leis, 1993; D'Alessandro *et al.*, 2007; Kaunda-Arara *et al.*, 2009), and with large-scale factors such as inter-annual variability in ocean conditions (Doherty, 1987). In terms of the lunar cycle, greater larval settlement onto reef sites has been associated with new moon phases (Dufour & Galzin, 1993), perhaps as a strategy to avoid predation (Johannes, 1978). Environmental factors such as wind direction and speed can influence larval settlement at different temporal scales (Dufour & Galzin, 1993) and have been reported to affect larval distribution in nearshore habitats (Jenkins *et al.*, 1998). Despite the effects of currents and wind on larval transport, some late-stage larvae of fish are known to actively control their position and dispersal (Leis, 1993).

The composition, structure and timing of fish larval settlement from distant sites on reefs probably influence the population dynamics of the settled adult populations and their response to exploitation. Reefs with a high and diverse supply of fish larvae are likely to be less susceptible to and recover faster from the effects of overfishing (D'Alessandro *et al.*, 2007). Therefore, it is important to understand both the temporal and the spatial scales of larval supply to these habitats. Moreover, larval transport between reef sites influences levels of connectivity and hence the genetic differentiation of reef populations (Sinclair, 1988; Botsford *et al.*, 2009). Despite this, few studies have examined temporal and spatial variability in larval fish supply in the Western Indian Ocean (WIO) (but see Kaunda-Arara *et al.*, 2009). Patterns in larval supply to reefs in the WIO at fine temporal scales are virtually unknown. The temporal variability in fish larval occurrence was thus studied in Malindi Marine Park, Kenya, to assess diel and lunar patterns of larval abundance.

METHODS

Study site

The study was carried out in Malindi Marine Park (Fig. 1), a marine park created in 1968 which is 6.3 km² in extent and includes part of Kenya's continuous nearshore fringing reef and a patch reef system. The park encloses a shallow lagoon with interspersed sand, algae, coral rubble and live coral bommies. Beds of the seagrass *Thalassodendron ciliatum* and isolated coral heads dominated by species of *Porites* and *Galaxea* occur on the upper edges of the east and south-west slopes of the North Reef (Fig.1). Malindi Marine Park is surrounded by a marine reserve (a traditionally-fished area) which has been fished for many years. However, no resource extraction is allowed in the park.

Field sampling

Fish larvae were sampled monthly (March 2005 to December 2006) at stations 1-3 (Fig. 1) using a 2 m long plankton net with a mesh size of 500µm and mouth area of 0.2 m² towed behind a boat at a constant speed of ~1 m.s⁻¹ for six minutes. Three replicate tows were collected during the day at high tide at each station, working from close (1-3 m) to the bottom to just below the water surface at depths ranging from 10-18 meters. A calibrated General Oceanics flowmeter was installed at the center of the mouth of the net to measure volume of seawater filtered. After each tow, samples were preserved in 5% buffered formaldehyde in seawater.

