

Seasonality in fish larval assemblage structure within marine reef National Parks in coastal Kenya

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Abstract Variability of larval assemblages within marine habitats has an effect on population structure of adults, and on patchiness of populations in space and time. However, despite this effect, few studies have examined this variability in the Western Indian Ocean (WIO) especially in relation to marine park boundaries. In this study, we tested the hypothesis that seasonality and biophysical variables influence fish larval assemblage structure within two of the oldest marine parks in Kenya of differing reef structure. Monthly samples were obtained from the parks using oblique plankton tows for 14–24 months. A total of 38 families and 52 genera of fish larvae were obtained from Malindi Marine Park, while 20 genera in 20 families were sampled from the more enclosed Watamu Marine Park but with a connection to an estuarine system. The preflexion larvae comprised

over 80% of the total larvae in the parks with the dominant groups being; Gobiidae, Blenniidae, Engraulidae and Apogonidae. The availability of a wide size range of larvae for some groups like Blenniidae, Gobiidae, Engraulidae, Labridae and Scaridae indicated the possibility of some larvae completing their pelagic phase within the parks. Larval densities differed significantly between seasons and stations in both parks, with higher densities ranging between 95–311 larvae/100 m³ during the calm northeast monsoon (NEM) season, compared to 5–58 larvae/100 m³ during the stormy southeast monsoon (SEM) season. Stepwise multiple regression analysis indicated a significant positive influence of zooplankton density on fish larval abundance in Malindi Park, while a positive and significant influence of temperature was found in Watamu Park. Distinct assemblages of larvae occurred within the parks indicating within park patchiness in larval distribution and, perhaps existence of retention features. These results provide useful baseline data on larval distribution in the WIO, and will be useful in understanding population dynamics of adult populations when complimented with additional oceanographic data.

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Introduction

Larval assemblages are spatially and temporally dynamic with variations in structure occurring

horizontally and vertically at variable scales (Leis 1991). Many fish larval assemblages undergo temporal changes in composition, particularly on a seasonal basis with distinct taxa and groups showing intra-annual peaks (Gray and Miskiewicz 2000). While seasonal changes in the structure of assemblages are a common feature in the tropics (Johannes 1978; Leis 1993; Kaunda-Arara et al. 2009), the factors that regulate these changes are diverse. Physical oceanographic processes are highly influential in regulating the distribution of pelagic fish eggs and larvae (Harris et al. 1999; Muhling and Beckley 2007). Hydrographic features and circulation patterns such as upwelling, tidal and coastal fronts or wind-driven mixing, influence larval survival and contribute to formation of distinct larval assemblages at sites (Sanvicente-Anorve et al. 1998; Cowen 2002; Sampey et al. 2004; Muhling and Beckley 2007). Other processes which contribute to spatial and temporal variation in larval assemblages include spawning activity of adult fish (Leis 1993; Gray and Miskiewicz 2000; Nonaka et al. 2000), larval behavior (Leis 1993; Tzeng and Wang 1993), and seasonal changes in water conditions (e.g. temperature, salinity and turbidity) (Harris et al. 1999).

In coastal East Africa, the annual migration of the Inter Tropical Convergence Zone (ITCZ) causes two distinct monsoon seasons which affect the physical, chemical and biological processes of coastal waters. The northeast monsoon season (NEM) occurs from November to March, and the southeast monsoon (SEM) from April to October (McClanahan 1988). The SEM is characterised by high cloud cover, rain, wind energy and decreased temperatures and light, while the NEM season brings warmer waters, a shallow thermocline, calm conditions and higher salinities. Current speeds along the coast are affected by wind patterns, downwelling is strongest during the SEM but breaks down during the NEM when the current direction reverses (McClanahan 1988). Due to high temperatures and the stable nature of the waters during the NEM, high phytoplankton and zooplankton are reported in coastal waters (Bryceson 1982; Kimaro 1986; Okemwa 1990; Mwaluma 1997; Osore et al. 2004). The influence of this oceanographic variability on ichthyoplankton has received scanty attention in Eastern Africa.

The community structure of adult fish assemblages are well described in coastal Kenya (McClanahan and Kaunda-Arara 1996; McClanahan and Graham 2005)

and, most of the Western Indian Ocean (WIO) (Jiddawi and Stanley 1999). However, studies on seasonality in biological systems have mainly been restricted to zooplankton communities (e.g., Reay and Kimaro 1984; Mwaluma 1997; Mwaluma et al. 2003 and Osore et al. 2004) with limited work on fish larvae (Little et al. 1988; Kaunda-Arara et al. 2009). In this study, we describe the seasonal patterns in fish larval assemblages in two of the oldest marine parks in Eastern Africa (Malindi and Watamu, created, 1968), and relate assemblage structure to biophysical factors.

