COMMUNITY STRUCTURE AND SPATIO-TEMPORAL VARIABILITY OF ICHTHYOPLANKTON IN KENYAN COASTAL WATERS

By

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DECLARATION BY THE CANDIDATE

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DEDICATION

This thesis is dedicated to My Father Evan Mwaluma Mwandawiro and My Mother Phidilora Mgoi who worked tirelessly to ensure that I got an education. I would not have achieved this without you. Thanks Lucy, Lesley and Allan for your patience.

ABSTRACT

Temporal and spatial variability in abundance and distribution of fish larvae contributes to structuring populations of adults within coral reef habitats and influences connectivity of reef sites. However, few studies have examined this variability at different spatial and temporal scales in the Western Indian Ocean (WIO). In an effort to bridge this gap, this study examined patterns of fish larval supply in Malindi and Watamu Marine National Parks between March 2005 - March 2007. Additionally, the study examined large-scale spatial variations in larval assemblages along lagoonal reef sites at a span > 160 Kms, and the inter-annual variability in alongshore assemblages of fish larvae at this scale. Larvae were sampled using a combination of plankton nets and light-traps. A total of 56 families, 45 genera and 21 species of larvae were identified in Malindi Marine Park, while, 21 families, 14 genera and 6 species were sampled in Watamu Marine Park. The dominant taxa at both sites were; Blenniidae (*Parablennius* sp. and *Omobranchus* sp.), Engraulidae (*Stolephorus commersonii*), Gobiidae n.d, and Pomacentridae (*Abudefduf* sp.). Seasonality was found to have an effect on the occurrence of larvae over the two parks, with segregation of distinct larval groups within and between the parks on a small spatial scale. Inter-annual variations in distribution of larvae and larval assemblage structure suggested annual differences in spawning patterns. Correspondence Analysis, indicated differences in species-site associations between years. Data suggested overall spawning by fishes on the north Kenyan coast with subsequent likely transport of larvae to the south.

Hatch dates derived from otolith analysis of commerson's anchovy, *Stolephorus commersonii*, were; January - March 2005, August - September 2005, December - February 2006. Monthly growth rates for *S. commersonii* larvae and juveniles were highest in the northeast monsoon months of December (0.207 cm.day⁻¹) and March 2005 (0.119 cm.day⁻¹), and lowest in southeast monsoon months of July $(0.056 \text{ cm. day}^{-1})$, and April $(0.0105 \text{ cm. day}^{-1})$ 2006, respectively. Finescale temporal variation in larval supply to Malindi Marine Park indicated that larval supply to the park was mostly nocturnal, with a peak during spring tides. Time-series spectral analysis showed that larval supply to Malindi Marine Park occurred after a 30 day cyclical period associated with the new moon lunar phase. This study provides, for the first time, a synoptic account of the taxonomy, distribution and relative abundance of nearshore fish larval assemblages in lagoonal waters of coastal Kenya, and contributes in providing baseline data useful in understanding fish population replenishment in lagoonal reefs.

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CHAPTER 1

INTRODUCTION

Field investigations of larvae of marine fishes originated in the 1800's. Motivations for the investigations were mainly assessment of adult spawning patterns and larval distribution, and the desire to understand how environmental variations and changes in the abundance of larvae interact to regulate the abundance of fish populations (Heath 1992).

The replenishment of fish populations by arrival of new young individuals is referred to as "recruitment" (Heath 1992). Factors affecting recruitment, particularly those related to the survival of larvae, are perceived to be of key importance in larval studies (Heath 1992). In spite of approximately 100 years of research, the process of recruitment as affected by larval dynamics is still not well understood, and is the subject of continuing studies (see reviews in Sponaugle *et al.* 2002; Sale 2004; Watson and Munro 2004; Pineda *et al.* 2007). Individual investigations have usually concentrated on particular aspects of early life history, examining factors affecting recruitment (e.g. dispersal, growth or mortality) which are perceived to be important in determining abundance (Heath 1992), or examining connectivity, that is, the degree to which a population is receiving recruits from other areas (Sponaugle *et al.* 2002).

Self-recruitment refers to levels of larval retention that substantially affect abundance of a local population (i.e. populations exhibiting high self-recruitment are those whose numbers are significantly influenced by recruitment of their own offspring) (Sponaugle *et* *al.* 2002; Warner and Cowen 2002). Physical variables influencing self-recruitment include site isolation, coastal complexity and flow variability (Leis 1993; Sponaugle *et al.* 2002). Long distance dispersal of larvae coupled with self-recruitment has the potential to affect population structure of fishes at different spatial scales creating metapopulations patterns with varying complexity (Sponaugle *et al.*, 2002)

Larval transport and dispersal through ocean currents, fronts, eddies, upwelling zones and counter currents also provide the opportunity for retention of larvae and therefore of selfrecruitment. These physical factors may enable retention of passive larvae (physical retention) or lead to retention with active behavioral input by larvae such as vertical orientation and strong swimming capabilities (Leis 1993; Cowen *et al.* 2000; Sponaugle *et al.* 2002; Swearer *et al.* 2002).

The objectives of field studies of fish larvae can be grouped under three headings (Heath 1992):

1. Estimation of the numbers or biomass of exploitable populations

of fish populations from a relationship between the abundance or distribution of larval stages and the abundance or distribution of spawning adult fish. These studies necessitate extensive research on the spawning behaviour of adult fish in addition to investigations on the spatial and temporal distribution of eggs and larvae.

2. Determination of the underlying processes affecting survival and recruitment to parent populations. Fluctuations in the size of fish populations may occur as a consequence of changes in the annual influx of larvae or recruiting juveniles. The

fluctuations could also be due to human exploitation affecting parent stocks among other factors. Consequently, research on fish larval supply is important in understanding factors affecting recruitment to parent stocks.

 3. Studies on stages of fish life history are important for evaluating mechanisms that regulate the dynamics of marine biological systems. This can be done by monitoring the dispersal and survival of larval stages of fish species.

1.1 Statement of the problem

East African coastal reefs are important ecosystems supporting a diversity of fisheries resources (Kaunda-Arara *et al***.** 2009). These resources are believed to be over exploited (McClanahan and Obura 1995, Jidawi *et al*. 1999, Kaunda-Arara *et al.* 2003), but continue to support large populations of artisanal fisheries. The extent to which fisheries decline in Kenya is attributed to environmental variability and recruitment success is unknown. Larval supply to reef sites is important for both conservation, design and fisheries replenishment, however, the pattern of larval supply to reefs and especially within marine reserve boundaries has received little attention in the Western Indian Ocean (WIO) region. However, these data are important in designing effective marine reserves for ecosystem conservation (Kaunda-Arara *et al.* 2009). Additionally, the extent to which recruitment variability affects fisheries production is largely unknown for most exploited reefs in the WIO, but may be significant (Miller *et al.* 2000).

While much work has been done on the functional biology of reef fishes in Kenya's coastal lagoons (Nzioka 1979; Nzioka 1985; Ntiba and Jaccarini 1990; Kaunda and Ntiba 1997; Kulmiye *et al.* 2002), there is little work on the ecology and population dynamics of fish larvae in Kenya and most of the WIO region. Taxonomic and ecological data on planktonic larvae originates mainly from general zooplankton studies (e.g. Reay and Kimaro 1984; Mwaluma 1997; Mwaluma *et al.* 2003 and Osore *et al.* 2004) with limited work on fish larvae (but see, Little *et al.*1988; Kaunda-Arara *et al.* 2009). To date no comprehensive study has been done on fish larval ecology in coastal lagoons and within marine parks, thus the extent to which fish stocks may be limited by larval supply and settlement is unknown. Understanding the composition and pattern of larval supply to reef sites is important in determining factors contributing to temporal and spatial variability of adult populations, and their conservation potential. The quantity and composition of fish larvae arriving on a reef site (larval supply or replenishment) is dependant on oceanographic conditions, larval ecology, and spawning regimes among other factors (Leis 1993; Leis *et al.* 2003; Alemany *et al.* 2006). In Kenya, marine parks have a long history, having been established over 30 years ago to protect reefs and fishing grounds. A lot of work has been done on the ecology and benthic populations within these parks (McClanahan and Nyawira 1988). However, the pattern of fish larval supply to these parks remain unknown, but may be important in understanding population dynamics within parks and adjacent fisheries (Kaunda *et al.* 2009).

1.2 Justification of the study

Data on the scale of distribution of reef fish larvae based on abundance and assemblage composition are important for designing and management of conservation areas and fisheries. The spawning seasons, distribution of spawned larvae in relation to hydrographic factors are important parameters for managing fisheries and marine protected areas. Moreover, there is a poor taxonomic database on reef fish larvae of the

WIO but these are neccessary for biodiversity conservation. Abundance and distribution of coral reef fish larvae have direct influence on the magnitude of juvenile recruitment and connectivity of reef fish populations. The spatio-temporal variation in abundance and distribution of larvae in relation to marine park boundaries may help in identifying optimal locations for protected sites. Data on the within and between-year variation in larval abundance at reef sites are important in understanding the processes controlling larval supply at fine temporal scales. In Kenya and most of the Western Indian Ocean region, studies on fish larval dynamics are scarce despite the fact that these data are important in designing effective marine reserves for ecosystem conservation and fisheries management.

1.3 Overall Objective

The overall aim of this study was to describe; the composition, spatio-temporal variability in larval abundance and distribution in shallow coastal lagoons of Kenya.

1.4 Specific Objectives

The specific objectives of this study were to:

- 1. Describe the seasonal variability in composition and abundance of fish larvae within the Malindi and Watamu Marine Parks in coastal Kenya.
- 2. Determine the spawning season of fish species based on relative temporal abundance of larval stages in the plankton.
- 3. Determine alongshore abundance, composition and diversity of fish larvae in coastal Kenya.
- 4. Determine growth variability between larval and juvenile fish and assess spawning period based on hatch date distribution using otolith studies.
- 5. Determine the effects of diel cycles, lunar and tidal rhythms on the abundance and distribution of larvae within the Malindi Marine Park, Kenya**.**

1.5 Hypotheses

This study was guided by the following statistical null hypotheses:

- 1. There is no temporal and seasonal variation in larval composition, abundance and diversity in Malindi and Watamu Marine Parks.
- 2. Spawning time has no influence on growth of larvae and juveniles of selected fish species in Malindi Marine Park.
- 3. There are no alongshore differences in distribution, abundance, composition and diversity of fish larvae in coastal Kenya.
- 4. There is no influence of diel and lunar cycles on the patterns of larval supply to Malindi Marine Park.

CHAPTER 2

LITERATURE REVIEW

2.1 Hydrography and Climate

The Kenyan coastline is about 600 Kilometers long and is characterized by a continuous fringing coral reef running parallel to the coast. The continental shelf is narrow (3-8 km) except in the northern Kenyan Banks and Ungwana Bay where it extends to 15-60 km wide (Fig. 2-1) (UNEP 1998). The East African waters have distinct seasonality in physical, chemical and biological parameters. These seasonal patterns are influenced by the annual movements of the Inter-Tropical Convergence Zone (ITCZ) which creates two distinct seasons, the northeast monsoon (NEM) and the southeast monsoon (SEM).

The SEM prevails from April to October and is characterized by high cloud cover, high wind energy and low solar insolation and temperatures (McClanahan 1988). Current speeds are high and achieve speeds such as 200 cm s^{-1} (Johnson *et al.* 1982). Lowest salinities occur at the onset of the SEM when river discharge and rainfall are high (McClanahan 1988). In contrast, the NEM which blows from November to March brings warmer waters, lesser rainfall, shallow thermocline, calm conditions, and high salinity. Current speeds are reduced and to 100 cm s-1 (Johnson *et al.* 1982).

Fig. 2-1. Map showing bathymetry, direction of the monsoons, and the major surface ocean currents (SEC= South Equatorial Current, MC = Mozambique Current, EACC= East African Coastal Current, ECC = Equatorial Counter Current (Modified from: Osore 2003)

Due to high water temperatures and calm waters during the NEM, high phytoplankton and zooplankton production are reported in coastal waters (Bryceson 1982; Kimaro 1986; Okemwa 1990; Mwaluma 1997; Osore *et al.* 2004). Consequently, fisheries production for both pelagic and demersal fish is highest during the NEM season in Kenya and Tanzania (McClanahan 1988).

The Kenyan coast is characterized by two rainfall seasons, which occur within the two monsoons. These are the long rains which conventionally occur in April/May and the short rains that fall in November/December transitional months. Relative humidity is comparatively high all year round, reaching its peak during the wet months of April to July (UNEP 1998). Mean monthly rainfall recorded for Malindi (one study site) between 2005-7 ranged between 80.6 - 360 mm during the SEM season, compared 0.3 - 66.4 mm during the NEM season (Fig. 2-2).

Overall average wind speeds on the Kenyan coast are highest during the SEM $(8.2 - 9.8)$ knots) and lowest during the NEM months of March (5.5 knots) and November (5.8 knots) as shown in Figure 2-2 (UNEP 1998).

2.2 Tides

The tides on the Kenyan coast are mixed semi-diurnal with two maxima and two minima per day. In each month the coast experiences two spring tides (during full and new moon) and two neap tides with a tidal range of about 4.0 m (Brakel 1982). The average tidal range for Malindi is 2.0 m at neap tide and 2.9 m at spring tide.

 Fig.2-2. Monthly (a) wind speed and (b) mean monthly rainfall for Malindi pooled for 2005-7. ± represents S.E of means (Source: Meteorological Department Malindi).

Lowest tides occur persistently during the NEM since the prevailing winds drive water offshore (UNEP 1998).