Six 24-hour sampling sessions were undertaken at Station 1 (Fig. 1) to determine diel variation in larval abundance. Sampling was undertaken during neap and spring tides on 15-16 March 2005 (spring tide), 18-19 March 2005 (neap tide), 27-28 May 2005 (spring tide), 29–30 June (neap tide), 24 –25 January 2007 (spring tide) and 29-30 March 2007 (neap tide). The tidal state and amplitude on sampling dates were derived from the Kenya Port Authority tide tables. Tows were
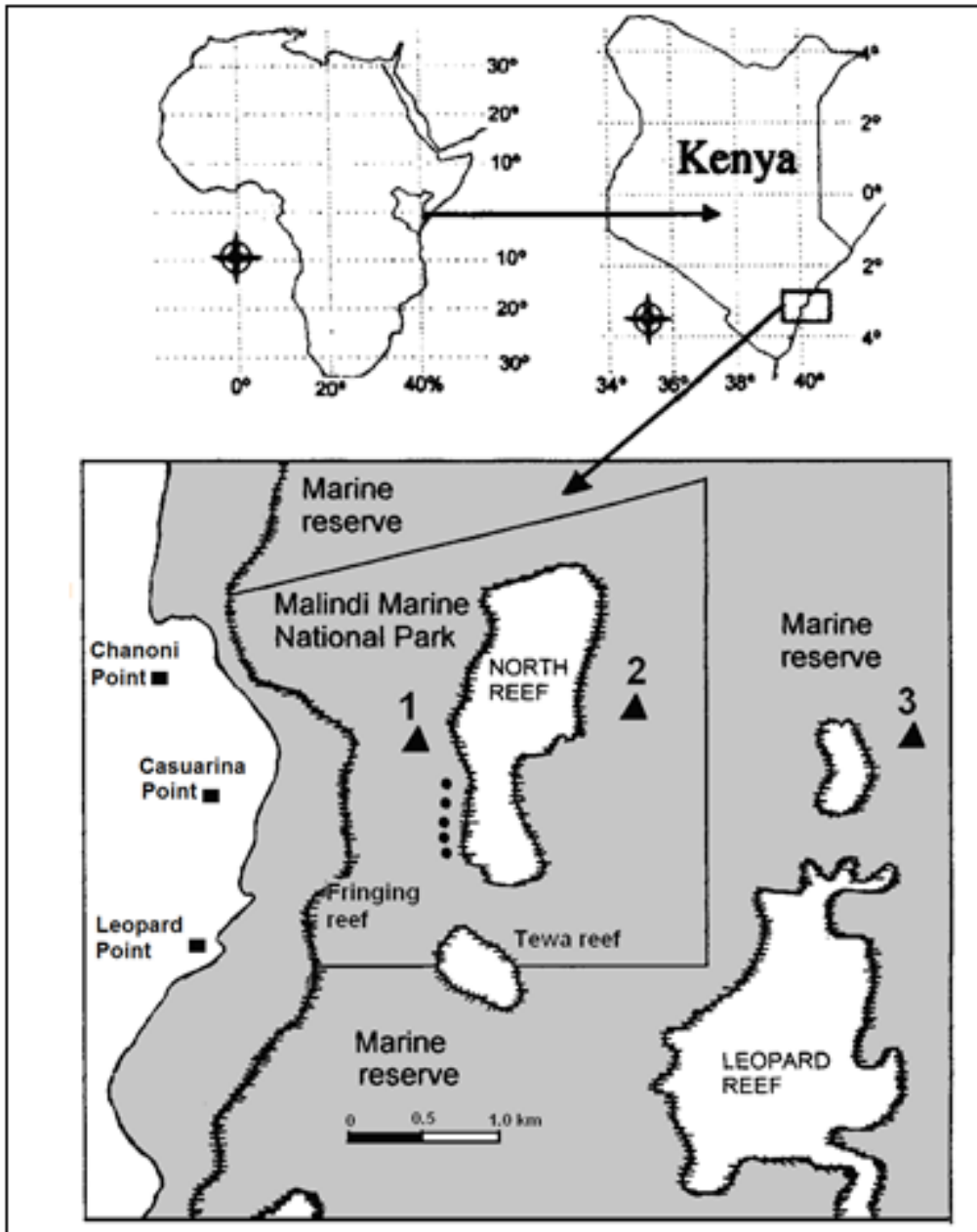
Figure 1. Map of Malindi Marine National Park, Kenya, showing the stations (1-3) sampled monthly for fish larvae and the location of transects for the 24-hr sampling sessions (●).

conducted using the net described above along randomly selected transects parallel to the shore (Fig. 1) at six-hour intervals beginning at 1200 hrs noon to 1200 hrs the next day. A total of five samples were collected from five tows during each sampling session.

All fish larvae were separated from the samples under a Wild Heerbrugg M3C stereo microscope in the laboratory and identified to the lowest taxonomical level using keys provided by Leis and Rennis (1983), Leis and Trnski (1989) and Leis and Carson-Ewart (2000).

Table 1. Differences in mean (±SE) fish larval abundance (larvae.100 m^{-3}), total larvae and development stage (preflexion, pr; flexion, fl; and postflexion, po) between spring and neap tides during six 24-hr sampling sessions in Malindi Marine Park, Kenya. n.d. indicates undetermined species; the t-test compared spring vs neap tides.