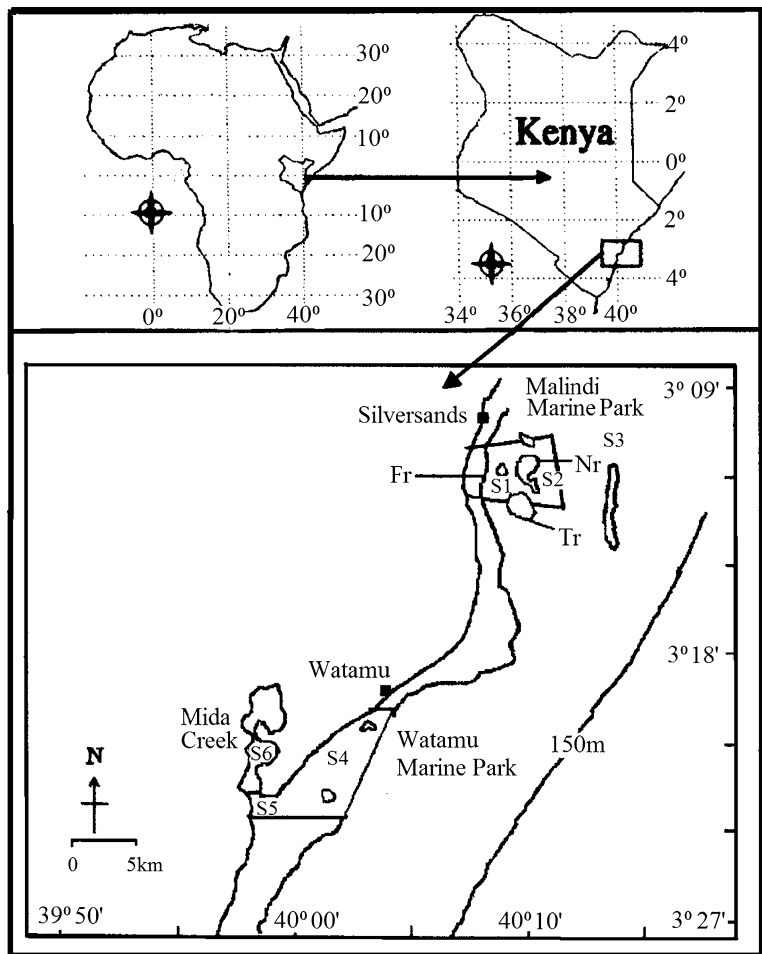
Materials and methods

Study area

The present research was done in Malindi (6.3 km²) and Watamu (10 km²) National Marine Parks (Fig. 1). Kenyan marine parks provide coral reefs with total protection from extractive exploitation, while adjacent areas designated as “reserves” receive limited protection from fishing. Both parks enclose lagoons with low and uniform topography dominated by mosaic of seagrass beds interspersed with varying cover categories (Kaunda-Arara and Rose 2004). Malindi Marine Park consists of a complex of reef platforms that are exposed to open waters. A patch reef system is located within the park approximately 1 km from shore. The park is surrounded by a marine reserve that has been fished for many years that extends to Watamu Park on the southern border. Watamu Marine Park is situated about 25 km south of Malindi Marine Park (Fig. 1). The Park has a near-shore fringing reef, enclosing a massive lagoon with conspicuous islands surrounded by patch reefs of flat eroded inner reef. The tidal cycle in both parks are mixed semi-diurnal with two maxima and two minima per day (Brakel 1982). The tidal range in the parks is about 2.0 m at neap tides and 2.9 m during spring tide.

In Malindi Marine Park, samples were collected from three stations; S1, S2 and S3 (Fig. 1). S1 was located within the shallow (10–12 m) park lagoon about 1 km from the shoreline. S2 was located in a back-reef site that is deeper (15–20 m). Station S3 was an offshore station 6 km from the shoreline and mostly consisting of a shallow reef platform (10–12 m). In Watamu, samples were collected from three

Fig. 1 A map of coastal Kenya showing location of sampling stations in Malindi (S1-S3) and Watamu (S4-S6) Marine Parks. (Nr, North reef; Fr Fringing reef; Tr, Tewa reef)



stations; S4, S5 and S6 (Fig. 1). S4 was a lagoonal seagrass station with patches of live corals and located 500 m from the shoreline with a high tide depth of about 10 m. S5 was located at the mouth of a creek (Mida Creek), connecting to the park and underlaid by a shallow (3–5 m) seagrass bed. S6 was located inside the creek, about 500 m from the creek mouth, with a depth of about 7 m during high tide.

Field procedures

In Malindi, fish larvae samples were collected for 24 months from March 2005 to March 2007 while, in Watamu sampling was done for 14 months from January 2006 to March 2007. Monthly plankton tows were carried out during high tides using a 2 m long, 500 µm mesh size plankton net with a mouth area of 0.2 m². At each station within the parks, three

replicate tows were made obliquely from close to the bottom (1–3 m) to just below the water surface at a boat speed of about 1 m·s⁻¹ each lasting 6 min. A calibrated General Oceanics flowmeter was installed at the center of the mouth of the net to estimate volume of seawater sampled. An average of 45 m³ of seawater was filtered per tow. After each tow, samples were preserved in 5% buffered formaldehyde in seawater. Surface water temperature and salinity were measured using an Aanderaa instruments (Norway) temperature-salinity sonde (display unit 3315). Surface water chlorophyll ‘a’ (mg·l⁻¹) was measured using Strickland and Parsons (1972) method.