2.3 Critical Habitats

The critical habitats that characterize the Kenyan coast include the coastal mangroves, seagrass beds and coral reefs (UNEP 1998). Living corals occur all along the length of the Kenyan coast. A fringing reef colonises the shallow parts of the continental shelf along most of the Kenyan coastline to a depth of about 45 m, and at a distance of between 200 m and 2.0 km from shore except where river systems create low salinities and high turbidity limiting coral growth (UNEP 1998). The extent, size and diversity of coral reef ecosystems decrease northwards along the coast due to increasingly poor conditions for reef development caused by river runoff and the Somali current system (Hamilton and Brakel 1984; Sheppard 1987).

2.4 Marine Fisheries

Marine fisheries in Kenya are based on a small number of species most of which are demersal caught by artisanal fishermen operating between the shoreline and the reef (UNEP 1998; Kaunda-Arara *et al.* 2003). Most fishermen use non-motorised boats such as outriggers, dhows, cataracts and canoes. Only about 10% of fishing crafts are motorized (UNEP 1998). Currently the offshore fisheries resources are under-exploited and localized over-fishing occurs mostly within reefs and the shallow coastal areas where fishermen have easy access (McClanahan and Obura 1995; Kaunda-Arara *et al.* 2003). There is limited semi-industrialised fishing in the form of licensed commercial trawlers. The most common demersal fish families in the fisheries are the scavengers (Lethrinidae) and the rabbitfish (Siganidae) each of which contribute about 20% of the demersal catch, while parrotfishes (Scaridae) and snappers (Lutjanidae) are the next most common and contribute between 6 and 8% of the catches respectively (UNEP 1998).

2.5 Larval ecology and population dynamics

Coral reefs are noted for their complex topography, hydrography and biota. This complexity has important implications for the biology of the fish larvae found in the waters near coral reefs, and for attempts to study their biology (Leis 1993). The structural complexity of coral reefs provides a variety of habitats most of which support fish larvae (Leis 1993). Distribution patterns of fish larvae in any region of the ocean are related to the reproductive activity of the adult population and to topographic and hydrodynamic features that affect the dispersal of the larvae (Nonaka *et al.* 2000). A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fish species during their early life history stages, as well as an understanding of adult spawning patterns and reproductive strategies adopted by these fish in response to physical and biological processes (Nonaka *et al.* 2000). In addition, abundance of coral reef fish larvae directly influence the magnitude of juvenile recruitment (Robertson *et al.* 1988; Doherty and Fowler 1994). This information is important for sustainable exploitation of fisheries resources and for understanding the ecological status of the component species in the marine ecosystem (Heath 1992; Nonaka *et al.* 2000).

 In temperate regions, the distribution and abundance patterns of larval fish have been the subject of research for decades, in contrast, relatively very few studies have been done in the tropics (Sampey *et al.* 2004).

Most tropical ichthyoplankton studies have been concentrated in Australian waters. In South-western Australia, Muhling and Beckley (2007) investigated horizontal and vertical structure of fish larvae and found distinct larval assemblages in the shelf and offshore waters associated with seasonal oceanographic conditions. In South-eastern Australian coastal waters, Gray and Miskiewicz (2000) found seasonal larval assemblages with no consistent cross-shelf differences in abundances, which were associated to dynamic nature of the currents, spawning activity of adults and larval behaviour. Similarly in north-western Australia, Sampey *et al.* (2004) found weak crossshelf patterns in abundance of larvae with no relationship to biophysical parameters. However, seasonal changes in abundance were attributed to spawning activities of adults and/or larval survival. In the Great Barrier Reef, Leis (1986, 1991) found consistent horizontal and vertical distribution of fish larvae with deeper distribution during the day as compared to night-time. In the same area, Leis and Goldman (1987) observed seasonal distribution in larval assemblages which he attributed to current circulation patterns that less favoured larval retention. Thorrold and Williams (1996) working in the same area found distinct nearshore larval assemblages in comparison to lagoon and outter-lagoon areas. In Western Australia, McIIwain (2003) found lunar cycles in larval abundance with peaks around new moon, which he associated with spawning behavior of adults among other factors. Of the lunar cycles, greater settlement of larvae into reef sites has

been associated with new moon phases (Dufour and Galzin 1993) perhaps as a strategy to avoid predation (Johannes 1978). Presettlement larvae of fish species are often transported by tidal currents to nearshore habitats (Jenkins *et al.* 1998) and hence environmental factors such as wind direction may influence patterns of larval settlement at diel and lunar scales (Dufour and Galzin 1993). Despite the effects of currents, some late-stage larvae of fish species are known to actively control position and dispersal distances (Leis 1993).

In the Caribbeans, Sponaugle and Cowen (1996) studied temporal and spatial patterns of larvae, and associated larval abundance and diversity with variation in lunar and tidal amplitude cycles, while in Hawaii, Leis (1982) found distribution patterns of inshore and offshore larvae related to tidal eddies and nearshore upwelling. In the eastern coast of Brazil, Nonaka *et al.* (2000) found two dominant fish larval groups: mesopelgic fish and coral-reef-associated fish which had spatio-temporal distribution strongly influenced by hydrographic features.

In Florida, Grorud-Colvert and Sponaugle (2009) found significant differences in larval supply and juvenile recruitment between sites in marine reserves with the same level of protection, suggesting that particular sites may be more or less suitable for protecting populations through establishment of marine reserves. Since local variability among sites can lead to spatial differences in population replenishment, characterisation of larval supply and recruitment to potential marine reserve sites may help to identify optimal locations in a region and contribute to more effective reserve design (Grorud-Colvert and Sponaugle 2009). In other studies in the same area, Sponaugle *et al.* (2003), also found temporal patterns of larval groups within the inner and outer shelf areas associated with movements of oceanic waters.

In Mediterranean lagoons, local features such as lagoon area, habitat heterogeneity and local hydrographical circulation patterns were found to significantly affect species richness and spatial distribution of larvae and lagoon use by fish (Pérez-Ruzafa *et al.* 2004; Franco *et al.* 2008). In the Gulf of Mexico, major factors affecting spatial and seasonal variations of ichthyoplankton assemblages were; main circulation patterns, continental water discharges, mixing processes and fish spawning (Sanvicente-Anorve *et al.* 2000; Flores-coto *et al.* 2000). Off the central Chile upwelling system, spatial and seasonal differences in fish larvae were identified and associated with physical and biological factors at different scales (Hernandez-Miranda *et al.* 2003; Landaeta *et al.* 2008).

Considerable ichthyoplankton work has been done in Southern Africa. Beckley (1986) studied nearshore ichthyoplankton assemblages of Algoa Bay and found relatively few larvae of coastal species which spawned outside the surf zone in order to avoid retention of larvae in the nearshore region. However, proximity of reefs and other coastal nurseries such as estuaries can also influence the composition of nearshore larval fish assemblages (Beckley 1986; Tilney and Buxton 1994). In St Lucia estuary, Harris *et al.* (1999) found spatial and temporal variations in the larval fish assemblage related to environmental conditions and ontogenic behavioural patterns of certain species. In the ocean-estuarine

gradient in northern KwaZulu natal, Harris *et al.* 2001 identified three distinct larval assemblages based on three different ecological zones namely nearshore, surf and estuary. The patterns in relative species abundance and diversity differed significantly between each environment suggesting that the assemblages may be considered as indicator species for the zones. The observed differences in community patterns were attributed to turbidity, salinity and temperature (Harris *et al.* 2001). Pattrick and Strydom (2008), studied larval fish assemblages in a proposed marine protected area in eastern Algoa Bay and found the presence of all developmental stages of dominant species within the study area suggesting self recruitment, and a suitable spawning and nursery area for many coastal fish species. Therefore the structure of larval assemmblages appear to be affected by a suite of factors that vary in scale. However this review indicates that few studies exist on fish larval assemblages in the Western Indian Ocean.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

Samples for this work were collected from five shallow coastal lagoons spanning a distance of approximately 160 km along the coast from south to northern coast of Kenya (Fig. 3-1). The sites included Mombasa, Watamu and Malindi Marine Parks and Nyali and Vipingo lagoonal reefs. Mombasa, Malindi and Watamu sites are designated as marine protected areas where no extractive exploitation of resources is allowed including fishing, while Nyali and Vipingo sites are non-protected.

Mombasa Marine Park (9.4 km², created in 1986) encloses a lagoon with extensive coral reef and a reef flat. The distance of the reef from shore is about 2.5 km and the average depth of the lagoon is about 10 m at high tide. Nyali reef is located about 5 km south of Mombasa Marine Park (Fig. 3-1). The average depth of this reef lagoon is about 12 meters at high tide. The distance of the reef from shore is about 5.0 km and regulated fishing is allowed at this site. The Vipingo reef lagoon is located about 40 km north of Mombasa site, and is a shallow lagoon of about 5.0 m at high tide and about 0.8 km from the shore. The lagoon was previously overfished but now is conserved under local management.

Fig.3.1 Map showing Kenya's coastline and location of study sites. The studied reef sites are Nyali, Mombasa, Vipingo, Watamu and Malindi.

Watamu Marine Park is situated about 25 km south of Malindi Park. The park is bounded by a linear fringing reef located at 3.5 km from the shore, inside the fringing reef is a massive lagoon carpeted by seagrass beds. Average depth within the park lagoon is about 7 m at high tide. The Malindi Marine Park (6.3 km², created 1968) is located approximately 160 km north of Mombasa town. The Park encloses both a continuous fringing reef located about 200 m off the high water mark and a pacth reef system about 1 km from shore (Kaunda-Arara and Rose 2004). The average depth at high tide in the park was about 10 m.

In Malindi Marine Park, fish larvae samples were collected from three stations S1, S2 and S3 (Fig. 3-2). S1 was located within the shallow (10-12 m, high tide) park lagoon about 1 km from the shoreline. S2 was located in a backreef site that is more deeper (15-20 m, high tide). Station S3 was an offshore station, 6 km from the shoreline and mostly consisting of a shallow reef platform (10-12 m, high tide) and coral rubble. Likewise in Watamu, samples were collected from three stations S4, S5 and S6. S4 was a lagoonal seagrass station within the Marine Park, consisting of patches of live corals and located 500 m from the shore line, 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 (3-5m at high tide) seagrass bed. S6 was located inside Mida Creek, about 500 m from the creek mouth, with a high tide depth of about 7m during high tide (Fig. 3-2).

Fig. 3-2. Location of sampling stations in Malindi (S1, S2 & S3) and Watamu (S4, S5 & S6) Marine Parks. (Nr, North reef; Fr, Fringing reef; Tr, Tewa reef)

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. A series of six 24 hour sampling was also carried out at from a fixed point in Malindi Marine park lagoon (S1) over six different periods (Fig. 3-2). Sampling was done on neap and spring tide dates starting from; $15{\text -}16^{\text{th}}$ March 2005 (spring tide), 18- $19th$ March 2005 (neap tide), 27-28th May 2005 (spring tide), 29 – 30th June (neap tide), $24 - 25$ th January 2007 (spring tide) and 29- 30th March (neap tide). In the same park, juveniles of the commerson's anchovy were caught using light- traps from March 2005 to June 2006. Three to five traps were deployed monthly in Malindi Marine park lagoon (S1), backreef (S2) and offshore (S3) sites at dusk and retrieved in the morning after remaining submerged for 10-12 hrs.

3.2 Fish larvae sampling

Monthly and diel (24 hrs) tows for fish larvae in Malindi and Watamu marine parks were carried out during high tides using a 3-meter long, 500µm mesh size plankton net with a mouth area of 0.2 m². At each station, three replicate tows each lasting 6 minutes were made obliquely, from close to the bottom (1-3 m) to just below the water surface at a speed of about 1 m.s^{-1} . 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 \pm 14 m³ of seawater was filtered per tow. Monthly sampling at Malindi and Watamu marine parks covered 10-14 days in a month.

For alongshore sampling in March 2007 and April 2008, 10 replicate tows lasting 20 minutes per site were made filtering an average of 442 m^3 of seawater per tow. This was done in order to obtain as much representative sample as possible. After each tow,
samples were preserved in 5% buffered formaldehyde in seawater. In the laboratory, fish larvae were removed from the samples using a Wild Heerbrugg M3C stereo microscope, and identified to the lowest taxonomic level possible using keys from Leis and Rennis (1983), Leis and Trinski (1989) and Leis and Carson-Ewart (2000). Developmental stages of the larvae (e.g. preflexion, flexion and postflexion) were determined according to Leis and Rennis (1983) and Leis and Carson-Ewart (2000). Preflexion larvae were those larvae whose developmental stage began at hatching and ended with the start of upward flexion of the notochord. Flexion larvae were identified as larvae whose developmental stage began with flexion of the notochord and ended with the hypural bones assuming a vertical position. Postflexion larvae described developmental stage from formation of the caudal fin to attainment of full external meristic complements (fin rays and scales) (Leis and Rennis 1983). The total length of each larvae was measured to the nearest 0.1mm using a microscope eyepiece graticule. The remaining samples were used to estimate monthly zooplankton density (numbers.m⁻³).