| Taxa	Stage	Spring tide		Neap tide		t-test	
		Mean abundance	Total larvae	Mean abundance	Total larvae	t	p
Acanthuridae							
Acanthurus sp.	pr	10 ± 10	50	-	-	-	-
Apogonidae							
Archamia sp.	pr	20 ± 20	100	-	-	-	-
Apogon sp.	pr	8 ± 8	40	28 ± 9	142	-0.66	0.52
Balistidae							
Balistid sp.	pr	1 ± 1	7	-	-	-	-
Blenniidae							
Blenniidae n.d.	pr,fl,po	131 ± 41	465	46 ± 25	230	0.53	0.60
Parablennius sp.		-	-	96 ± 48	482	-	-
Bothidae							
Bothus pantherinus	pr	-	-	4 ± 4	20	-	-
Caesionidae							
Pterocaesio sp.	pr	-	-	6 ± 4	30	-	-
Carangidae							
Caranx sp.	pr	-	-	2 ± 2	4	-	-
Scomberoides sp	fl	-	-	2 ± 2	11	-	-
Dactylopteridae							
Dactyloptena sp.	pr	-	-	2 ± 2	2	-	-
Engraulidae							
Stolephorus commersonii	pr,fl,po	360 ± 252	1802	117 ± 84	533	0.71	0.49
Gerreidae							
Gerres sp.	pr	1 ± 1	4	-	-	-	-
Gobiidae							
Amblygobius sphynx	po	1 ± 1	7	7 ± 7	33	-1.43	0.17
Gobiidae n.d.	pr,fl,po	31 ± 18	157	18 ± 14	73	-0.17	0.87
Haemulidae							
Pomadysis maculatum	pr,fl	5 ± 5	25	-	-	-	-
Labridae							
Labridae n.d.	pr,fl,po	215 ± 215	1075	1 ± 1	6	-	-
Lethrinidae							
Lethrinus sp.	pr	2 ± 2	8	7 ± 7	33	-1.36	0.19
Lutjanidae							
Lutjanus argentimaculatus	pr	2 ± 2	8	1 ± 1	5	-0.66	0.51
Monocanthidae							
Monacanthus ciliatus	pr	1 ± 1	7	4 ± 4	20	1.13	0.27
Aluterus scriptus	pr	2 ± 2	8	-	-	-	-
Nemipteridae							
Nemipteridae n.d.	pr	-	-	3 ± 3	13	-	-
Platycephalidae							
Thysanophyrs arenicola	fl	1 ± 1	2	-	-	-	-
Platycephalidae n.d.	fl	-	-	1 ± 1	7	-	-
Pomacentridae							
Chromis sp.	pr	5 ± 5	25	-	-	-	-
Abudefduf sp.	pr,fl	-	-	22 ± 20	108	-	-
Pomacanthidae							
Pomacanthidae n.d.	pr	2 ± 2	8	-	-	-	-
Scaridae							
Leptoscarus vaigiensis	pf,fl,po	100 ± 100	500	-	-	-	-
Calotomus sp.	pr	3 ± 3	13	-	-	-	-
Scaridae n.d.	pr	-	-	6 ± 5	30	-	-
Siganidae							
Siganus sutor	pr	20 ± 20	100	-	-	-	-
Siganus canaliculatus	pr,po	7 ± 7	33	4 ± 4	20	0.64	0.53
Sparidae							
Sparidae n.d.	pr	-	-	4 ± 4	20	-	-
Sphyraenidae							
Sphyraena barracuda	po	11 ±10	57	-	-	-	-
Sphyraena jello	fl,po	10 ± 10	50	2 ± 2	4	1.93	0.07
Sygnathidae							
Coryoichthys sp.	pr	1 ± 1	3	1 ± 1	4	-	-
Sygnathidae n.d.	fl	-		9 ± 3	47	-	-
Tetraodontidae							
Arothron sp.	pr	2 ± 2	8	-	-	-	-
Totals		951 ± 408	4562	394 ± 260	1890	2.10	0.03

a)

b)
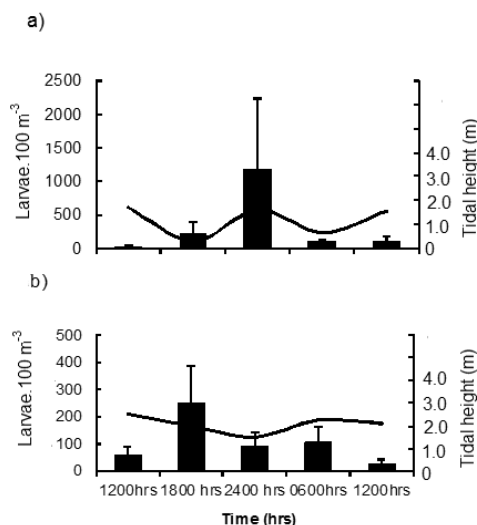
Figure 2. Diel variation in mean fish larval abundance (vertical bars represent the SE) with tidal heights for six 24-hr sampling sessions during a) spring tides and b) neap tides in Malindi Marine Park, Kenya.

Data analysis

Data from all three stations were pooled to represent monthly supply of larvae into the park environment as no significant difference was detected in the monthly larval abundance between stations (2 way-ANOVA, F = 1.62, p = 0.198). The data were standardised according to the volume of water sampled to obtain larval abundance per day. The total daily abundances were then averaged to obtain mean daily abundances (larvae.100 m^{-3}) which were then subjected to time-series spectral analysis to examine fine-scale temporal variations of larval abundance in the park (Taylor, 1984). In addition, Autocorrelation Function (ACF) plots were used to validate significant periodicities identified by the power spectra (Platt & Denman, 1975; Taylor, 1984).