In the laboratory, the monthly plankton samples were observed under a Wild Heerbrugg M3C stereo microscope, and all fish larvae were isolated and identified to genus level using keys from Leis and Rennis (1983), Leis and Trnski (1989) and Leis and Carson-Ewart (2000). Size (mm) and developmental stage of each larvae (e.g.,

preflexion, flexion and post flexion) was measured and determined according to Leis and Rennis (1983) and Leis and Carson-Ewart (2000). The remaining zooplankton in the samples were used to estimate monthly zooplankton density (numbers/m³) in the parks.

Data analyses

Prior to analysis, all data sets were log₁₀ ($x+1$) transformed to fulfill the homoscedasticity and normality requirements for parametric statistical procedures. Stepwise multiple regression analysis was used to determine the sub-set of environmental variables (temperature, salinity, chlorophyll-a and zooplankton density) that explained the greatest variability in larval abundance in each park. Density was expressed as larvae/100 m³ for fish larvae, and numbers/m³ for zooplankton. The interaction between season and station in influencing larval abundance was tested using a 2-way ANOVA. Data were grouped and analyzed according to the two seasons (NEM and SEM). Monthly data were considered as replicates in each season. For those variables differing significantly among factors, Tukey's Honestly Significant Difference (HSD) test was performed to identify the significantly different means. Cluster analysis based on group average linkage with Bray-Curtis measure of similarity was used to examine the associations of dominant family groups based on log transformed larval densities within each site. Statistical analysis was performed using STATISTICA version 6.0 software.

Results

Taxonomic composition

In Malindi Marine Park, a total 4017 fish larvae belonging to 38 families and 52 genera were sampled during the study. The larval pool in this park was dominated by the preflexion larvae (83.6%), with the flexion and postflexion stage larvae comprising 11.5 and 4.9% of all larvae, respectively. The dominant species during both NEM and SEM seasons were larvae from non-pelagic shore fishes including Blenniidae (*Parablennius* sp., Blenniid sp., and *Exallias* sp.) and Gobiidae (*Microgobius* sp. and Gobiid sp.) (Table 1). The family Engraulidae (e.g., *Stolephorus* sp.) dominated the pelagic larval pool. In Watamu

Marine Park, a total of 2296 larvae belonging to 21 families and 20 genera were sampled. Similar to Malindi, this park was also dominated by preflexion stage larvae (87.3%) with relatively smaller proportions of the flexion (5.9%) and postflexion (6.8%) stage larvae. Fish larvae mainly from the families Blenniidae, Gobiidae, Engraulidae, Labridae, Scariidae and Pomacentridae, were available in a complete range of stages (preflexion, flexion and postflexion) in this park (Table 1). However, some species were either available in preflexion (e.g. *Archamia* sp., *Carangoides* sp., *Myripristis* sp., *Haliophores* sp., *Xyrichtys* sp., *Lethrinus* sp., *Lutjanus* sp., *Parupeneus* sp.) or postflexion (e.g. *Cheilodipterus* sp., *Gnathodon* sp., *Drepane* sp., *Scolopsis* sp.) stages (Table 1).

Biophysical parameters

Peaks in zooplankton density, temperature and salinity, occurred during the NEM months in both parks during 2005 and 2006 (Fig. 2). Chlorophyll-a however was, highest during the SEM months (August and September) of 2006 (Fig. 2). In Malindi Park, stepwise multiple regression analysis of environmental variables on larval abundance indicated a significant relationship between larval abundance and zooplankton density ($t=0.45$, $p=0.012$), however, there was lack of significant relationship between larval abundance and salinity ($t=-1.28$, $p=0.203$). In Watamu, a significant relationship of larval abundance with temperature was found ($t=2.50$, $p=0.01$).

The mean water temperature and salinity were significantly higher (ANOVA, $p<0.05$) during the NEM compared to the SEM season (Table 2). Similarly, significant differences (ANOVA, $p<0.05$) in temperature and salinity occurred between stations, with lower mean monthly temperatures in the outer oceanic stations (S3) as compared to inshore ones (S1, S2, S5) while the reverse was true for salinity (Tukey HSD test, Table 2). Significant interaction effects of season and station on larval densities were found, indicating that the factors had conditional influence on larval abundance.

Seasonal variation in larval density

Larval density in Malindi Park peaked during the NEM season (March and December) ranging between 95–311 larvae/100 m³ compared to 9–58 larvae/100 m³ during the SEM season (Fig. 2). Similarly,

Table 1 Taxa composition, mean density (larvae/100 m³), size (mm) and development stage (preflexion-pr, flexion-fl and postflexion-po) of fish larvae from Malindi and Watamu Marine Parks during the southeast (SEM) and northeast (NEM)

monsoon seasons. (Spawning mode (SM) given as: *P*=Pelagic; *N*=non-pelagic; Un = Unknown, and Dev. Stage after Leis and Rennis 1983, Leis and Trnski 1989)