3.3 Measurement of biophysical parameters

Surface water temperature (ºC) and salinity (ppt) were measured using an Aanderaa instruments (Norway) temperature-salinity probe (display unit 3315). Samples for chlorophyll-a analysis was collected monthly from Malindi (20 months) and Watamu Marine parks (11 months) by filtering 1L of seawater from three stations per site and filtering it through a Whatman glass fibre filter paper (47 mm diameter and pore size 0.5). As the seawater was being filtered, a few drops of magnesium carbonate in sea water were added to prevent acidity on the filter paper. Since analysis did not proceed immediately, the filter papers were labelled and stored at minus 20 ºC in a freezer. In the laboratory, the filter papers were centrifuged for 10-15 min using 15ml of 90% acetone in order to extract the pigments. The supernatent was decanted into a 10 ml path length spectrophotometer cuvette in order to measure the extinction at wavelenghths 750, 664, 647 and 630 nm. Each extinction was corrected for a small turbity blank by substracting the 750 from 664, 647 and 630 nm absorbtions. Calculation for chlorophyll-a $(mg/m⁻³)$ was then done according to Parson et al (1984) where;

(Ca) Chlorophyll-a = 11.85 E_{664} -1.54 E_{647} -0.08 E_{630}

Where E stands for the absorbance at the different wavelengths and Ca the amount of chlorophyll-a in ug/ml derived as:

Mg chlorophyll/m⁻³ =
$$
\frac{C x v}{V x 10}
$$

where ν is the volume of acetone in ml (15ml), V is the volume of seawater in liters and Ca is the amount of chlorohyll-a substituted for C in the above equation.

3.4 Estimation of zooplankton and larval abundance

Due to the sparse nature of the larvae, data were $log_{10} (x+1)$ prior to analysis to fulfill normality requirements for parametric tests. Density of larval fishes and zooplankton were calculated by dividing total numbers counted in each sample by volume of seawater filtered (no. of revolutions x volume in $m³$ per revolution). Density was expressed as numbers.100 m⁻³ for fish larvae and numbers.m⁻³ for zooplankton.

A one-way ANOVA (α = 0.05) was used to test for significant differences in temporal abundance of larvae between sites and Tukey HSD test used for *post hoc* analysis. Differences in temperature, salinity, chlorophyll-a, zooplankton and fish larval abundance between seasons (where NEM = November to March and SEM =April to October) were asssessed using students *t*-test.

A stepwise multiple regression analysis was used to determine the sub-set of environmental variables (temperature, salinity, chlorophyll-a and zooplankton density) that explained the largest variability in larval abundance in both parks. Diversity indices (Margalef's Species richness, Eveness, and Shannon-Wiener) were derived using PRIMER v 6.0 statistical package (Clark and Gorley 2006) from monthly species abundance data, and compared between seasons (NEM and SEM months) using students *t-*test. The formulae for these indices being expressed as;

Shannon diversity index (H)

$$
H' = -\sum_{i=1}^{s} pi \ln pi
$$

where S is the total number of species in the community and *pi*, is the proportion of S made up of the *i* th species. This index provides a rough measure of diversity, which is much less biased by sample size than species richness (Shannon-Weiner 1949).

Species evenness: $J' = H'/H'_{\text{max}}$, where *H*['] is the Shannon index as defined above, H'_{max} = ln *S*, and *S* is the number of species observed. This index determines how evenly the proportions of taxa are distributed in a sample.

Margalef's index (species richness): $d = (S - 1)/\ln N$, where *N* is the number of individuals. This index provides a measure of species richness that is roughly normalized for sample size without using more complex rarefaction techniques (Margalef 1968).

Cluster analysis based on group average linkage with Euclidean distance as a measure of similarity was used to examine the associations of dominant family groups based on larval abundances ($log_{10} (x+1)$ transformed) within each site. All data analysis followed Zar (1999) and Sokal and Rolf (1995).

In order to examine differences in species dominance and diversity between alongshore sites, K-dominance curves (Lambshead *et al.*1983) were generated by plotting percentage cumulative abundance of larvae against species rank (*k)* on a logarithmic scale. The most elevated curve indicates a site of least diversity, and hence of high species dominance (Clark and Warwick 2001). The curves were generated for 2007 and 2008 using PRIMER V6 software (Clark and Gorley 2006).

In order to determine species associations (or assemblages) within sites and assemblage constancy between years, a simple multivariate Correspondence Analysis (CA) was performed on log transformed abundances (larvae.100 m^{-3}) of the 15 most dominant fish larval species in March 2007 and April 2008 using SPSS V 13 software. Statistical analysis followed Zar (1996) and Sokal and Rohlf (1981).

3.4.2 Light trap fabrication and deployment

Light traps were fabricated locally and used to sample presettlement larvae in Malindi Marine park. The main body of the trap was made up of an 18.5 L transparent plastic water dispenser supported by a three legged metal frame, measuring about 1.2 m in height (Fig. 3-3a). The frame had a support base on which a diver's dry box was tightly fastened using a rubber hose (Fig. 3-3a). The water dispenser bottle was perforated to make 8 uniform holes of about 10 cm diameter. Bottle necks (tapering to about 2 cm) cut from ordinary plastic drinking water bottles (1L) were then glued to the holes using araldite glue. These then formed entry windows for larvae to enter the bottle (Fig 3-3a) The light unit consisted of a water proof 11 watt DC energy saving bulb (Fig. 3-3a) bought from a local electrical shop for US \$15 and powered by a Jacobs's lead-acid battery (12V 7Ah/20hr) which costed US 15\$ (Fig.3-3a). The lamp terminals were connected by clips $(+ve$ and $-ve$) which fitted easily and firmly onto the battery terminals. The battery was housed in a Seemann (Germany) diver's dry box which costed US \$20. The dry box measures 23 x 20 x 9 cms and comes with an O- ring seal which was coated in grease to ensure that no leakages occurred while underwater (Fig. 3- 3a).

Collection buckets (10L) with fish from the traps

Fig. 3.3 The locally fabricated light trap showing the original (with metal frames) design (a) collection bottle (b) a mixture of larval and post larval fish catches in collection buckets.

 A 1-liter collection bottle was initially secured at the bottom of the dispenser (Fig. 3-3a); however, this was later replaced by a 10 L bucket (with a sieve of 1 mm mesh size as a drainage panel) by enlarging the bottom of the dispenser bottle for more efficient collection of fish larvae (Fig. 3-3b). The frame supporting the trap was tied to floaters using a 15 m nylon twine. The floats ensured that the locations of the trap were known during retrieval and the sinkers helped to hold the trap upright and firmly at the bottom.

The traps were deployed within Malindi Marine National Park, Kenya, to sample presettlement fish larvae at coral, seagrass and sandy habitats from a motorized boat every evening at 1800 hrs and recovered after about 12 hours (overnight). Deployment occurred during high tide, at depths varying between 10-18 m

On average three traps were deployed per site. During deployment, the lamp was lit by directly connecting the lamp terminals to the battery while aboard the boat. The use of switches proved inconvenient due to frequent malfunctioning. With the light on, the trap was lowered slowly using the surface floater rope until the sinker hit the bottom. The traps were then left overnight for retrieval at dawn the following day. All the trapped fish settled at the bottom of the collecting bucket and were removed and placed in labeled containers and fixed in 70% alcohol.

In a later version (Fig. 3-4), the metal frames were eliminated and instead floaters tied at the rim of the bottle by 1 m manila twine. These provided the tension to keep the traps afloat at about 1-2 m from the bottom.

Fig. 3-4 A schematic diagram of the light trap without iron frames for deployment in mid water. Floaters and a sinker ensure upright positioning of the trap at a desired depth.

3.4.3 Otolith treatment and analysis

From the light traps, a total of 287 larvae and 946 juveniles of *Stolephorus commersonii* were used for otolith extraction. Trapped juveniles of *S. commersonii* were separated from pre-settlement fish larvae and juveniles of other fish, and were initially identified using guides by Smith and Heemstra (1998) and Whitehead *et al.* (1988). They were then measured for total length (TL) and Standard length (SL) to the nearest 0.1 mm before otolith extraction. Both sagittal and lapillus otoliths were dissected out of the fish head, extracted and viewed using an ordinary stereo microscope for gross morphology. Those with better ring formation were used for ageing. The otolith was then mounted on glass slides convex side up using glue and labelled accordingly, after which it was ground and polished using a 3M 261X imperial lapping film $(3 \text{ and } 30 \mu \text{m})$ to produce a thin transverse section that contained the nucleus and rings. Otoliths obtained from *S. commersonii* larvae were not ground as they had easily discernible rings which were counted after mounting them on slides. The selected otoliths were then viewed under a Leica DM IRB inverted microscope (10x ocular, adjustable PL Fluotar with C Plan: 4x, 10x, 20x, 40x and 63x objectives) fitted with a digital camera Leica DFC 320 connected to an image display unit at the Kenya Marine and Fisheries Research Institute (KMFRI) laboratory. The entire otoliths were photographed at 40x (for juveniles) and 400x (for larvae) enlargement, for area measurement and general view of ring formation. Using the IM500 software, each otolith was then measured for total area (μm^2) and three independent counts of the rings made from the nucleus to the outer margin in three different directions (Fig. 3-5).

Fig.3-5 Sagittal otolith (right) of *Stolephorus commersonii* larvae (17mm T.L) viewed from the lateral surface, showing daily growth rings (-17 days) and directions of counts (1-3) from primordium to rostrum. Arrows indicate direction of count. Magnification = x 400

Photographs for age counting were taken at 200x magnification for juveniles and 400x or 630x for larvae depending on the size. Increments were counted from selected optimal photographs of either left or right sagittae or lapillus. It was assumed that the increment closest to the nucleus of the otolith was formed at or within a day of hatching (Mikaela *et al.* 2002), with subsequent deposition at a daily rate (Campana and Neilson, 1985). Therefore total counts of the increments were taken to represent age of the fish in days. The highest count was considered conservative and used to represent age of the fish in days (Vidar Øresland pers comm.).

3.4.4 Estimation of hatch-dates and monthly growth rates

Hatch dates of monthly samples of *S. commersonii* larvae and juveniles were obtained from back calculation using derived age at capture and the catch-date. The median date of the monthly sampling date was used as the catch-date. The monthly distribution of the hatch date frequencies were then used to derive the spawning period based on the modal frequencies (Wells and Rooker 2004). Fish were considered to spawn at months of modal hatch-date frequency. Monthly growth rates $(cm. day^{-1})$ were also derived from regressions of length on age for both larvae and juveniles. Periods of low larval growth were determined from deviations of monthly growth from the overall mean growth rate. Deviations lower than the overall mean were considered to represent sub-optimal growth periods (Wells and Rooker 2004). Analysis of variance test (ANOVA) was used to evaluate differences in growth rates between months.

3.4.5 Estimation of growth parameters

A non-linear growth model based on Schnute (1981) was fitted to larval and juvenile growth patterns as:

$$
Y(t) = \left[Y_1^b + (Y_2^b - Y_1^b) \underbrace{1 - \exp(-a(t - \tau_1))}_{1 - \exp(-a(\tau_2 - \tau_1))} \right]^{1/b}
$$
 (1)

Where Y (t) = Total length at time t (in days) after hatch, τ_1 and τ_2 = upper and lower limits, respectively, of age range in the data, Y_1 = predicted size at age τ_1 , Y_2 = predicted size at age τ_2 , and *a* and *b* = parameters of the growth curve. The growth parameters K (growth co-efficient) and t_0 (hypothetical age at length $= 0$) were estimated for *S*. *commersonii* juveniles from the von Bertalanffy plot of $-\text{In}(1-L(t)/ L_{\infty})$ against age (t) years (Sparre and Venema, 1998), where L_t is the total length (cm) at age t (years), L_{∞} (cm) is the asymptotic length.

The largest fish in the samples (TL = 9.7 cm) was taken to represent L_{∞} . Length at age data of the species was then fitted into three growth models; von Bertalanffy (VBGF), Gompertz and Logistic for both larvae and juveniles in order to determine the appropriate growth model as:

von Bertalanffy (VBGF):
$$
L_t = L_\infty (1-\exp(-K(t-t_0)))
$$
 (2)

Gompertz
$$
L_t = L_\infty \exp(-\exp(-K(t-t_0)))
$$
 (3)

Logistic $L_t = L_{\infty}/(1 + \exp(-K(t-t_0)))$ (4)

The best fitting model was selected on the basis of the AIC (Akaike's Information Criterion) values derived as:

$$
AIC = n \ln Y_{\min} + 2p \tag{5}
$$

Where n is the number of specimens used for the analysis, Y_{min} is the minimum value of the residual sum of squares, and *p* is the number of estimated parameters (Puentes *et al.* 2004). Akaike's information criterion is a measure of the goodness of fit of an estimated statistical model offering a relative measure of the information lost or variance in model construction. Given a data set, several competing models may be ranked according to their AIC values, with the one having the lowest AIC being of the best fit (Puentes *et al.* 2004).

3.4.6 Time series analysis and diel cycles

Data sets from all the three stations were pooled to represent monthly supply of larvae into the park environment as no significant difference in abundance was detected between stations (ANOVA, F=1.62, $p = 0.198$). The larvae from replicate tows were summed up and standardized by total volume of water sampled to obtain larval abundance per day. The total daily abundances were then averaged to obtain mean larval abundance per month (larvae.100 $m⁻³$). Data was then subjected to time-series analysis in order to examine fine-scale temporal variation in larval abundance. Spectral analysis was used to determine periods of significant larval abundance in the park. In the spectral analysis, the dominant cycling frequency corresponds to periods of abundance with the greatest spectral power revealed by the periodiograms (Platt and Denman 1975). In addition, autocorrelation graphs were used to establish with greater precision any statistically significant periodicities identified by the power spectra (Platt and Denman 1975).

The number of larvae collected in the 24-hour sampling were standardised to number of larvae.100 $m⁻³$ using volumes of water calculated from the flow meter. Prior to analysis this data set was $\log_{10} (x+1)$ transformed to stabilize the variance caused by unpredictable occurrence of the rare species. A 2-factor nested ANOVA with tide (spring and neap) and time (day and night) as main factors was used to examine the influence of tidal regime and time of sampling on larval abundance. A *post Hoc* Tukey HSD test was used to partition the difference within the 24-hour series. Simple linear regression analysis was used to examine the relationship between tidal height and larval abundance for the dominant species. Statistical analyses followed Zar (1999).