The numbers of larvae collected in the 24-hour sampling regime were also standardised (number of larvae.100 m^{-3}). The data were Log$_{10}$ (x+1) transformed to stabilise the variance caused by zero values and the unpredictable occurrence of rare species. The data were grouped according to season (NE and SE monsoon) and time of day (day or night) and a two-factor ANOVA was used to examine for seasonal or diel variation. Factor analysis was used to describe the relationship between tidal height and larval abundance. Statistical analyses followed Zar (1999).

RESULTS

Diel cycles

A total of 394 larvae were collected from the six 24-hour samples, comprising 39 species in 27 families (Table 1), mainly Blennidae, Gobiidae, Engraulidae, Labridae and Scaridae in a complete range of stages (principally preflexion, but also flexion and postflexion; Table 1). During neap tides, *Stolephorus commersonii* (Engraulidae), an *Apogon* sp. (Apogonidae), *Parablennius* sp. (Blenniidae) and a *Gobiidae* sp. (not determined, n.d.) dominated the park samples, while Stolephorus commersonii, *Leptoscarus vaigiensis* (Scaridae), Labridae n.d. and *Parablennius* sp. were the dominant larvae during spring tides. The total mean abundance (100 m^{-3} ± SE) of larvae in the park was significantly higher during spring tides (951 ± 408) than neap tides (395 ± 261; t = 2.02, p < 0.05; Table 1).

During spring tides, the mean larval abundance (100 m^{-3} ± SE) increased from 205.3 ± 197 at 1800 hrs to a peak of 1 184 ± 1060 at 2400 hrs (Fig. 2a). Larval abundance

Species	Season		Time of day		Season and time of day	
	F	p	F	p	F	p
Total catch	0.575	0.455	1.771	0.195	2.003	0.169
Stolephorus commersonii	2.014	0.168	2.504	0.126	2.341	0.138
Blenniidae n.d.	3.520	0.124	0.801	0.378	1.198	0.283
Gobiidae n.d.	0.06	0.806	2.41	0.132	0.03	0.851

was lowest in the park at 1200 hrs (26.0 ± 13.3) during spring tides (Fig. 2a). During neap tides, the mean larval abundance (100 m^{-3} ± SE) increased from 57.1 ± 47.4 at 1200 hrs to a peak of 246.3 ± 210.4 at 1800 hrs (Fig. 2 b). Thereafter, the larval occurrence in the park declined to levels of 90 ± 50.8 and 103 ± 68.1 at 2400 and 0600 hrs, respectively. No significant effects of season (p = 0.455), time of day (p =.195) or their interactions (season x time of day; p= 0.169) were found on larval abundance in the park (Table 2). Similarly, no significant effect season or time of day were found on the occurrence of the most abundant taxa, *Stolephorus commersonii* (p = 0.168 and p = 0.126), Gobiidae n.d. (p = 0.806 and p = 0.132) and Blennidae n.d. (p = 0.124 and 0.378)