Taxa	SM	Malindi Marine Park				Watamu Marine Park				
		Size (mm)	Dev. Stage	Mean density		Size (mm)	Dev. Stage	Mean density		
				SEM	NEM			SEM	NEM	
Atherinidae										
<i>Hypoantherina</i> sp.	N	3–5	fl	–	–	6–11	fl,po	0.7±0.7	1.5±1.5	
Apogonidae										
<i>Apogon</i> sp.	N	2–13	pr,fl,po	43.3±17.1	63.8±34.9	3–14	pr,fl,po	11.3±6.1	0.5±0.5	
<i>Archamia</i> sp.	N	2–3	pr	70.7±37.4	9.1±3.2			–	–	
<i>Cheilodipterus</i> sp.	N	8	po	0.0	1.4±1.4			–	–	
Balistidae										
Balistid sp.	N	2–3	pr	2.1±1.8	0.7±0.7			–	–	
Blenniidae										
<i>Entomacrodus</i> sp.	N	2–5	pr	12.6±5.1	1.2±1.1			–	–	
Blennid sp.	N	2–14	pr,fl,po	8.7±2.6	120.3±61.7	2–3	pr	0.4±0.4	12.4±9.0	
<i>Parablennius</i> sp. 1	N	2–4	pr	6.8±3.1	3.8±3.6	13	po	29.1±21.3	42.6±37.5	
<i>Parablennius</i> sp. 2	N	2–5	pr	145.2±64.3	369.6±162.0	2–11	pr,fl,po	5.9±5.5	1.7±1.7	
<i>Exallias</i> sp.	N	2–6	pr,fl	51.5±24.7	22.9±12.7	2–3	pr	7.1±5.6	6.0±4.5	
<i>Omobranchus</i> sp.	N	2–3	pr	0.0	0.4±0.4	2–9	pr,fl,po	116.1±61.4	45.6±29.8	
Bothidae										
<i>Engyprosopon</i> sp.	P	2–6	pr,fl,po	4.2±2.7	1.6±1.2			–	–	
Bythtidae										
<i>Dinematichthys</i> sp.	N	2–8	pr,fl,po	2.2±1.1	2.2±2.1			–	–	
Caesionidae										
<i>Pterocaesio</i> sp.	N	2–24		3.6±2.3	5.6±3.6			–	–	
Carangidae										
<i>Caranx</i> sp.	P	2–7		10.1±2.4	22.4±12.9	3–4	pr	0.5±0.5	0.0	
<i>Scomberoides</i> sp.	P	3–7		0.9±0.5	4.7±3.1					
<i>Gnathodon</i> sp.	P	24–48		1.9±1.8	15.9±8.0	30–36	po	1.9±1.0	1.9±1.2	
<i>Elagatis</i> sp.	P	7		0.5±0.5	2.5±1.6			–	–	
<i>Carangoides</i> sp.	P	3–5	pr	1.9±1.1	12.9±7.7			–	–	
Centriscidae										
Centriscid sp.	Un	–	pr	–	–	3–4	pr	2.6±1.8	0.0	
Dactylopteridae										
<i>Dactyloptena</i> sp.	P	7		0.0	2.1±1.4			–	–	
Drepaneidae										
<i>Drepane</i> sp.	Un	19		0.3±0.2	0.0			–	–	
Engraulididae										
<i>Stolephorus</i> sp.	P	2–61	pr,fl,po	76.5±23.7	101.6±48.5	5–10	pr,fl	1.6±1.1	7.4±6.8	
Fistularidae										
<i>Fistularia</i> sp.	P	7		1.7±1.0	0.0			–	–	
Gobiidae										
Gobiid sp.	N	2–12	pr,fl,po	16.4±7.8	32.0±10.4	2–14	pr,fl,po	55.9±28.5	829.5±484.0	

Table 1 (continued)

Taxa	SM	Malindi Marine Park				Watamu Marine Park			
		Size (mm)	Dev. Stage	Mean density		Size (mm)	Dev. Stage	Mean density	
				SEM	NEM			SEM	NEM
<i>Microgobius</i> sp.	N	2–8	pr,fl,po	22.6±6.5	92.6±58.0	2–5	pr,fl	7.2±6.4	0.0
<i>Bathygobius</i> sp.	N	4–5		2.3±1.9	0.0			–	–
<i>Coryphopterus</i> sp.	N	2–5		0.9±0.7	0.0			–	–
Gobiesocidae									
Gobiesocid sp.	N	–		–	–	3–4	pr	0.0	1.6±1.6
Haemulidae									
<i>Plectorhynchus</i> sp.	P	4–15	pr,fl,po	1.8±1.4	3.1±2.9			0.4±0.4	0.0
Holocentridae									
<i>Myripristis</i> sp.	P	3	pr	0.3±0.2	1.3±1.2			–	–
Labridae									
Labrid sp.	P	2–13	pr,fl,po	18.1±6.4	35.3±6.2	2–10	pr,fl,po	14.1±6.1	1.6±1.6
<i>Chelinius</i> sp.	P	3–10	pr,fl,po	1.3±0.8	3.7±1.5			–	–
<i>Thalossoma</i> sp.	P	6–10	pr,fl,po	9.4±6.5	0.0			–	–
<i>Halichoeres</i> sp.	P	3–4	pr	0.0	3.3±3.2			–	–
<i>Xyrichthys</i> sp.	P	3–5	pr	1.3±1.0	3.8±3.6	5	pr	0.4±0.4	0.0
Lethrinidae									
<i>Lethrinus</i> sp.	P	2–6	pr	8.1±3.2	8.4±5.3			–	–
Leiognathidae									
<i>Leiognathus</i> sp.	P	2–8	pr,fl,po	1.8±1.5	15.4±6.8			–	–
Lutjanidae									
<i>Lutjanus</i> sp.	P	3–4	pr	6.6±2.8	17.2±8.7	2–4	pr	2.1±1.3	0.0
Mullidae									
<i>Parupeneus</i> sp.	P	2–5	pr	2.7±2.2	0.7±0.7			–	–
Nemipteridae									
<i>Scolopsis</i> sp.	P	18	po	0.0	11.4±7.4			–	–
Opistognathidae									
Opistognathid sp.	N	3	pr	0.0	1.1±1.1			–	–
Pegasidae									
<i>Europegasmus</i> sp.	P	2–3	pr	0.2±0.2	1.3±1.2	3	pr	0.7±0.7	0.0
Platycephalidae									
<i>Thysanophrys</i> sp.	P	2–12	pr,fl,po	3.68±2.5	3.0±3.0			–	–
Platycephalid sp.	P	2–16	pr,fl,po	2.7±2.1	3.2±1.6	4–6	pr,fl	2.3±1.2	3.1±3.1
Pleuronectidae									
Pleuronectid sp.	Un	12	po	0.0	1.1±1.1			–	–
Pomacentridae									
<i>Abudefduf</i> sp.	N	4–15	pr,fl,po	3.0±2.7	17.3±9.7	4–5	fl	1.1±1.1	3.1±3.1
<i>Chromis</i> sp.	N	5–10	pr,fl,po	0.5±0.5	2.1±2.0			–	–
<i>Pomacentrus</i> sp.	N	3–4	pr	0.2±0.2	2.2±2.1	4	pr	0.6±0.6	0.0
Psettodidae									
<i>Psettodes</i> sp.	P	3–5	pr	2.0±1.2	0.0			–	–
Pseudochromidae									