CHAPTER 4

RESULTS

4.1 Seasonality of larval supply to Malindi and Watamu National Marine Parks

4.1.1 Biophysical parameters

Larval abundance was highly synchronized with temperature, salinity, chlorophyll-a and zooplankton peaks during the NEM months (Nov-March) in both parks (Fig. 4-1). In Malindi Marine Park, significant differences in temperature (t = 3.63, df = 20, p = 0.001), salinity (t = 3.57, df = 20, p = 0.001) and zooplankton density (t = 3.09, df = 21, p= 0.005) occurred between seasons, with higher values during the NEM season (Table 4-1).

Similarly, in Watamu Park, significant differences in temperature ($t = 2.64$, $df = 11$, $p =$ 0.022), salinity (t = 2.47, df = 11, p = 0.031) and chlorophyll-a abundance (t = 2.10, df = 42, $p = 0.04$) occurred between seasons, with higher values during the NEM period (Table 4-1). However, no significant difference in zooplankton density occurred between seasons in Watamu Park (t = 1.44, df = 12, p = 0.176) (Table 4-1).

A stepwise multiple regression analysis of larval abundance on biophysical variables (zooplankton density, chlorophyll-a, temperature and salinity) in Malindi Park, indicated a significant relationship between larval abundance and zooplankton density ($t = 2.47$, p $= 0.012$, $r^2 = 0.25$). There was lack of significant relationship between larval abundance and salinity (t = 1.30, p = 0.205), temperature (t = 1.67, p = 0.108) and chlorophyll-a (t = -1.34 , $p = 0.719$).

Fig. 4-1 Monthly variations in mean $(\pm \text{ SE})$ temperature, salinity, chlorophyll-a, zooplankton density and fish larval abundance in Malindi and Watamu Marine Parks.

Table 4-1: Seasonal variation in mean larval abundance (larvae.100m⁻³ \pm SE and biophysical parameters at Malindi and Watamu Marine Parks during the northeast (NEM) and southeast (SEM) monsoon seasons. \pm represent SE.

 $(no.m^{-3})$

* indicates significant seasonal difference at α = 0.05

In Watamu, a significant relationship of larval abundance with temperature was found (t $= 2.50$, p = 0.02, r² = 0.34). However, no significant relationship occurred between larval abundance and salinity (t = 1.87, p = 0.08), chlorophyll-a (t = 0.74, p = 0.470) and zooplankton density ($t = 0.96$, $p = 0.355$).

4.1.2 Taxonomic composition of larvae

In Malindi Marine park, a total 4017 fish larvae belonging to 56 families, and 45 genera and 21 species were collected during the study. The dominant species during both NEM and SEM seasons were from non-pelagic shore fishes such as Blenniidae (*Parablennius* sp., Blenniidae n.d., and *Exalias brevis*), and Gobiidae (*Microgobius* sp. and Gobiidae n.d.). The Engraulidae (*Stolephorus commersonii*) dominated the pelagic larval species in the samples (Table 4-2).

In Watamu Park, a total of 2296 larvae were collected belonging to 21 families with 14 genera and 6 species. The dominant groups in this park were from the families Gobiidae (Gobiidae n.d.) and Blenniidae (*Omobranchus* sp., *Parablennius* sp.)(Table 4-2).

Table 4-2: Mean density (larvae.100m⁻³) of fish larvae sampled in Malindi (2005-2007) and Watamu Marine Park (2006-2007) during the southeast (SEM) and northeast (NEM) monsoon seasons (spawning mode given as: $P =$ Pelagic egg; N= non-pelagic egg; Un = Unknown, after Leis and Rennis 1983, Leis and Trnski 1989). \pm indicate SE.

Taxa	Spawning Malindi Marine Park			Watamu Marine Park			
	mode	SEM	NEM	SEM	NEM		
Atherinidae							
Hypoantherina tropicalis	N			0.7 ± 0.7	1.5 ± 1.5		
Apogonidae							
Apogon sp.	N	43.3 ± 17.1	63.8 ± 34.9	11.3 ± 6.1	0.5 ± 0.5		
Archamia sp.	${\bf N}$	70.7 ± 37.4	9.1 ± 3.2				
Cheilodipterus sp.	N	0.0	1.4 ± 1.4				
Balistidae							
Balistidae n.d	$\mathbf N$	2.1 ± 1.8	0.7 ± 0.7				
Blenniidae							
Entomacrodus striatus	${\bf N}$	12.6 ± 5.1	1.2 ± 1.1				
Blenniidae n.d.	${\bf N}$	8.7 ± 2.6	120.3 ± 61.7	0.4 ± 0.4	12.4 ± 9.0		
Parablennius yatabei	N	6.8 ± 3.1	3.8 ± 3.6	29.1 ± 21.3	42.6 ± 37.5		
Parablennius sp.	N	145.2 ± 64.3	369.6 ± 162	5.9 ± 5.5	1.7 ± 1.7		
Exallias brevis	N	51.5 ± 24.7	22.9 ± 12.7	7.1 ± 5.6	6.0 ± 4.5		
Omobranchus sp.	N	0.0	0.4 ± 0.4	116.1 ± 61.4	45.6 ± 29.8		
Bothidae							
Engyprosopon sp.	$\mathbf P$	4.2 ± 2.7	1.6 ± 1.2				
Bythtidae							
Dinematichthys sp.	$\mathbf N$	2.2 ± 1.1	2.2 ± 2.1				
Caesionidae							
Pterocaesio sp.	${\bf N}$	3.6 ± 2.3	5.6 ± 3.6				
Carangidae							
Caranx sp.	${\bf P}$	10.1 ± 2.4	22.4 ± 12.9	0.5 ± 0.5	0.0		
Scomberoides sp.	${\bf P}$	0.9 ± 0.5	4.7 ± 3.1				
Gnathodon speciosus	P	1.9 ± 1.8	15.9 ± 8.0	1.9 ± 1.0	1.9 ± 1.2		
Elagatis bipinnulata	P	0.5 ± 0.5	2.5 ± 1.6	\overline{a}	$\overline{}$		
Carangoides sp.	\mathbf{P}	1.9 ± 1.1	12.9 ± 7.7		-		
Centriscidae							
Centriscidae n.d.	Un			2.6 ± 1.8	0.0		
Dactylopteridae							
Dactyloptena sp.	${\bf P}$	0.0	2.1 ± 1.4		-		
Drepaneidae							
Drepane puncata	Un	0.3 ± 0.2	0.0				
Engraulidae							
Stolephorus commersonii	\mathbf{P}	76.5 ± 23.7	101.6 ± 48.5	1.6 ± 1.1	7.4 ± 6.8		
Fistularidae							
Fistularia commersonii	P	1.7 ± 1.0	0.0				
Gobiidae							
Gobiidae n.d.	N	16.4 ± 7.8	32.0 ± 10.4	55.9 ± 28.5	829.5 ± 484.0		
Microgobius sp.	N	22.6 ± 6.5	92.6 ± 58.0	7.2 ± 6.4	0.0		
Bathygobius sp.	N	2.3 ± 1.9	0.0				
Coryphoterus sp.	N	0.9 ± 0.7	0.0				
Gobiesocidae							
Gobiesocid n.d.	N			0.0	1.6 ± 1.6		

4.1.3 Seasonal variation in larval supply and diversity

In Malindi Park, larval abundance (larvae. $100m⁻³$) varied significantly between seasons (t $= 2.20$, df $= 22$, p $= 0.038$) with higher abundance recorded during the NEM (1292 \pm 240) compared to the SEM (599 \pm 203) (Table 4-1). No significant differences in diversity (t = $- 0.26$, df = 22, p = 0.795), richness (t = $- 0.03$ df = 22, p = 0.969), and evenness (t = $-$ 0.14, $df = 22$, $p = 0.885$) occurred between seasons (Table 4-1). However, these diversity indices were higher during the SEM season. Similarly, in Watamu Park, no significant difference in larval abundance (t = 1.46, df = 9, p = 0.179), species diversity (t = -1.19 , df = 9, p = 0.263), richness (t = -1.14, df = 9, p = 0.280) and evenness (t = -0.78, df = 9, p $= 0.453$) occurred between the two seasons (Table 4-1).

4.1.4 Temporal and spatial trends in larval abundance

In Malindi Park, peaks in larval abundance occurred in the NEM months of March and December 2005 (Fig. 4-1). ANOVA test indicated significant difference in the monthly larval abundance in the park ($F = 4.90$, $df = 21$, $p < 0.001$). SNK test showed the March 2005 samples contributed significantly to the temporal variability in larval supply to the park. No significant difference in larval abundance occurred between the three stations (S1, S2 & S3) across the park (F = 2.83, df = 2, p = 0.069).

In Watamu Park, peaks in larval abundance similarly occurred during the NEM months of February, March and December (Fig. 4-1). As in Malindi, ANOVA indicated a significant abundance in the temporal variability in larval supply in the park ($F = 3.83$, df $=10$, $p = 0.001$) caused by the March 2007 samples (SNK test). No significant differences

in larval abundance occurred between the three stations $(S4, S5 \& S6)$ in the park including the creek (F = 0.73, df = 2, p = 0.483).

4.1.5 Spatial distribution of larval assemblages

A multivariate cluster analysis divided the larval assemblages into three distinct groups in Malindi and two in Watamu Parks (Fig. 4-2). The most dominant family in Malindi, the Blenniidae, formed Group 1 (Fig. 4-2a), these were mainly distributed in stations S1 and S2 (Fig. 4-3a). The Carangidae, Labridae, Gobiidae, Apogonidae and Engraulidae comprised Group 2 (Fig. 4-2a). This group was moderately abundant, and did not show any clear spatial pattern of segregation except Engraulidae which was abundant at S1 (Fig. 4-3a). Group 3 was the least abundant assemblage, comprising of Scaridae, Sphyraenidae, Leiognathidae, Lutjanidae, Syngnathidae, Lethrinidae and Platycephalidae (Fig. 4-2a). This group mostly consisted of larvae of species that produce pelagic eggs.

In Watamu, the Blenniidae and Gobiidae separated into a distinct Group 1 (Fig. 4-2b) distributed in stations S4, S5 and S6 in varying magnitude (Fig. 4-3b). The Gobiidae were, however, mostly abundant at S6 (Fig. 4-3b). The Centriscidae, Trichonodontidae, Engraulidae, Platycephalidae, Pomacentridae, Carangidae, Siganidae Syngnathidae, Scaridae, Apogonidae and Labridae clustered into a separated Group 2 with the Scaridae and Syngnathidae being more prominent in S4 and S5, respectively (Fig. 4-3b).

Fig 4-2 Cluster analysis of dominant groups of fish larvae in (a) Malindi and (b) Watamu Marine Parks. (Vertical line represents the Euclidean distance chosen for group separation I, II or III) $Bl = Blenniidae$, $Ca = Carangidae$, $La =$ Labridae, Go = Gobiidae, AP = Apogonidae, En = Engraulidae, Sc = Scaridae, $Sp = Sphyraenidae$, Leo = Leiognathidae, Lut = Lutjanidae, Syn = Syngnathidae, Le = Lethrinidae, Pl = Platycephalidae, Cen = Centriscidae, Tri $=$ Trichonodontidae, Po $=$ Pomacentridae, Si $=$ Siganidae.

Fig. 4-3 Distribution of dominant larval family groups across sampling stations in (a) Malindi (S1-S3) and (b) Watamu (S4-S6) Marine Parks in coastal Kenya. $n =$ numbers of larvae, \pm represents SE.

4.1.6 Early life history stages

In Malindi Marine Park, out of 4017 larvae sorted out during the study, 3358 (83.6 %) were at preflexion stage, 462 (11.5 %) flexion, and 197 (4.9%) in postflexion stage. The temporal variation in occurrence of the larval stages in Malindi park parks is shown in Figure 4-4a. The proportion of preflexion larvae in the park was greater than flexion and postflexion stages in all the months ranging between $66 - 98$ % of total larvae. There was a consistent reduction in preflexion stage larvae corresponding to an increase in flexion and postflexion stage larvae in March 2005, March 2006 and January 2007 (northeast monsoon months), suggesting settlement of larvae during these months (Fig. 4-4a).

In Watamu Park, out of 2296 larvae sorted out, 2004 (87.3 %) individuals were preflexion larvae, 135 (5.9 %) flexion, and 156 (6.8%) in post flexion stage. Like in Malindi Park, the preflexion larvae were dominant in most of the months ranging between 64 and 97 % of total larvae except in July (40%) and December 2007 (23.3%) when their abundance dipped, however, the abundance of flexion and postflexion stages increased during the periods of low preflexion abundance (Fig. 4-4b).

Fig. 4-4 Monthly variation in percentage frequency of stages of development of fish larvae in (a) Malindi and (b) Watamu Marine Park during the study period.

In Watamu, the months with higher occurrence of the ready-to-settle stages were July and November 2006; this differed with Malindi, perhaps indicating spatial difference in settlement time of the larvae.

4.2 Alongshore distribution of fish larvae in lagoonal reefs

4.2.1 Species composition

A total of 2644 fish larvae were sampled during the study period, 949 in March 2007 and 1695 in April 2008. In total, 26 families comprising of 37 species were sampled in March 2007 as compared to 43 families containing 73 species sampled in April 2008. The dominant (≥ 30.0 larvae.100 m⁻³) species of fish larvae in both years were from the families Gobiidae; Gobiidae n.d., *Coryphoterus dicrus*, Blenniidae; *Parablennius* sp., Blenniidae n.d., *Omobranchus punctatus*, Gerreidae; *Gerres* sp. and Pomacentridae; *Abudefduf* sp. (Table 4-3). Fish larvae hatched from pelagic eggs were rare and constituted only 8% of total abundance, while the remaining 92% were from demersal mode of spawning.