The larval supply of the dominant species (e.g. *Stolephorus commersonii*, Labridae n.d. *Parablennius* sp. and Gobiidae n.d.) to the park was highest during nocturnal spring tides (2400 hrs; Fig. 3), suggesting that these larvae entered the park mostly under these conditions. However, during daytime spring tides, the abundance of most species was low except for the *Parablennius* spp. at 0600 hrs (Fig. 3). During neap tides, larvae of these species were almost absent during the day and appeared at night in comparatively low numbers (Fig. 3). The cardinalfish, *Apogon* sp., was not caught during spring tides most of the time except at 0600 hrs. However, during neap tides, this species, unlike the others, was more abundant during the day at 1200 hrs and
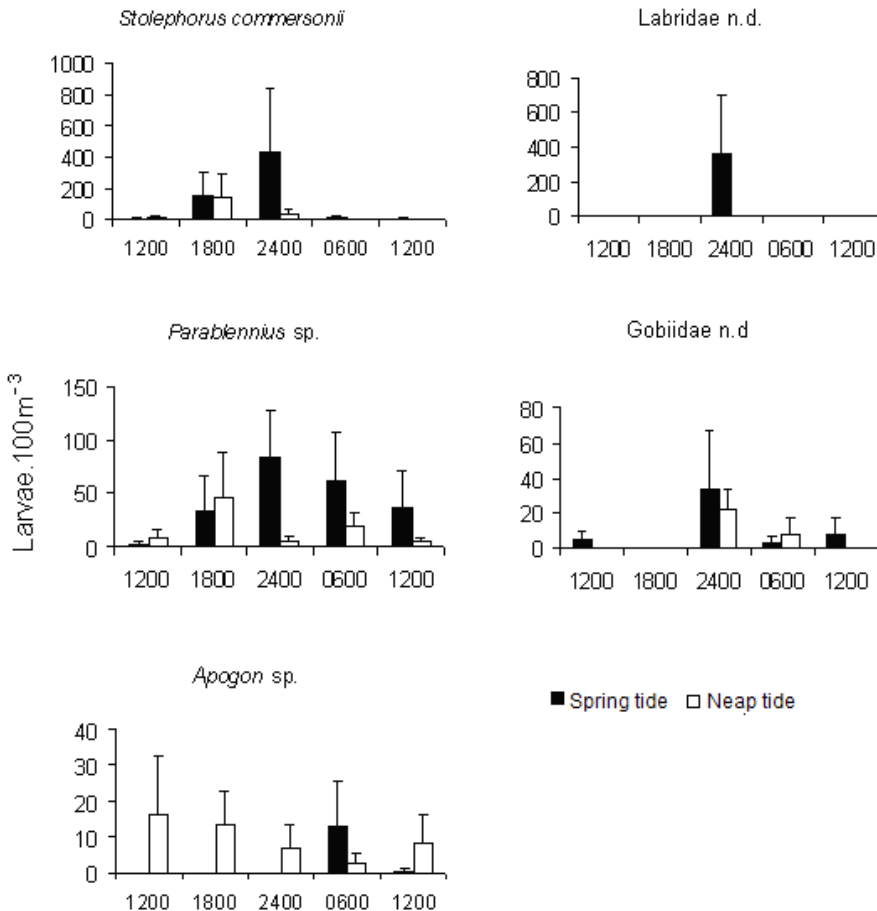

Figure 3. Diel variation in abundance (vertical bars represent the SE) of the dominant fish larval species collected during six 24-hr sampling sessions in Malindi Marine Park, Kenya.

at 1800 hrs (Fig. 3). Larval abundance was positively correlated with tidal height (r = 0.58), suggesting that larvae used high tides to enter the park.

Lunar patterns

The number of larvae sampled during new moon periods (2 886 larvae) was higher than during the full moon periods (2 824 larvae). However, no significant differences in mean larval abundance were detected between the two lunar periods for the comparable sample sizes of 204 and 200 tows during the new and full moon periods respectively (t = 1.84, p = 0.066). Spectral analysis of total larval (all families) and dominant species data revealed that peak larval supply occurred in a 25-30 days cycle, as shown in the spectral analysis periodiogram

(Fig. 4). This observation was corroborated by the Autocorrelation Function plot (ACF) that revealed a significant peak in larval arrival at 30-day intervals (p <0.05; Fig. 4).

The Blenniidae n.d. manifested a major peak in larval abundance at 30 days and a minor peak at 15 days with significant activity in the AFC plot at 30-day intervals (Fig 5). This pattern is suggestive of a lunar and semi-lunar frequency in its larval supply to the park. The *Stolephorus commersonii* larvae also manifested a strong peak in larval abundance in the park at 30-day intervals, and a minor peak at 27 days; the 30-day cycle again being confirmed by the ACF plot (Fig. 6). Finally, the Gobiidae n.d. larvae manifested some evidence of a similar pattern to the preceding in its abundance in the park (Fig. 7).
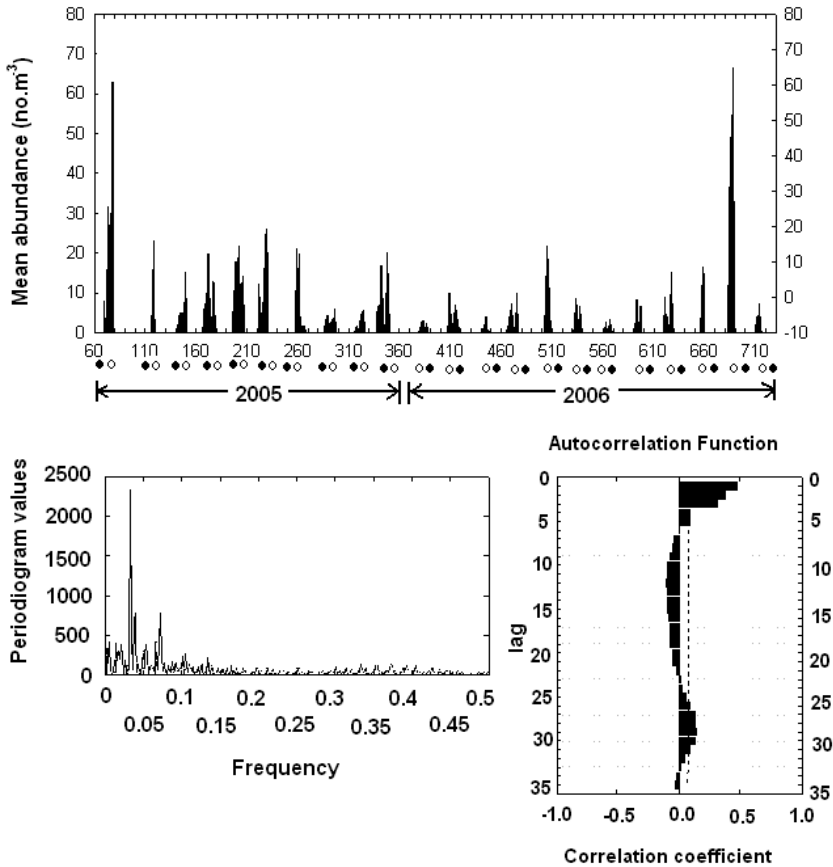