Table 1 (continued)

Taxa	SM	Malindi Marine Park				Watamu Marine Park			
		Size (mm)	Dev. Stage	Mean density		Size (mm)	Dev. Stage	Mean density	
				SEM	NEM			SEM	NEM
Pseudochromid sp.	N	2–3	pr	2.0±2.0	1.3±1.2			–	–
Scaridae									
<i>Calotomus</i> sp.	P	3–13	pr,fl,po	11.2±3.0	20.5±12.2	2–14	pr,fl,po	1.0±1.0	7.1±2.6
<i>Leptoscarus</i> sp.	P	5–8	pr,fl,po	0.5±0.3	10.8±10.2				
Scarid sp.	P	2–9	pr,fl,po	17.1±4.4	85.4±25.7	2–14	pr,fl,po	15.6±6.0	9.7±3.8
Scombridae									
Scombrid sp.	O	3–4	pr	0.8±0.8	3.6±2.5			–	–
Scorpaenidae									
<i>Pterois</i> sp.1	N	12	po	0.4±0.4	1.5±1.5			–	–
<i>Pterois</i> sp. 2	N	15	po	1.1±0.5	0.0			–	–
Serranidae									
<i>Epinephelus</i> sp.	N	7	po	0.3±0.2	1.1±1.1			–	–
Siganidae									
<i>Siganus</i> sp.	N	2–26	pr,,po	4.4±2.9	3.1±2.9	2–4	pr	6.3±5.5	0.0
Solenostimatiidae									
<i>Solenostomus</i> sp.	N	5–8	fl	0.4±0.3	3.7±2.2	5	fl	0.0	0.4±0.4
Sphyraenidae									
<i>Sphyraena</i> sp.1	P	3–30	pr,fl,po	1.9±0.9	18.3±10.7	5	fl	0.9±0.9	0.0
<i>Sphyraena</i> sp.2	P	4–5	pr	1.7±1.4	0.0			–	–
Syngnathidae									
<i>Corythoichthys</i> sp.	N	6–13	pr,fl,po	5.8±1.4	14.8±3.4	6–10	pr,fl,po	10.7±5.9	5.6±2.0
<i>Syngnathus</i> sp.	N	6–16	pr,fl,po	2.7±1.8	4.6±3.1			–	–
Terapontidae									
Terapontid sp.	P	5	pr	0.0	4.4±2.8			–	–
Tetraodontidae									
Tetraodontid sp.	N	12	po	0.0	4.8±2.4	3	pr	1.1±1.0	1.2±1.2
Trichonotidae									
<i>Trichonotus</i> sp.	Un	7–25	pr,fl,po	0.7±0.5	5.9±3.6	4–5	fl	1.7±0.9	1.5±1.5
Tripterygiidae									
<i>Tripterygion</i> sp.	N	7	fl	0.0	1.1±1.1			–	–
Others				5.4±4.8	2.5±1.4			–	–
Total				612.1	1211.6			299.0	984.1