Table 4-3. Abundance (larvae.100 m⁻³) of fish larvae sampled from Kenyan lagoonal reef sites in March 2007 and April 2008. Mombasa (MOM), Nyali (NYA), Vipingo (VIP), Malindi (MAL) and Watamu (WAT). (Spawning mode SM given as; $D =$ demersal egg; $P =$ pelagic egg; $V =$ vivipary $Un =$ Unknown, after Leis and Rennis 1983, Leis and Trnski 1989).

		March 2007				April 2008					
TAXA	${\rm SM}$	MOM	NYA	MAL	WAT	MOM	NYA	VIP	MAL	WAT	
Acropomatidae											
Acropoma sp.	D	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\mathbf{0}$	$\boldsymbol{0}$	0.5	$\boldsymbol{0}$	
Aluteridae											
Osbeckia scripta	D	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\mathbf{0}$	0.8	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	
Antherinidae											
Hypoantherina	D	$\boldsymbol{0}$	0.2	$\boldsymbol{0}$	$\boldsymbol{0}$	0.2	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	
tropicalis											
Apogonidae											
Apogon sp.	$\mathbf D$	0.5	0.2	4.4	$\boldsymbol{0}$	4.3	1.8	2.2	3.4	3.6	
Pseudamia sp.	D	θ	θ	θ	$\overline{0}$	θ	θ	θ	0.5	Ω	
Cheilodipterus sp.	D	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\overline{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	1.2	
Belonidae											
Tylosurus crocodilus crocodiles	\mathbf{P}	$\boldsymbol{0}$	$\boldsymbol{0}$	$\mathbf{0}$	$\mathbf{0}$	$\mathbf{0}$	$\boldsymbol{0}$	$\mathbf{0}$	$\boldsymbol{0}$	0.4	
Blenniidae											
Blenniidae n.d.	D	$\boldsymbol{0}$	0.2	4.4	47.1	0.7	$\boldsymbol{0}$	$\boldsymbol{0}$	0.5	$\boldsymbol{0}$	
Parablennius											
pilicornis	$\mathbf D$	0.2	0.9	8.7	$\boldsymbol{0}$	6.1	7.7	2.2	0.5	7.6	
Omobranchus											
punctatus	D	0.5	3.8	$\boldsymbol{0}$	35.3	14.0	7.5	12.9	0.5	13.6	
Petroscirtes											
breviceps	$\mathbf D$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	2.3	2.2	$\boldsymbol{0}$	6.8	
Parablennius sp.	D	4.5	2.5	30.4	182.4	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	3.4	$\boldsymbol{0}$	
Bothidae											
Engyprosopon											
grandisquama	${\bf P}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	0.2	0.3	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	
Bothus sp.	\mathbf{P}	$\mathbf{0}$	$\overline{0}$	$\overline{0}$	$\overline{0}$	$\overline{0}$	Ω	0.6	$\overline{0}$	$\boldsymbol{0}$	
Carangidae											
Caranx sp.	\mathbf{P}	4.5	0.2	4.4	$\boldsymbol{0}$	1.1	2.3	3.4	2.9	0.4	
Scomberoides sp.	\mathbf{P}	0.9	Ω	4.4	$\boldsymbol{0}$	2.7	1.0	2.2	1.0	2.0	
Gnathodon											
speciosus	\mathbf{P}	$\boldsymbol{0}$	$\boldsymbol{0}$	4.4	5.9	0.2	Ω	$\mathbf{0}$	$\mathbf{0}$	1.2	
Carangoides sp.	\mathbf{P}	1.1	0.5	$\boldsymbol{0}$	$\boldsymbol{0}$	2.3	0.3	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	
Seriolina											
negrofasciata	\mathbf{P}	$\boldsymbol{0}$	$\boldsymbol{0}$	4.4	$\boldsymbol{0}$	$\boldsymbol{0}$	0.8	$\mathbf{0}$	$\mathbf{0}$	$\boldsymbol{0}$	
Chanidae											
Chanos chanos	P	$\boldsymbol{0}$	0.2	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\mathbf{0}$	
Centriscidae											
Centriscidae n.d.	D	0.2	$\boldsymbol{0}$	$\mathbf{0}$	$\boldsymbol{0}$	0.2	0.8	$\boldsymbol{0}$	$\mathbf{0}$	$\boldsymbol{0}$	
Cirrhitidae											
Cirrhitops sp.	\mathbf{P}	$\boldsymbol{0}$	θ	θ	$\overline{0}$	0.5	θ	θ	θ	$\boldsymbol{0}$	

Table 4-3 continues

TAXA	SM	MOM	NYA	MAL	WAT	MOM	NYA	VIP	MAL	WAT
Tetraodontidae										
Tetraodontidae n.d.		0.2	θ	θ	θ	0.2	θ			
Canthigaster sp.		0.2	θ	θ	θ	θ	θ			
Trichonodontidae										
<i>Trichonotus</i> sp.	Un	0.2	0.7		5.9	0.5	0.8	3.9	0.5	
Total		47	57	235	2688	172	73	193	55	70

4.2.2 Larval abundance

There was a distinct gradient in larval abundance (larvae.100 m⁻³ \pm SE) along the coast during March 2007 (Fig. 4-5a). Peak abundance was observed on the north coast at Watamu Marine park (414 \pm 239) with progressive decline to the south at Mombasa Marine park (4.7 \pm 1.0) and Nyali (5.7 \pm 1.7). However, the extreme northward site of Malindi recorded lower abundance (31.0 ± 10.5) than Watamu (Fig. 4-5a), indicating variability in larval abundance at local scales. There was a significant difference in larval abundance between the four sites ($F = 14.6$, $p < 0.05$) with Tukey HSD test partitioning the difference between Mombasa and Malindi ($p < 0.05$), Mombasa and Watamu ($p <$ 0.001), Malindi and Nyali ($p < 0.05$) and Nyali and Watamu ($p < 0.01$).

In April 2008, overall larval abundance (larvae.100 m⁻³ \pm SE) declined northwards along the coast opposite to the pattern of 2007, perhaps reflecting annual differences in larval sources (Fig. 4-5b). Peak larval abundance occurred on the southern sites of Mombasa (16 ± 5.1) and Vipingo (19 ± 1.0) with the northern sites recording lower larval abundance at Watamu (8.0 \pm 1.8) and Malindi (6.0 \pm 0.9) (Fig. 4-5b). There was significant difference in mean abundance between sites ($F = 7.24$, $p < 0.05$) with Tukey HSD test revealing the differences to occur between Mombasa and Malindi ($p = 0.040$), Vipingo and Nyali ($p = 0.007$), Vipingo and Malindi ($p \le 0.001$) and Vipingo and Watamu ($p < 0.05$), respectively.

Fig 4-5. The variation of mean fish larval abundance (larvae.100 m⁻³ ± SE) between sites along the Kenyan coast in (a) March 2007 and (b) April 2008.

4.2.3 Species diversity and richness

Species diversity and richness declined from southwardly located sites (Mombasa) to northerly ones (Watamu) during both March 2007 and April 2008. In March 2007, Mombasa site had the highest species diversity ($H' = 2.39$) and richness ($d = 4.01$) as compared to the northern Watamu site which had the least diversity $(H' = 1.93)$ and richness ($d = 2.93$). Nyali and Malindi sites had intermediate diversities of H' = 1.57 and 1.34 with corresponding richness of $d = 2.32$ and 2.18, repectively. In April 2008, the same trend was repeated with Mombasa having a diversity $H' = 2.09$ and richness $d = 3.36$ as compared to Watamu site with H' = 1.13 and $d = 1.63$. Species diversity in Nyali, Vipingo and Malindi sites was $H' = 2.34, 2.21,$ and 1.88, respectively, with corresponding richness $d = 3.87, 3.44$ and 3.02 respectively. The diversity values in 2008 were higher than in 2007, likely due to dominance of a few species like gobies and blenniids in the samples of 2007.

Relative abundance (%) of dominant families varied between sites and years, with the most dominant families being Gobiidae, Blenniidae and Pomacentridae (Fig. 4-6). In March 2007, the Gobiidae were dominant in Watamu (87.5%) and Nyali (64.4%), while in April 2008, the Gobiidae were dominant in Mombasa (67.5 %), Vipingo (49.0%) and Malindi (22.4%). The Blenniidae occurred most in the northern sites of Malindi (22.2%) in March 2007 and Watamu (41.7%) in April 2008. The Pomacentridae were found mainly distributed in Mombasa (23.7%) and Malindi (20%) in March 2007 and in Nyali (32.1%) and Vipingo (23.7%) in April 2008 (Fig. 4-6).

Fig.4-6 The variation in relative abundance (%) of the dominant families of fish larvae between sites along the Kenyan coast in March 2007 and April 2008.
Other families that varied in abundance within sites over the two years were; Carangidae, Labridae, Scaridae, Apogonidae, Terapontidae and Engraulidae (Fig. 4-6).

In 2007, the species cumulative dominance curve for Watamu site was highly elevated as compared to other sites (Fig. 4-7a), suggesting that the site was characterized by high dominance of species and lowest species diversity. Mombasa and Malindi sites had low curvatures suggesting low dominance of species; however, Mombasa site had higher species ranking which suggested a higher diversity (Fig. 4-7a). Species abundance curve for Nyali site was in between that of Watamu, Mombasa and Malindi sites, indicating an intermediate dominance of species and diversity (Fig. 4-7a).

In 2008, a different pattern in species dominance and diversity was observed (Fig. 4- 7b). For example, the species curve for Mombasa site was highly elevated, suggesting high dominance and low diversity of species unlike in 2007 (Fig. 4-7b), while Vipingo, Watamu and Nyali sites had intermediate diversities and dominance. Malindi Marine Park showed highest diversity and low dominance of species not observed in 2007 (Fig. 4-7b).

Fig. 4-7. Cumulative species dominance curves from reef sites on The Kenyan coast during (a) March 2007 (b) April 2008.

4.2.4 Spatial patterns of larval assemblages

Correspondence Analysis plot for 2007 showed that the southern sites of Mombasa and Nyali had similar larval assemblage mainly dominated by *Chromis* sp. (Pomacentridae) (Fig. 4-8a), while the northern sites of Watamu and Malindi showed distinct larval assemblages. Species of larvae associated with Watamu were Blenniidae n.d., *Parablennius pilicornis* (Blenniidae), Gobiidae n.d. (Gobiidae), *Corythoichthys amplexus* (Syngnathidae) and Platycephalidae n.d. (Platycephalidae) (Fig. 4-8a) while, those associated with Malindi were Nemipteridae n.d. (Nemipteridae), *Sphyraena jello* (Sphyraenidae), Leiognathid n.d. (Leiognathidae), *Stolephorus commersonii* (Engraulidae), *Abudefduf* sp. (Pomacentridae), *Parablennius* sp. (Blenniidae), Labridae n.d. (Labridae), and *Calotomus* sp. (Scaridae) (Fig. 4-8a).

In 2008, there was similarity in larval assemblage between Malindi and Mombasa not observed in 2007 (Fig. 4-8b). The sites were dominated by *Stolephorus commersonii*, *Apogon* sp. (Apogonidae), *Caranx* sp.(Carangidae), Labridae n.d. and *Coryphoterus dircus* (Gobiidae)(Fig. 4-8b). The larval pool of *Petroscirtes breviceps* (Blenniidae), *Terapon theraps* (Terapontidae), *Parablennius pilicornis*, *Omobranchus punctatus* (Blenniidae), *Corphoterus dircus*, *Sphyraena jello*, *Bathygobius soporator* (Gobiidae), Gobiidae n.d*.* and *Abudefduf* sp. was more closely associated with Nyali site (Fig. 4-8b), although the same species were represented in Watamu and Vipingo. The species *Paramonacanthus cingalensis* (Monacanthidae) and *Gerres* sp. (Gereidae) were more associated with Watamu and Vipingo sites, respectively (Fig.4-8b.)

Fig. 4-8 Simple Correspondence Analysis ordination of 15 dominant fish larval species from different sites along the Kenyan coast in (a) March 2007 and (b) April 2008.

4.2.5 Spatial distribution of early life history stages

The percentage abundance of preflexion, flexion and postflexion stage larvae varied between sites and years (Fig. 4-9 a & b). In 2007, preflexion larvae were found to increase northwards from Mombasa (18.2%) to Watamu (86.4%), while postflexion larvae reduced along the same longitudinal axis (Mombasa 59.3%, Nyali 43%, Malindi 40.8% and Watamu 6.8%) (Fig. 4-9a). The percentage of flexion larvae was similar at Mombasa (22.5%), Nyali (28.6%) and Malindi (24.5%), but lower in Watamu (8.5%).

In 2008, a reverse trend was observed, with preflexion larvae reducing northwards from Mombasa Park (76 %) to Watamu Marine Park (2 %) (Fig. 4-9b). Postflexion larvae increased from 18.9% in Mombasa to 94.8% in Watamu (Fig. 4-9b), while flexion stage larvae showed variable random distribution between sites; Watamu (1.2%), Mombasa (3.0%), Nyali (17%), Malindi (19.3%) and Vipingo (28.7%).