Figure 4. Time-series of mean total fish larval abundance from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.
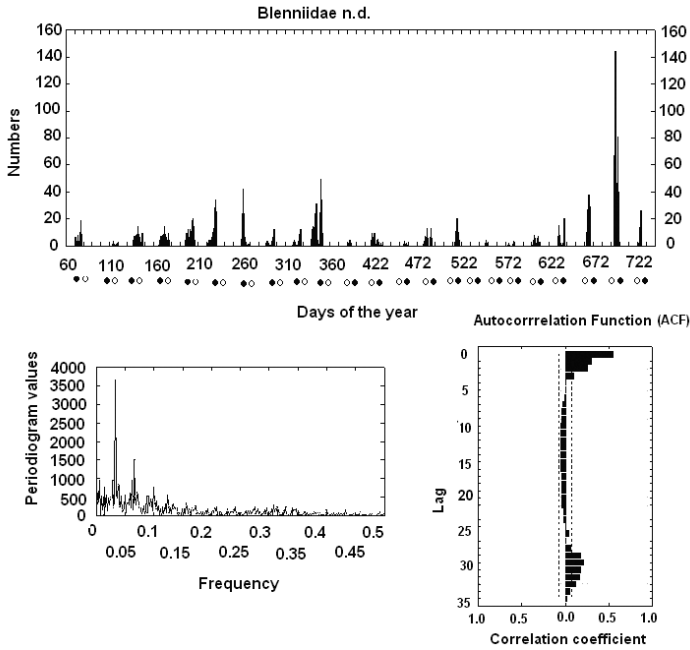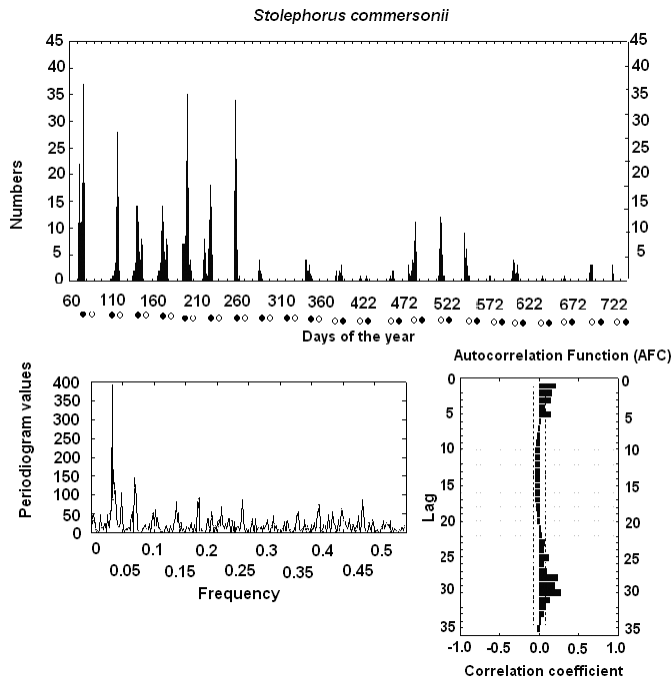
Figure 5. Time-series of larval abundance of a *blenniid* sp. from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph;   = full moon and   = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.
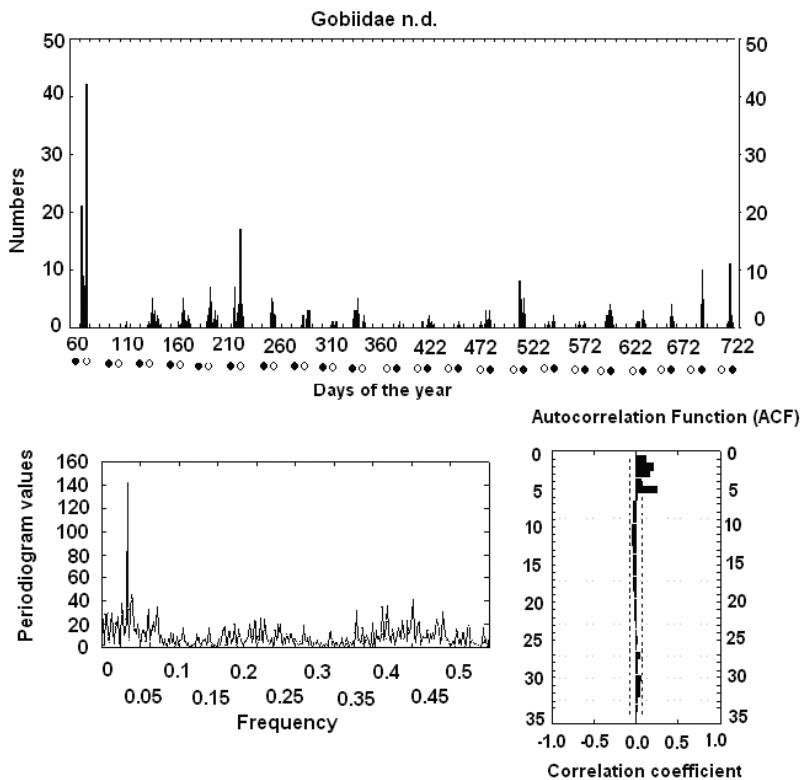