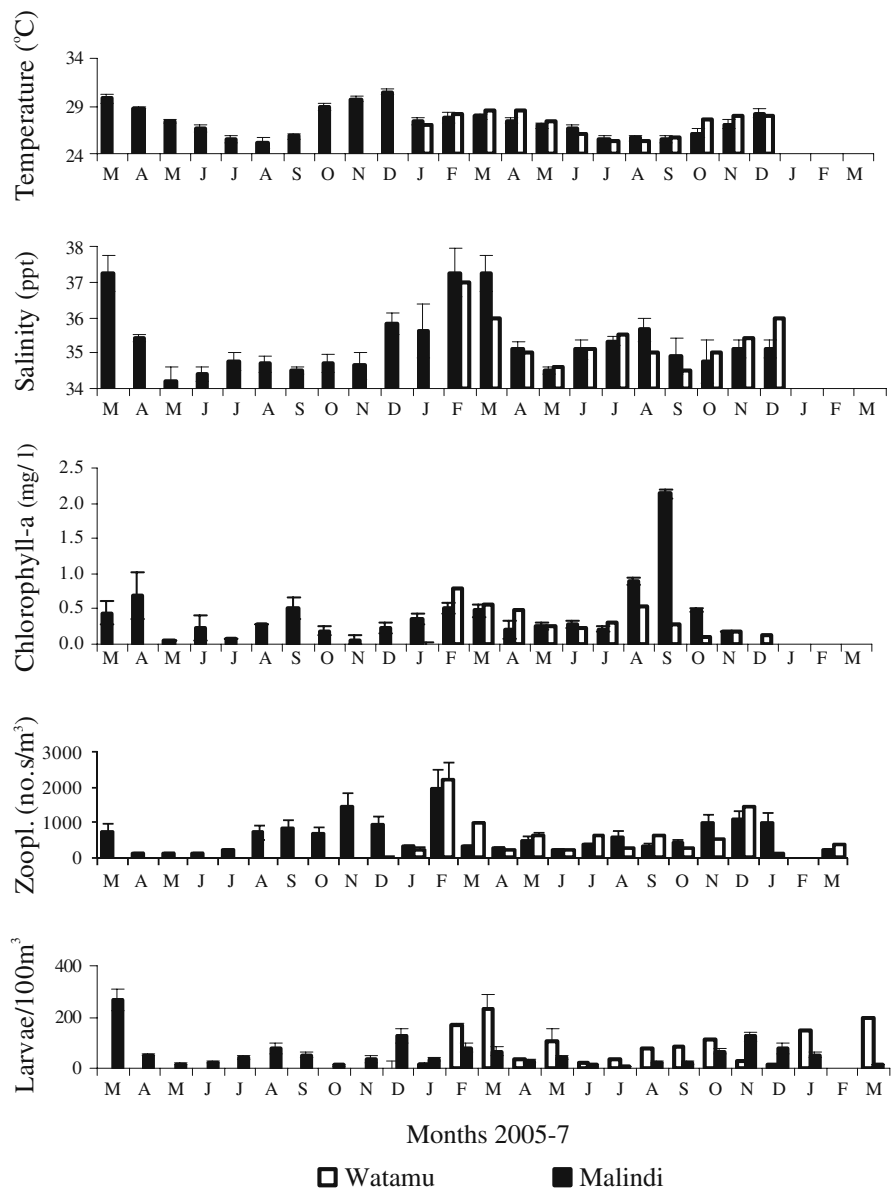
in Watamu Park, peak larval abundance occurred during the same season (February, March and December) and ranged between 247–256 larvae/100 m³ compared to 15–25 larvae/100 m³ during the SEM season (Fig. 2). There was significant difference in larval density between seasons ($p < 0.05$) and stations ($p < 0.05$), and a significant interaction effect of seasons and stations (interaction

effect $p < 0.05$), indicating conditional influence of both factors on larval abundance in the parks (Table 2).

Spatial patterns of larval assemblages

A multivariate cluster analysis divided the larval assemblages into three distinct groups in both Malindi

Fig. 2 Monthly variation in fish larval density and biophysical variables in Malindi and Watamu Marine Parks, Kenya. \pm indicate SE



and Watamu Parks (Fig. 3a, b). The most dominant family in Malindi Park, the Blenniidae, formed Group 1 (Fig. 3a), which was mainly distributed in the shallow lagoonal stations, S1 and S2 (Fig. 4a). The Gobiidae, Engraulidae, Apogonidae Carangidae, Labridae and Scaridae, comprised Group 2 (Fig. 3a). This group was moderately abundant and did not show any distinct spatial distribution pattern, except the Engraulidae which was abundant at S1 (Fig. 4a). Larval Group 3 was the least abundant in Malindi Park, comprising of Platycephalidae, Leiognathidae, Lethrinidae, Lutjanidae and Syngnathidae

(Fig. 3a). This group comprised of species of larvae that produce pelagic eggs, and were relatively less abundant in the park (Fig. 4a, Table 1).

In Watamu Park, the Blenniidae and Gobiidae separated into a distinct Group 1 (Fig. 3b) distributed in the shallow within-park stations S4, S5 and S6 in varying proportions (Fig. 4b). The Gobiidae were, however, mostly abundant at the within-creek station, S6 (Fig. 4b). The Scaridae, Syngnathidae, Labridae and Apogonidae clustered into a distinct assemblage, Group 2 (Fig. 3b); with Scaridae and Syngnathidae being more prominent in the within-park stations S4

Table 2 Two-way ANOVA results on the influence of stations, seasons and interaction between stations and seasons on the abundance (number per 100 m³) of fish larvae within Malindi and Watamu Marine Park, Kenya. SS, MS, df and F are test parameters