The early life history stages of the dominant species in the samples (Gobiidae n.d., *Abudefduf* sp., *Parablennius* sp., and *Omobranchus punctatus*) showed variation between sites and years (Fig. 4-10). Gobiidae n.d. occurred in high percentages as preflexion stage larvae on the northward sites of Malindi and Watamu in both years, while the southward sites of Mombasa and Nyali had high prevalence of flexion and postflexion stage larvae of the species (Fig. 4-10). *Abudefduf* sp. occurred in high percentage as postflexion stage larvae at all sites over the two years, with preflexion larvae of the species being consistently abundant at Nyali site. This perhaps indicated a possible spawning site for this species (Fig. 4-10).

Fig 4-9. Percentage abundance of preflexion, flexion and postflexion stages of all fish larvae sampled from reef sites along the Kenyan coast in (a) March 2007 and (b) April 2008.

Fig. 4-10 Variation in percentage abundance of preflexion, flexion and postflexion stage of larval fish species sampled from reef sites along the Kenyan coast in 2007 and 2008.(Mom = Mombasa, Nya = Nyali, Vip = Vipingo, $Mal = Malindi$, Wat = Watamu)

High predominance of preflexion stage larvae of *Parablennius* sp. occurred in Mombasa and Malindi sites in both years, while Vipingo and Watamu had high postflexion stage larvae of this species in 2008. The gobiid *Omobranchus punctatus,* occurred in high proportion as flexion and postflexion stages in the southward sites such as Mombasa and Nyali in 2007, however, in 2008, high proportion of postflexion larvae were sampled in northward sites such as Vipingo, Malindi and Watamu (Fig. 4-10).

4.3 Hatch date distribution and growth variability of the commerson's

anchovy, *Stolephorus commersonii* **(Lacepede, 1803) larvae and juveniles**

4.3.1 Hatch date distributions

Analysis of the hatch dates of *S. commersonii* juveniles from the 2005 samples indicated the existence of three major spawning periods January-March, August-October, and December 2005. This conclusion is derived from the modal frequencies of the monthly samples (Fig. 4-11 a-j). For example, the March $12th$ samples indicated that spawning occurred during January-February with a peak in late January (Fig. 4-11 a). For samples collected in April $28nd$, spawning occurred in early March (Figure 4-11 b), while those collected in September, suggested spawning to occur in mid August to early September (Fig. 4-11 d).

Fig. 4-11. Hatch date distribution of juvenile *Stolephorus commersonii* in monthly samples (a-j) from Malindi Marine Park, Kenya, during 2005 and 2006.

Specimens collected in 22nd October were likely spawned in late August with a little spillover to early September (Fig. 4-11e). Low sample sizes of May 2005 precluded definite conclusions on spawning time from the sample.

Analysis of hatch dates of the monthly samples in 2006 identified two major spawning periods to occur from December 2005-February 2006 and from May-June (Fig. 4-11 fj). For example, specimens collected on $23rd$ January and $21st$ February indicated spawning to occur from mid-December 2005 (Fig. 4-11 f) to early January 2006 (Fig. 4- 11g). The specimens collected on $18th$ April 2006 and $26th$ May indicated spawning to occur from mid to end of February 2006 (Fig. 4-11 h and i). Spawning in late May to early June 2006 was detected from the June $24th$ samples (Fig. 4-11j). The derived spawning seasonality for the species are summarised in Table 4-4.

Table 4-4 Summary of hatch dates (spawning period) of *Stolephorus commersonii* juveniles collected from Malindi Marine Park from March 2005 to June 2006. (No larvae were collected from May-July 2005)

The monthly growth rates derived from regression of length on age of *S. commersonii* larvae and juveniles obtained from plankton and light trap samples of 2005 and 2006 are shown in Table 4-5. Growth rates of *S. commersonii* larvae varied greatly between months. Fastest absolute growth rate was obtained in the northeast monsoon month of December $(0.206 \text{ cm}.day^{-1})$, while the lowest was in the southeast monsoon month of July 2005 (0.056 cm.day⁻¹) (Table 4-5 a). There was a significant difference (F = 6.90, p \leq 0.05) in growth rate between the months and Tukey's HSD test subsequently attributed the difference to the higher growth rates in March and September 2005 (Table 4-5 a).

For the juveniles, fastest growth occurred in the intermonsoon months of March (0.119 cm.day⁻¹) and September (0.099 cm.day⁻¹) of 2005 (Table 4-5 b). Slowest growth occurred in the southeast monsoon months of April 2005 $(0.044 \text{ cm}.day^{-1})$, April 2006 $(0.010 \text{ cm. day}^{-1})$ and May 2006 (cm.day⁻¹). There was significant difference in growth rates between months ($F = 7.91$, $p < 0.05$), and Tukey's HSD test attributed the difference to the months of March 2005, January 2006 and June 2006. There was no significant inter-annual variability in growth rate (cm.day⁻¹) of juveniles with a growth rate of 0.075 ± 0.036 and 0.049 ± 0.026 in 2005 and 2006, respectively.

Table 4-5 Monthly growth functions of *Stolephorus commersonii* for (a) larvae and (b) juveniles derived from regression of length (TL cm) on age (days). The x coefficient represents monthly growth rate (cm.d⁻¹). n = number of larvae or juveniles analysed.

(a)		T.L	T.L			ANCOVA
Larvae	$\mathbf n$	Min	Max	Equation	\mathbf{R}^2	$F = 6.90, p < 0.05$
Mar 2005	11	0.5	1.8	T.L (cm) = $0.120x +0.097$	0.96	0.05 (Mar. > all months)
Apr	8	0.4	1.5	$T.L$ (cm) = 0.131x + 0.187	0.79	${}_{0.05}$
May	36	0.3	1.3	T.L $(cm) = 0.132x + 0.086$	0.78	${}_{0.05}$
June	39	0.3	2.2	T.L $(cm) = 0.132x - 0.076$	0.76	${}_{0.05}$
July	70	0.3	1.1	$T.L$ (cm) = $0.056x + 0.151$	0.28	${}_{0.05}$
Aug	44	0.4	1.2	$T.L$ (cm) = $0.099x + 0.011$	0.29	${}_{0.05}$
Sept.	47	0.4	1.7	T.L $(cm) = 0.084x + 0.098$	0.47	< 0.05 (Sept.> all months)
Dec.	12	0.4	1.9	T.L $(cm) = 0.206x - 0.537$	0.89	${}_{0.05}$
(b)						ANCOVA
Juveniles				Equation	\mathbf{R}^2	$F = 7.91$, p < 0.05)
Mar 2005	62	1.4	7.8	$T.L(cm) = 0.119x + 1.004$	0.95	0.05 (Mar. > all months)
Apr	218	5.5	7.8	$T.L$ (cm) = 0.044x + 4.28	0.22	${}_{0.05}$
May	15	5.2	7.9	T.L (cm) = $0.078x + 3.64$	0.35	${}_{0.05}$
Sept	40	2.9	9.4	T.L (cm) = $0.099x + 3.50$	0.75	${}_{0.05}$
Oct.	101	4.2	9.4	T.L (cm) = $0.093x + 2.64$	0.54	${}_{0.05}$
Dec.	37	2.8	8.4	T.L (cm) = $0.022x + 5.69$	0.26	${}_{0.05}$
Jan 2006	95	3.5	7.7	$T.L$ (cm) = $0.068x + 2.28$	0.53	< 0.05 (Jan. $<$ all months)
Feb	94	6.4	7.8	T.L $(cm) = 0.048x + 3.96$	0.11	${}_{0.05}$
Apr	86	4.5	7.8	T.L (cm) = $0.010x + 6.63$	0.03	${}_{0.05}$
May	95	2.6	8.0	$T.L$ (cm) = $0.042x + 4.49$	0.15	${}_{0.05}$
June	98	2.6	8.0	$T.L$ (cm) = $0.078x + 1.45$	0.64	< 0.05 (June $<$ all months)

The deviations of monthly growth rates from the overall (all months) growth of *S. commersonii* larvae and juveniles are shown in Figure 4-12. The overall growth rates (cm day ⁻¹) for larvae and juveniles were 0.11 ± 0.04 and 0.064 ± 0.03 respectively.

For the larvae, positive growth was registered in December, while below average growth rates occurred in the southeast monsoon months of July and October (Fig. 4- 12a). Juveniles had highest positive growth during the NE monsoon month of March and December 2005. Unlike the larvae, juveniles registered net growth in the southeast monsoon months of May, September and October 2005 and June 2006 (Fig. 4-12b). However, below average growth were also registered in the southeast monsoon months of April 2005, and October 2005 (- 0.05 cm day⁻¹) and May 2006 (- 0.022 cm day⁻¹) (Fig. 4-12 b)

A stepwise multiple regression analysis of biophysical variables (zooplankton abundance, chlorophyll-a, temperature and salinity) on larval growth rate indicated a significant relationship between growth rate and temperature (t = 4.59, p = 0.01, r^2 = 0.62). There was, however, lack of significant relationship between larval growth rate and salinity (t = - 2.57, $p > 0.05$), zooplankton abundance (t = 1.33, $p > 0.05$) and chlorophyll-a (t = -0.47 , p > 0.05). A significant relationship occurred between juvenile growth and with chlorophyll-a (t = 2.47, p < 0.05, $r^2 = 0.4$), but none was detected between juvenile growth and salinity (t = - 2.12, p > 0.05), temperature (t = 1.84, p > 0.05), and zooplankton abundance ($t = 0.43$, $p > 0.05$).

Fig. 4-12. Deviations of monthly growth rates of *Stolephorus commersonii* from the overall mean growth rates for (a) larvae and (b) juveniles in Malindi Marine Park, Kenya, between March 2005 - June 2006. Positive values indicate months of higher rates, while negative values indicate months of slow growth.

4.3.2 Growth models

The von Bertallanffy plot of length-at-age data for *S. commersonii* juveniles yielded the following equation:

$$
-\text{In (1-L (t)/L\infty)} = 8.329 \text{ (t)} + 0.0581 \text{ r}^2 = 0.44 \text{ (Fig. 4-13)}
$$

The growth coefficient *K* was then derived from the slope of the equation $(K = b)$ as 8.3296 per year, while t_0 was derived from $t_0 = -a/b$ (Sparre and Venema 1998) as 0.00696 cm yr¹.

Having derived the growth parameters K and t_o , the growth models were then fitted as:

VBGF =
$$
L_t = 9.7 \{1-\exp[-8.329(t+0.00696)]\}
$$

($r^2 = 0.97$; AIC = 4379.6) (7)

Gompertz
$$
L_t = 9.7 \exp(-\exp(-8.329(t - 0.00696)))
$$
 (8)
\n $(r^2 = 0.94; \text{ AIC} = 4512.6)$

Logistic
$$
L_t = 9.7/(1 + \exp(-8.329(t - 0.00696)))
$$
 (9)
\n $(r^2 = 0.94; \text{ AIC} = 4824.4)$

Fig. 4-13. The von Bertalanffy plot for estimating growth parameters *K* and *to* for *Stolephorus commersonii*.

The models predicted different growth patterns for younger fish but converge for older fishes approaching asymptotic length (Fig. 4-14). Older fish showed slower growth approaching asymptotic size and low variability of length-at-age. The VGBF, Gompertz, and Logistic growth curves predicted an asymptotic length of about 8.5 cm for juveniles which differed from the observed maximum size of 9.7 cm used in this study.

The Logistic model predicted a larger size of 6.4 cm for the youngest fish in the sample at 0.015 yr old (Fig. 4-14) as compared to 4.4 cm and 1.8 cm predicted by Gompertz and VBGF, models, respectively, for the same fish. This indicates the choice of model to use is critical for younger fish. The minimum value of *AIC* was generated by the von Bertalanffy model ($AIC = 4379.6$) indicating that it was relatively the best fitting model.

The combined data of juveniles and larvae fitted to the non-linear Schnute (1981) model is shown in Figure 4-15. The growth curve possesses an upper asymptote and a monotonic lower linear curve. This indicates an intitial period of rapid growth by the larvae which smoothly declines to represent juvenile growth (at inflexion age of 26 days indicated by x, see Fig. 4-15) to asysmptotic length.

Fig. 4-14 The pattern of growth of *Stolephorus commersonii* juveniles from Malindi Marine Park predicted by von Bertalanffy,Gompertz and Logistic models.

Fig 4-15 Growth curve of *Stolephorus commersonii* larvae and Juveniles (combined data) fitted to a non-linear Schnute (1981) model**.** Notice the inflexion growth point $x = 26$ days.

4.4 Diel and lunar variations in larval supply to Malindi Marine Park

4.4.1 Diel cycles

From the six 24-hour sampling series, a total of 394 larvae were collected representing 39 species from 27 families (Table 4-6). During neap tides, *Stolephorus commersonii* (Engraulidae), *Apogon* sp. (Apogonidae), *Parablennius* sp. (Blenniidae) and Gobiidae n.d. (Gobiidae) dominated the park, while during spring tides *Stolephorus commersonii*, *Leptoscarus vaigensis* (Scaridae), Labridae n.d. and *Parablennius* sp. were dominant (Table 4-6). The mean abundance (larvae.100m⁻³ \pm SE) of larvae during spring tide was 951 \pm 408 and was significantly higher (t = 2.02, p < 0.05) than that recorded during neap tides (395 ± 261) (Table 4-6).

During spring tides, mean larval abundance (larvae.100m⁻³ \pm SE) had a distinct nocturnal peak with abundance increasing from 205.3 ± 197 at 1800 hrs to a peak of 1184 ± 1060 at 2400 hrs (Fig. 4-16 a), which was about 13 fold greater than day time concentrations of 88.3 \pm 45.0 (at 0600 hrs) and 90.4 \pm 88.0 (at 1200 hrs). Larval abundance was lowest in the park at 1200 hrs (26.0 ± 13.3) during the spring tide (Fig. 4-16 a).