Figure 6. Time-series of larval abundance of *Stolephorus commersonii* from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph;   = full moon and   = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.

Figure 7. Time-series of larval abundance of a *gobiid* sp. from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.

DISCUSSION

The supply of fish larvae to Malindi Marine Park seems to be both diel and lunar in pattern. Overall, greater numbers of larvae entered the park at night compared to the day, with evidence of lunar periodicity. Larval abundance was highest at 2400 hrs during spring tides, with abundances being twice that of neap tides and about 13 times more in the night compared to the day for a given tidal regime. It has been hypothesised that larvae are predominantly spawned or dispersed during the night or new moon to reduce the risk of mortality from visual predators (Johannes, 1978; Taylor, 1984; Dufour & Galzin, 1993). Additionally, it is likely that olfactory and sound cues for dispersal and settlement onto reefs may be more enhanced at night (Kingsford *et al.*, 2002; Wright *et al.*, 2005).

Among species with pelagic eggs and oceanic larvae (e.g. *Stolephorus commersonii* and the Labridae n.d. found in this study), a possible strategy in reproduction is to time spawning to coincide with the ebb of spring tides to maximise the offshore tidal transport of larvae to reduce predation (Johannes, 1978). Among demersal spawners (e.g. the *Parablennius* sp., Gobiidae n.d., *Apogon* sp. found in this study), hatching is similarly believed to occur predominantly at dusk or at night to prevent predation (Johannes, 1978; Dufour & Galzin, 1993). The presence of all stages of larvae in the families Gobiidae, Blennidae, Engraulidae, Labridae and Scaridae in this study suggested that they completed their pelagic larval phase within the lagoon (Mwaluma, 2010; Pattrick & Strydom, 2008).

In this study, fish larval abundance was cued to lunar phases in cyclical patterns of 30 days (with a semi-lunar peak in the Blenniidae). If larval supply was cued entirely to lunar or tidal cycles, then two peaks (pulses) in larval supply would occur in the park every month. However, sampling effort in this study had to be concentrated in the second half of the month for logistical reasons, thus missing potential semi-lunar peaks. The dominant species of larvae (Blenniidae n.d., *Stolephorous commersonii* and Gobiidae n.d) nevertheless manifested a synchronous abundance at 28-30 days, indicating similarities in factors that regulated their larval supply in the park. These results are similar to those reported by D'Alessandro *et al.* (2007) in the Florida Keys where the fish larval abundance peaked between 21 and 30 days. Factors related to the arrival of pre-settlement larvae at reef sites in different lunar phases have been associated with adult spawning behaviour (Taylor, 1984; Robertson, 1991; D'Alessandro *et al.*, 2007), larval behaviour (Thorrold *et al.*, 1994), spawning prior to recruitment (McIIwain, 2003) and passive delivery by currents (D'Alessandro *et al.*, 2007). However, in this study, data were lacking to determine whether there environmental regulators determine lunar-based supply of fish larvae to the park.