Parameter	Factor	SS	df	MS	F	P	Tukey HSD
Larval density (no/100 m ³)	Season	21.13	1	21.13	13.73	*0.000	NEM > SEM
	Station	64.52	5	12.90	8.38	*0.000	S6>all stations
	Season × Station	86.41	5	17.2	11.23	*0.000	NEM S6>all
	Error	807.7	5	1.53			
Temperature (°C)	Season	114.0	1	114.0	214.7	*0.000	NEM>SEM
	Station	16.80	5	3.40	6.3	*0.000	S3<S1,2 &S5
	Season × Station	21.30	5	4.30	8.0	*0.000	NEM S1-6
	Error	278	525	0.5			>SEM S1-6
Salinity (ppt)	Season	50.60	1	50.6	279	*0.000	NEM > SEM
	Station	5.30	5	1.1	6	*0.000	S3 > S4-6
	Season × Station	5.70	5	1.1	6	*0.000	NEM S1-6
	Error	95.3	5	0.2			>SEM S1-6

*indicates significant difference at $\alpha=0.05$

and S5, respectively. Group 3 comprised of Centriscidae, Platycephalidae, Carangidae Pomacentridae, Engraulidae, and Siganidae (Fig. 3b), and had no clear pattern of distribution within the park.

Discussion

The ichthyoplankton assemblage found in this study is comparable to those reported from other shallow temperate and tropical systems (Harris and Cyrus 1995; Harris et al. 1995; Patrick and Strydom 2008). Over 50% of the larvae sampled were from non-pelagic or benthic mode of spawning dominated by Blenniidae, Gobiidae, Apogonidae, and Engraulidae. Most larvae of known adult fish within the parks (e.g., Lutjanidae, Lethrinidae and Siganidae) were in preflexion stage of development, with the exception of Scaridae, suggesting that they did not complete their pelagic phase in the lagoon (Leis et al. 2003). In Watamu Park, these larvae were relatively less abundant possibly due to physical exclusivity of Watamu from oceanic waters.

Preflexion larvae comprised over 80% of the total number of larvae in both parks, suggesting that the parks, situated in shallow lagoons, are important spawning and nursery grounds for fish. The observed variation in proportions of developmental stages of larvae in the parks could be indicative of temporal differences in

spawning activity of adults, settlement of larvae, mortality or larval transport (Leis 1993). The presence of all developmental stages of certain blenniids, gobiids, engraulids, labrids, scarids and pomacentrids within the parks, suggests completion of pelagic larval phase within these lagoonal reef sites (Patrick and Strydom 2008). However, the availability of only preflexion or postflexion stage for some species indicated they complete only part of their life cycle in the park lagoons (Leis et al. 2003). It has been suggested that remaining inshore is advantageous for finding a suitable settlement habitat at the end of larval stage (Hickford and Schiel 2003), however, Hamilton et al. (2008) showed that post-larval survivorship of bluehead wrasse was higher for individuals that spent part of their pelagic phase outside the lagoon than those that completed their entire cycle in a lagoon. The existence of a wider size range and high proportion of preflexion larvae in Watamu Park suggests that more fish complete their entire life cycle within Watamu as compared to Malindi Park.

Larval density in both Malindi and Watamu Parks was higher during the calm NEM season as compared to the rough SEM season perhaps due to optimal conditions for food production and warmer temperatures during this season (McClanahan 1988; Kaunda-Arara et al. 2009). In Malindi Park, seasonal zooplankton density was strongly correlated with larval abundance, while in Watamu; temperature was the more important determi-

Fig. 3 Cluster analysis of dominant groups of fish larvae in (a) Malindi and (b) Watamu Marine Parks, Kenya. (vertical line represents the chosen distance for group separation) Bl=Blenniidae, Ca=Carangidae, La=Labridae, Go=Gobiidae, Ap=Apogonidae, En=Engraulidae, Sc=Scaridae, Sp=Sphyraenidae, Leo=Leognathidae, Lut=Lutjanidae, Syn=Syngnathidae, Le=Lethrinidae, Pl=Platycephalidae, Cen=Centriscidae, Tri=Trichonodontidae, Po=Pomacentridae, Si=Siganiidae