During neap tides, mean larval abundance increased from 57.1 ± 47.4 at 1200 hrs to a peak of 246.3 ± 210.4 at 1800 hrs (Fig. 4-16 b). Thereafter, larval abundance in the park declined to levels of 90 ± 50.8 and 103 ± 68.1 at 2400 and 0600 hrs, respectively

Table 4-6. Differences in mean abundance $(larvae.100m⁻³)$ of fish larvae between spring and neap tides during six 24 hr sampling series in Malindi Marine Park, Kenya. (-) indicates lack of larvae, \pm indicate standard error of the mean.

Fig 4-16 Variation of the total fish larval abundance with tidal heights for the six 24hr- sampling series during (a) spring tides and (b) neap tides in Malindi Marine Park, Kenya. (vertical bar represent SE.)

No significant effect of tidal regime, time of day and interaction effect (tidal regime x time) were found on larval abundance (Table 4-7). Similarly, no significant effect of tidal regime and time of day were found for abundance of *Stolephorus commersonii* and Gobiidae n.d. (Table 4-7), however a significant effect of tidal regime was found for abundance of Blenniidae n.d. (Table 4-7) suggesting a lunar pattern of larval supply, but not for the interaction effect of tidal regime x time (Table 4-7).

Larval supply to the park of the dominant species (e.g. *Stolephorus commersonii*, Labridae n.d., *Parablennius* sp. and Gobiidae n.d.) was maximum during nocturnal spring tide hours (2400 hrs) (Fig. 4-17), suggesting that these larvae mostly immigrated into the park during spring night-time. However, during day time spring tides, abundance was low for most species except for the *Parablennius* sp. at 0600hrs (Fig 4- 17).

During neap tides, larvae of these species were almost absent during the day while appearing in comparatively low numbers at night (Fig. 4-17). The cardinal, *Apogon* sp., was absent during spring tides for most of the time except at 0600 hrs, however, during neap tides, the species unlike the others, was more abundant during the day at 1200 hrs and at 1800 hrs (Fig. 4-17).

Table 4-7 Two-way ANOVA results on the influence of tidal regime (spring vs. neap), Time of sampling (night vs. day) and interaction effects on the mean larval abundance (larvae.100m⁻³) of the common fish larvae families within Malindi Marine Park, Kenya. * significant at p < 0.05

Fig. 4-17 Diel variation in abundance of dominant larval species during six 24-hr sampling series at Malindi Marine Park, Kenya. (vertical bar represent SE)

A regression analysis of total larval abundance on tidal heights for the whole 24-hr sampling data set indicated a lack of significant relationship (r^2 = 0.015. F = 0.430, P = 0.517), (see also Fig. 4-16 a & b). The dominant species *Stolephorus commersonii*, Labridae n.d., *Parablennius* sp., Gobiidae n.d., and *Apogon* sp. similarly showed insignificant relationship with tidal height (*Stolephorus commersonii* $r^2 = 0.004$, F = 0.114, P = 0.738), Labridae n.d. $(r^2 = 0.002, F = 0.056, P = 0.813)$, *Parablennius* sp., $(r^2 = 0.006, F = 0.187, P = 0.668)$, Gobiidae n.d. $(r^2 = 0.021, F = 0.608, P = 0.441)$ and *Apogon* sp. (r^2 = 0.032, F = 0.080, P = 0.767).

4.4.2 Lunar patterns

The total number of larvae sampled was higher during new moon periods ($n = 2886$) as compared to full moon $(n = 2824)$. However, no significant differences in mean larval abundance was detected between the two lunar cycles for comparable number of samples of 204 and 200 for new and full moon, respectively ($t = 1.84$, $p = 0.066$). From the spectral analysis of total larvae (all families) and dominant species, lunar patterns of fish larval abundance were identified. Peak larval supply for all larvae to Malindi Marine Park occurred after a 30 and 25 day cycles as shown by the spectral analysis periodiogram (Fig. 4-18). This observation is further supported by the Autocorrelation Function plot (ACF) that revealed significant peak larval abundance ($p < 0.05$) arriving in the park at 30 days intervals (Fig. 4-18).

Fig. 4-18 Time-series spectral analysis of mean total fish larval abundance from March 2005 to December 2006 in Malindi Marine Park, Kenya. Lower left spectral density plot shows the two cycling peaks within the time series (period in days) of the larvae confirmed by Autocorrelation Function plots (lower right) of the raw data where vertical lines are 2 X SE). Full moon (\circ) and new moon phase(\bullet).

For Blenniidae n.d., the periodiogram showed a major peak at 30 days and a minor peak at 15 days validated by a significant activity on the AFC plot at 30 day intervals (Fig. 4-19). This pattern indicating a lunar and semi-lunar supply of the species to the park.

The *Stolephorus commersonii* larvae showed a strong peak in larval abundance in the park at 30 day cycle, and a minor peak at 27 days. These peaks were confirmed on the ACF plot with a significant peak at 30 days (Fig. 4-20). Similarly, the Gobiidae n.d. showed strong evidence of lunar based abundance in the park, with a peak at 30 and 25 days intervals as shown by the periodiogram and supported by the ACF plot (Fig. 4- 21).

Fig. 4-19 Time series spectral analysis of Blenniidae n.d. from March 2005 to December 2006 in Malindi Marine Park. Lower left spectral density plot shows the two cycling peaks within the time series of the larvae confirmed by Autocorrelation Function plots (lower right) of the raw data where vertical lines are $2 \times SE$). Full moon (\circ) and new moon $phase($.

Fig. 4-20 Time series spectral analysis of *Stolephorus commersonii* from March 2005 to December 2006 in Malindi Marine Park. Lower left spectral density plot shows the two cycling peaks within the time series of the larvae confirmed by Autocorrelation Function plots (lower right) of the raw data where vertical lines are 2 X SE). Full moon (\circ) and new moon $phase (\bullet)$.

Fig.4-21 Time series spectral analysis of Gobiidae n.d. from March 2005 to December 2006 in Malindi Marine Park. Lower left spectral density plot shows the two cycling peaks within the time series of the larvae confirmed by Autocorrelation Function plots (lower right) of the raw data where vertical lines are $2 \times SE$). Full moon (\circ) and new moon $phase (\bullet)$.

4.5 Light trap evaluation and performance

4.5.1 Light trap catch rates

Total catch rates expressed as number of fish caught per hour (fish.hr⁻¹) was used to estimate larval abundance. The highest catch rates were observed during March-April of a two year study period. These catch rates, costs and comparisons with other traps are shown in Table 4-8. The catch rates which ranged from $1.3 - 263$ fish hr⁻¹ in March (peak season) were higher than that of Stobutzki and Bellwood trap $(5.4 - 42.1)$ fish hr^{-1}) and the bucket trap (29.1 – 30.4 fish hr^{-1}) (Watson *et al.* 2002) (Table 4-8).

4.5.2 Species composition

A total of 25 families and 65 species of fish larvae were caught using the light trap. Mean sizes and taxa sampled are summarised in Table 4-9. The dominant fish larvae caught were from families; Caesionidae, Tetraodontidae, Lutjanidae and Apogonidae, in order of decreasing abundance. The traps also caught juveniles of pelagic fish species like the Engraulidae (*Stolephorus commersonii*), Pristigasteridae (*Pellona ditchella*) and other clupeidae (Table 4-9). Other organisms that were captured by the light traps included different groups of crustaceans; Copepoda, Amphipoda, Ostracoda, Caridea (Palaemonid larvae), Brachyuran megalopa (Portunidae), Brachyuran larvae, Stomatopoda, Mysiidacea, Polychaeta, Hydromedusae (Jelly fish), Opisthobranchia (Sea slugs), Pycnogonids, Syllaridae (Lobster larvae), and Cephalopoda (Squid larvae) among others.

Table 4-8. Catch rates and cost implications of different light trap designs.

*** most abundant ** moderately abundant * abundant

DISCUSSION

5.1 Seasonality of larval supply to Malindi and Watamu National Marine Parks

Larval abundance in both Malindi and Watamu Parks was more pronounced during the calm NEM season. This observation suggests that spawning by most fish was likely taking place during this period. Significantly lower abundances of fish larvae occurred during the SEM season in both parks likely due to turbulent conditions that prevail along the Kenyan coast, causing unfavourable conditions for larval survival, and enhancement of larval transport offshore in this season (Kaunda-Arara *et al.* 2009). This seasonal larval dominance concurs with findings in Kenya (Nzioka 1979; McClanahan 1988; Kulmiye *et al.* 2002; and Kaunda-Arara *et al.* 2009) and Seychelles (Robinson *et al.* 2004), where spawning and abundance of pre-settlement larvae were found to be highest during the NEM season. It is likely that the calm conditions and elevated temperatures during this season provide conditions necessary for successful spawning.

The synchrony in larval abundance and zooplankton density in Malindi Park indicated that environmental productivity had an influence on larval supply to the park. However, this correlation was not significant for Watamu Park indicating that overriding factors controlling larval abundance varied spatially. Temperature and zooplankton abundance significantly correlated with larval abundance in Malindi, while temperature alone seemed important in Watamu Park. Temperature has been confirmed as an important environmental variable influencing ichthyoplankton assemblages (Belyanina 1986;

Kingsford 1998; Tzeng and Wang 1993; Harris *et al.*1999). Synchrony of zooplankton production and larval abundance has previously been reported in other studies including from the shelf waters of KwaZulu-Natal (Carter and Schleyer 1978) and St Lucia Estuary, South Africa (Harris *et al.*1999).

Species richness and diversity were not significantly different between seasons, however, diversity was found to be lower during the NEM season compared to the SEM season mainly due to predominance of a few species from the families Blenniidae and Gobiidae.

In this study, Blenniidae, Gobiidae, Pomacentridae and Engraulidae were common during the NEM season while, Apogonidae and Siganidae were abundant during the SEM, suggesting that spawning could also be occurring during the SEM season. The ichthyoplankton composition at the family level in both parks is comparable with results from other tropical systems. For example the families; Gobiidae, Clupeidae, Tripterygiidae, Engraulidae, Blenniidae and Labridae are dominant groups in South African subtropical habitats (Harris and Cyrus 1995; Harris *et al.* 1995). In many temperate and tropical estuarine and coastal habitats, gobies are a particularly large component of fish larval assemblages (Blabber *et al.*1997).

The temporal synchrony in larval abundance in both parks indicated that processes affecting larval supply were similar at the between-park spatial scale. Larval groups between the parks were found to be different with more larvae with pelagic mode of spawning (e.g. *Stolephorus commersonii*) being found in Malindi Park compared to

Watamu, which had a higher proportion of larvae from demersal spawning mode (e.g. Gobiidae n.d.). This could be attributed to differences in habitat types. Watamu Park is a shallower and more sandy habitat with restricted access to the open sea as compared to Malindi which has a deeper lagoon and more open channels to the sea. The segregation of larval groups at within-park scale may indicate existence of features that contribute to larval retention and patchiness as could have been the case for Watamu Park. 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 parks.

Preflexion larvae comprised over 80% of the total number of larvae in both parks indicating the parks and the adjacent vicinity are important spawning grounds for fish. The observed variation in percentage frequency of developmental stages of larvae is indicative of temporal differences in spawning activity of adults, settlement of larvae, mortality or transport of larvae from distance or natal sources (Leis 1993). For example in Malindi Park, the concomitant increase in flexion and postflexion stage larvae and consequent reduction in preflexion larvae in March, 2005, 2006 and January 2007 (NEM months) may have suggested settlement activity during this period. Likewise in Watamu, similar trends were observed in July (SEM month) and November (NEM month) 2006 likely indicating differences in settlement period of larvae between parks.

5.2 Alongshore distribution of fish larvae in lagoonal reefs

In this study a total of 69 families and 110 species of fish larvae were recorded from the reef sites on the Kenyan coast. The ichthyoplankton of the near shore reef lagoons in Kenya were therefore found to be diverse and typical of coastal tropical ichthyoplankton. Of the larvae sampled, 92% were hatched from demersal eggs while only 8% were from pelagic eggs. The demersal groups Gobiidae; Blenniidae and Pomacentridae accounted for 88 % of the larvae in both 2007 and 2008 reinforcing the notion that small demersal shore fishes often dominate ichthyoplankton assemblages over continental shelves (McIIwain 2003; Munk *et al.* 2004; Sampey *et al.* 2004). The proportion of the three dominant families along the five sites did not vary significantly; they likely represent the typical taxa of fish larvae to be expected in shallow coastal lagoons of Kenya.

There was a gradient in total larval abundance in 2007 from low densities in southward sites (e.g. Mombasa) to high densities in northern sites of Malindi and Watamu. This gradient may have been caused by spatial variation in spawning patterns along the coast and may suggest northward location of spawning sites in 2007. However, lack of distinct pattern in distribution of larval stages in 2008 likely indicates inter-annual variation in spawning sites. The within and between-year variation in larval abundance at sites indicated that the factors controlling larval supply to reef sites were variable. The middle to northward sites (e.g.Vipingo to Malindi and Watamu) had consistently higher abundances of gobiid and blenniid species perhaps indicating a northward source of these larvae.

Species diversity and richness were found to decline from southward sites (e.g. Mombasa) to northward locations (e.g. Watamu) during both years. This trend was attributed to dominance of gobiid and blenniid larvae in the northward sites. Except for the Mombasa Marine Park, the larval pool from the other marine protected sites (e.g. Malindi and Watamu Marine Parks) was less diverse than the unprotected sites (Vipingo and Nyali). This likely indicates lack of influence of area protection on planktonic processes and that factors other than area protection influence structure of larval pools on reef sites (Cudney-Bueno *et al.* 2009; Grorud-Colvert and Sponaugle 2009).