Spectral analysis nevertheless revealed that larval fish supply to the park at a temporal scale is significant within a narrow diel and lunar period or window; this may be linked to environmental productivity (Johannes, 1978; Cushing, 1987), favourable oceanic conditions (McClanahan, 1988) and increased spawning activity (Mwaluma *et al.*, 2011).

Larval fish supply to Malindi Marine Park thus appears to be influenced by lunar cycles with larvae arriving in the park in cycles of 30 days within a narrow window. The larvae displayed a tidally-induced diel, peak abundance during spring tides at midnight, suggesting a behavioural component in their replenishment. These results are useful for modelling of their dispersal and recruitment, needed to elucidate the population dynamics of coral reef fish communities.

References

Botsford LW, Coffroth MA, Jones GP, Paris CB, Planes S, Shearer TL, Thorrold SR, White JW (2009) Measuring connectivity and estimating resilience of coral reef metapopulations in MPAs: matching empirical efforts to modelling needs. Coral Reefs 28: 327-337

Cushing DH (1987) Population biology and the management of fisheries. Trends Ecological Evolution 2: 138-139

D'Alessandro E, Sponaugle S, Lee T (2007) Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. Marine Ecology Progress Series 331: 85-100

Doherty PJ (1987) Light - traps: selective but useful devises for quantifying the distributions and abundances of larval fishes. Bulletin of Marine Science 41: 423-431

Dufour V, Galzin R (1993) Colonisation patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. Marine Ecology Progress Series 102: 143-152

Jenkins GP, Welsford DC, Keough M, Hamer PA (1998) Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctuate* in relation to feeding and vertical distribution of prey in a temperate bay. Marine Ecology Progress Series 170: 239-248

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes 3: 65-84

Kaunda-Arara B, Mwaluma J, Gamoe A, Oresland V, Osore M (2009) Temporal variability in fish larvae supply to Malindi Marine Park, coastal Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems 19: S10-S18

Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70: 309-340

Leis J M, Rennis DS (1983) The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Kensington, Australia, 268 pp

Leis J M, Trnski T (1989) The Larvae of Indo-Pacific Shore fishes. New South Wales University Press, Kensington, Australia, 372 pp

Leis JM (1993) Larval fish assemblages near indo-Pacific coral reefs. Bulletin of Marine Science 53: 362-392

Leis JM, Carson-Ewart BM (2000) The larvae of Indo-Pacific coastal fishes. An identification guide to marine fish larvae. Fauna Malesiana Handbooks 2, EJ Brill, Leiden, 870 pp

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199

McIIwain JL (2003) Fine-scale temporal and spatial patterns of larval supply to fringing reef in Western Australia. Marine Ecology Progress Series 252: 207-222

Mwaluma JM, Kaunda-Arara B, Rasowo J, Osore MK, Øresland V (2011) Seasonality in fish larval assemblage structure within marine reef National Parks in coastal Kenya. Environmental Biology of Fishes 90: 393-404

Pattrick P, Strydom NA (2008) Composition, abundance, distribution and seasonality of larval fishes in the shallow nearshore of the proposed Greater Addo Marine Reserve, Algoa Bay, South Africa. Estuarine, Coastal and Shelf Science 79: 251-262

Platt T, Denman KL (1975) Spectral analysis in ecology. Annual Review of Ecology, Evolution and Systematics 6: 189-210

Richards WJ, Lindeman KC (1987) Recruitment dynamics of reef fishes: Planktonic processes, settlement and demersal ecologies, and fishery analysis. Bulletin of Marine Science 41: 392- 410

Robertson DR (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale PF (eds) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, USA, pp 356-386

Sinclair M (1988) Marine populations: An essay on population regulation and speciation. University of Washington Press, Seattle, Washington, 252 pp

Taylor MC (1984) Lunar synchronization of fish reproduction. Transactions of the American Fisheries Society 113: 484-493

Thorrold SR, Shenker JM, Mojica R, Maddox ED, Wishinski E (1994) Temporal patterns in the larval supply of summer-recruitment reef fishes to Lee stocking Island, Bahamas. Marine Ecology Progress Series 112: 75-86

Valles H, Sponaugle S, Oxenford HA (2001) Larval supply to a marine reserve and adjacent fished area in the Soufriere Marine Management Area, St Lucia, West Indies. Journal of Fish Biology 59: 152-177

Wright KJ, Higgs DM, Belanger AJ, Leis JM (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). Marine Biology 147: 1425-1434

Zar JH (1999) Biostatistical analysis. 4th Edition, Prentice Hall Inc., Upper Saddle River, NJ, USA, 931 pp