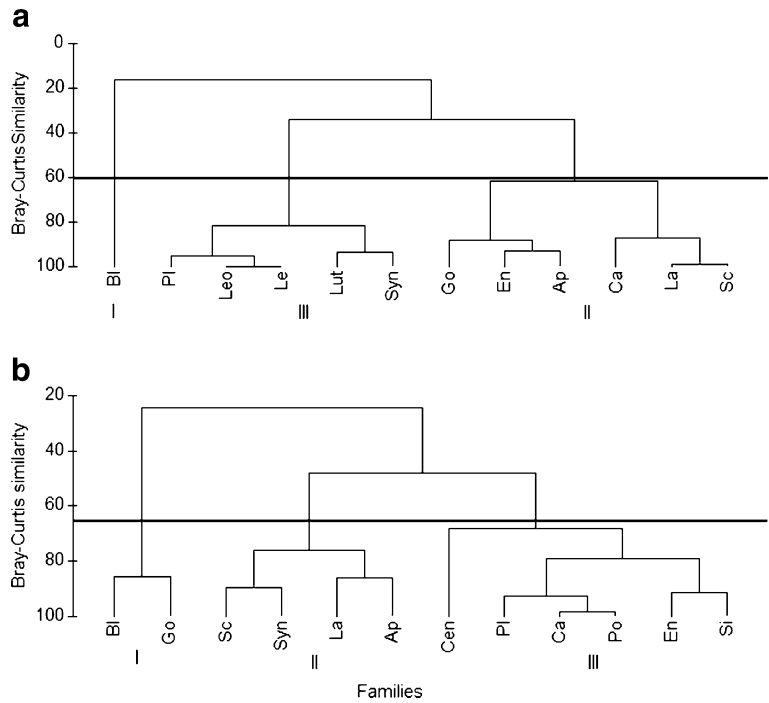
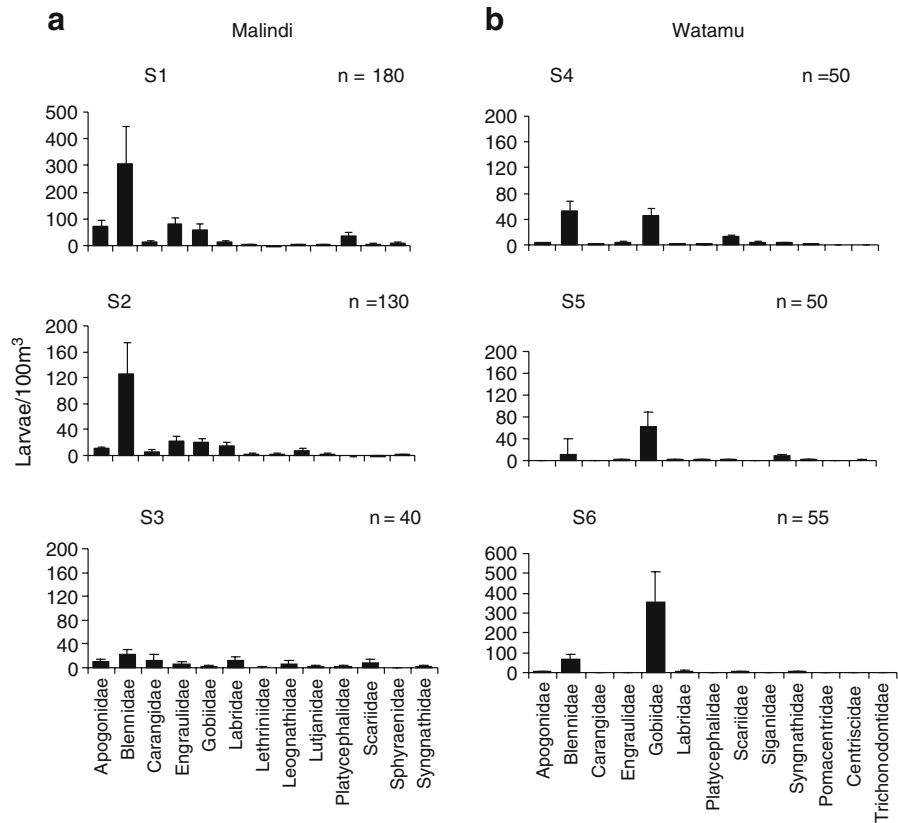


Fig. 4 Distribution of dominant family groups across stations in (a) Malindi (S1-3) and (b) Watamu Marine Parks (S4-S6) in coastal Kenya. *n*=total number of tows



nant. These results concur with studies done elsewhere, where temperature (Belyanina 1986; Tzeng and Wang 1993; Kingsford 1998; Harris et al. 1999) and zooplankton production (Carter and Schleyer 1978; Harris et al. 1999) were found to positively influence larval abundance. The dominance of larvae during NEM season further suggests preponderance of spawning during this season, however, some groups (e.g., Apogonidae and Siganidae) appeared to spawn during the SEM season.

In this study, Watamu Park which is more enclosed with restricted connection to open waters was found to be dominated by fish larvae from demersal spawners; the more open Malindi Park was, however, dominated by the larval pool from pelagic spawners. Consequently, seascape and oceanographic features appear to influence larval pools on these parks, and may form important consideration in locating marine parks (Leis et al. 2003). The segregation of larval groups at within-park scales may indicate existence of features that contribute to larval retention and patchiness within parks. However, more robust data is needed to determine the existence and scale of larval retention within these parks. If larval retention is found to be prevalent, this will have implications for the design and management of these and other marine parks (Swearer et al. 1999).

Conclusions

Fish larval occurrence in Malindi and Watamu Marine parks is strongly influenced by seasonal patterns of the yearly reversing NEM and SEM seasons. High larval densities were encountered during the NEM season with zooplankton density and temperature being the most important biophysical parameters influencing density. Dominance of preflexion stage larvae in both parks is suggestive of a high degree of local spawning occurring perhaps within the parks and the adjacent areas. Adult spawning behavior and oceanographic features may have been responsible for differences in distribution of fish larval assemblages between stations. Synchrony in larval peaks during the NEM season between the parks for some families and species indicated that factors controlling larval occurrence and distribution were similar at small (10–15 km) spatial scales. The results of this study provide a synoptic account of nearshore fish larval assemblages in lagoonal waters of coastal Kenya and the WIO region, and will contribute to providing baseline data

necessary in understanding population replenishment in marine reef parks. A greater challenge lies in enhancing the taxonomic database of fish larvae in the WIO region by sampling further offshore and employing genetic techniques to aid in taxonomy and systematics of the large larval pool in this region.

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