Cumulative species abundance curves suggested relatively lower diversity and high dominance at Watamu site in 2007 likely caused by high occurrence of preflexion larvae of Gobiidae n.d. and *Parablennius* sp. (Blenniidae) at this site. In 2008, dominance of preflexion stage *Coryphoterus dicrus* (Gobiidae) resulted in low species diversity at Mombasa site.

Correspondence Analysis revealed existence of distinct larval pools at sites, whose structure varied between years. Seasonal and intra-seasonal changes in structure of larval assemblages are a common feature in tropical waters (Leis 1993), and may reflect spawning activities of adults, differential larval survival, transport or a combination of these processes (Heath 1992; Leis 1993). Variability in larval distribution and abundance along a coast may be caused by factors such as site isolation, topographic complexity and flow variability (Sponaugle *et al.* 2002) as well as adult spawning behaviour, mode of spawning and larval behaviour (Leis 1993). The fact that most larvae were in the

preflexion stage in this study, suggests a high degree of local production at the study areas (Leis 1993).

Patterns of variation of preflexion and postflexion abundance can provide information on processes regulating assemblage structure (Leis 1993). It is expected that the bigger the larvae, the higher the chances of net avoidance which may bias the results when comparing preflexion and postflexion larvae. However in this study, net avoidance was minimized as much as possible by towing the net besides the boat as opposed to behind the boat. In 2007, there was high northward occurrence of preflexion stage larvae at Malindi and Watamu and high proportion of postflexion larvae in southwardly located sites of Mombasa and Nyali, suggesting possible spawning in the north coast with likely transport of the postflexion larvae to the southern sites. However, in 2008, preflexion stage larvae dominated the southwardly located sites of Mombasa and Nyali with high prevalence of postflexion larvae in the northern sites of Malindi and Watamu. This observation suggested that despite the likely overall spawning by species in the north, some species seem to indicate southward spawning.

The availability of all life history stages of some species from the families Blenniidae, Gobiidae and Pomacentridae at sites suggested possibility of larval retention and completion of life cycles at the same lagoons. However, sites such as Mombasa, Nyali and Malindi which had a higher proportion of larvae of pelagic origin like *Stolephorus commersonii*, (Engraulidae), *Caranx* sp., *Scomberoides* sp., *Gnathodon speciosus* (Carangidae), Scaridae n.d., Labridae n.d. and *Sphyraena jello* suggested they were more

open to the influence of oceanic waters and that the lagoons are important nursery habitats for these larvae.

5.3 Hatch dates and growth rates of *Stolephorus commersonii*

Hatch dates (or spawning period) of *S. commersonii* in Malindi Marine Park falling in January-March and August-October, were synchronized with periods of high larval growth of March-June and December in both 2005 and 2006, during warmer temperature months. Larvae spawned at periods favouring higher growth rate likely outgrow predation and enhance recruitment to benthic population (Houde 1987; Wilson and Meekan 2002). The spawning seasonality found in this study concurs with other studies done along the Kenyan coast which, have documented spawning of most species of fish to occur within the same period (Nzioka 1979; Kaunda-Arara and Ntiba 1997; Kulmiye *et al.* 2002). For both larvae and juveniles, significantly lower growth rates were observed in June-July period. These months coincide with the southeast monsoon season when productivity is low and current speeds are high on the Kenyan coast (McClanahan 1988). It is therefore likely that the severe conditions during these months preclude spawning by the species. Spawning therefore seems to be keyed to favourable environmental conditions of higher temperatures (Nzioka 1979; McClanahan 1988) and zooplankton productivity (Mwaluma *et al*. 2003, Osore *et al*. 2004) during the calm northeast monsoon season, likely to favour larval growth and survival. Faster growth of larvae has been suggested as an important factor in fish survival due to increased ability of larvae to capture food and to avoid predators (Gotceitas *et al*. 1996). Chlorophyll-a was an important predictor of growth for juveniles, while temperature was significantly correlated with growth of larvae. However, zooplankton density was poorly correlated

with both larval and juvenile growth. Many population dynamics models assume that growth is directly related to food availability and that food is limiting in the plankton (Ware 1975; Shepard and Cushing 1980). Despite the prevalence of this notion, few studies have demonstrated significant relationships between food densities and growth rates mostly due to the confounding effects of temperatures and turbulence (Meekan *et al.* 2003). In this study, however, a mis-match in zooplankton production and growth rates resulted in a weak correlation. Other studies have found that growth rates and pelagic larval duration are most strongly correlated with water temperatures (Heath 1992; Rilling and Hounde 1999; Bailey and Heath 2001; Meekan *et al*. 2003), with short term variations associated with food availability (Heath 1992; Meekan *et al*. 2003). Warmer water temperatures are often associated with higher primary and secondary production and thus better feeding conditions for larvae (Heath 1992; Bailey and Heath 2001; Wilson and Meekan 2002) and hence faster growth and better survival (Hounde 1989; Wilson and Meekan 2002).

The three models (VBGF, Gompertz and Logistic) appear to converge for older fishes around asymptotic size but predicted different growth patterns for younger fish, thus suggesting that the choice of a growth model appears inconsequential for older fish but maybe significant for younger fish. The von Bertalanffy growth model yielded the best model fit for juveniles, making it perhaps the preferable model to describe post-larval growth in this species. The non-linear Schnute model showed a concave shape with a clear inflection point on the continuum of larval-juvenile growth. Larvae were described by the linear portion of the Schnute model indicating a more rapid growth that transforms

into a slower juvenile growth. The Schnute model is easy to fit and quicker to achieve convergence regardless of the data set, and therefore useful in determining the appropriate functional form in fish growth (Lei and Zhang 2006).

Estimating the age of individual fish using otolith micro-increments has become a widely used tool in early life-history ecology (Bailey *et al.* 1996). The basic assumption of the method is that increments are formed on a daily basis, however, for slow growing larvae, daily increments have been found to be too narrow to be resolved under optical microscopy, resulting in underestimation of age (Campana *et al.* 1987; Fox *et al.* 2003). Similarly, during the first days after hatching daily increments are often not detected by light microscopy. Validation experiments are thus recommended or the use of Scanning Electron Microscopy which is capable of revealing increments of less than 200 nm width (Klink and Eckmann 1992). In this work, validation trials failed due to lack of permanent marking on the otoliths by alizarin stain, and the high mortality encountered by the marked larvae. The assumptions of daily growth may require further validation work and likely constrains the conclusions in this study.

5.4 Diel and lunar patterns of larval supply to Malindi Marine Park

The supply of larvae to Malindi Marine Park seem to have been influenced both by the effects of diel and lunar patterns. Overall, greater numbers of larvae were supplied to the park during the night-time as compared to the day, and during alternative full and new moon lunar cycles. Larval abundance was highest at 2400 hrs during spring tides with abundances being 2-times greater than at neap tides, and about 13 times more in the night compared to day time for a given tidal regime. The dominant species (*Stolephorus*

commersonii, Labridae n.d., *Parablennius* sp. and *Leptoscarus vaigensis*) were more abundant during spring night-time (2400 hrs) cycle. However, *Apogon* sp. (Apogonidae) was more dominant during the day-time (1200 hrs) neap tide cycle. The collection of greater numbers of fish larvae at night in this study is consistent with other results (e.g. Johannes 1978; Sponaugle and Cowen 1996; Jenkins *et al.* 1998; D'Alessandro *et al.* 2007; Bonecker 2009). Lunar based variation in fish larval abundance as reported in this study, has also been reported by Dufour and Galzin (1993) and Valles *et al.* (2001). It is hypothesized that larvae are predominantly spawned or dispersed during night-time or new moon phase (spring tides) in order to reduce the risk of mortality from visual predators (Johannes 1978; Taylor 1984; Dufour and Galzin 1993). Additionally, spawning synchronized with spring tides is thought to maximize offshore tidal transport as a predator avoidance, and or a dispersal mechanism (Johannes 1978).

Among species with pelagic eggs and oceanic larvae (e.g. *Stolephorus commersonii*, Labridae n.d. found in this study), one common strategy is the timing of spawning to coincide with ebbing of flooding spring tides to maximize on tidal transport of larvae, such species are known to have reproductive rhythms to spawn in the vicinity of spring tides (i.e. around new or full moon) (Johannes 1978). Among demersal spawners (e.g. *Parablennius* sp., Gobiidae n.d. *Apogon* sp. found in this study), hatching is also known to occur predominantly at dusk or at night as found in this study) perhaps as an antipredation response (Johannes 1978, Dufour and Galzin 1993).

In this study, larval abundance was cued to lunar phases of the moon in cyclic patterns of 30 days and a semi-lunar supply for the Blenniidae. If larval supply was cued entirely to lunar or tidal cycles, then it is expected that two peaks (pulses) in larval supply would occur in the park every month. However, in this study sampling effort was concentrated on the second half of the month thus missing out on the possible semi-lunar peaks. The dominant species of larvae in the park (Blenniidae n.d. *Stolephorous commersonii* and Gobiidae n.d.) had a synchrony in larval supply at 28-30 days indicating between species similarities in timing of larval replenishment to the Park. This further indicated similarity in factors that control supply to the park for the species. The lunar cycles in larval supply obtained in this study are similar to those reported by D'Alessandro *et al.* (2007) who found all larvae to be distributed over the lunar and tidal cycles in Florida Keys peaking between 21 and 30 days. Factors associated with arrival of pre-settlement larvae with different moon phases have been identified as adult spawning behavior (Taylor 1984; Robertson 1991; D'Alessandro *et al.* 2007), larval behavior (Thorrold *et al.* 1994; Leis *et al.* 2007), spawning effort preceding the recruitment event (McIIwain 2003), and passive delivery by currents (D'Alessandro *et al.* 2007). However, in this study data is lacking to determine the environmental correlates of lunar based supply of larvae to the park.

Spectral Analysis indicated that in the long term, larval supply to the park is significant over a small period (narrow window) falling within the northeast monsoon season. It is possible that this is related to environmental productivity (Robertson *et al.* 1988; Kaunda-Arara *et al.* 2009) but indicates an unstable pattern of larval replenishment to the park.

5.5 Light trap evaluation and performance

The light trap catch composition in this study was comparable with that of other traps in tropical regions (Hickford and Schiel 1999; Watson *et al.* 2002; Watson and Munro 2004) with a dominance of the Apogonidae and Caesionidae. The catch rates for the assembled light trap compare quite favourably with other traps assembled elsewhere.

In terms of costs, the present light trap is cheaper $(\sim 70\$) when compared to the other traps which use relatively expensive materials either for the lighting system or the main body (mostly plexiglass) (Table 4-8). The advantage of designing a cheaper trap is the ease of replication especially in situations where funds are limited. The catches from the bottom (Fig. 3-3 a) and suspended (Fig.3-4) versions of the traps did not differ significantly perhaps because of the shallow columns $(< 10$ m at high tide) in the study area. It is likely that the limited depth range of the study area excluded other species in the samples. Light-traps are useful tools for sampling pre-settlement fish larvae, however, most of them are expensive making them inaccessible to cash strapped projects. The light trap in this study attempted to overcome this problem by fabricating a low cost trap of comparable performance to other existing traps. The advantage with light traps is that they can be used to sample many different habitats, different depths and seasons. In this study, they were successfully used to sample nearshore lagoonal reefs.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Fish larval abundance in Malindi and Watamu Marine parks was strongly influenced by seasonal patterns of the yearly reversing SEM and NEM winds. Synchrony in larval supply within the parks for some families and species indicated that factors that control larval supply were similar at small $(10-15 \text{ km})$, but at larger scales $> 15 \text{ km}$, the assemblage structure of larvae was found to vary, with the greatest variability occurring at sites located furthest from each other such as Mombasa and Watamu sites (interval of 160 kms). In this study segregation of larval groups was found within and between parks and this may have important implications in selecting the range of habitats to include in Marine Protected Areas in order to enhance biodiversity within them. There is need therefore for further studies on fish recruitment within different habitats.

Temperature and zooplankton abundance were the most important biophysical parameters that influenced larval abundance. The results of this study provide a synoptic account of nearshore fish larval assemblages in lagoonal waters of coastal Kenya and the WIO, and will contribute in providing baseline data in understanding population replenishment in lagoons. A greater challenge lies in enhancing the taxonomic database of the fish larvae in the WIO region by sampling further offshore and employing other techniques (e.g. genetics) to aid in taxonomy and understanding population connectivity.

Variation in larval abundance and structure between sites and years indicated that processes controlling larval supply between sites and years are variable. The fish larval assemblages along shallow reef lagoons of Kenya were found to be dominated by Gobiidae, Blenniidae, Pomacentridae and the pelagic species, *Stolephorus commersonii* (Engraulidae). Malindi Marine Park is likely an important breeding and nursery area for the commercially important *S. commersonii*. This is likely an important function of most shallow lagoons common in coastal Eastern Africa.

Patterns of variation of preflexion and postflexion abundance can provide information on processes regulating assemblage structure (Leis 1993). In 2007, there was high northward occurrence of preflexion stage larvae at Malindi and Watamu and high proportion of postflexion larvae in southwardly located sites of Mombasa and Nyali, suggesting possible spawning in the north coast with likely transport of the postflexion larvae to the southern sites. However, in 2008, preflexion stage larvae dominated the southwardly located sites of Mombasa and Nyali with high prevalence of postflexion larvae in the northern sites of Malindi and Watamu. This observation suggested that despite the likely overall spawning by species in the north, some species seem to indicate southward spawning.

This study used presumed day-ring counts in otoliths to delineate spawning times of *S. commersonii* as being January-March, August-September, and December-February. Although the findings on spawning seasons support earlier results from gonad maturation, the frequency of otolith ring formation will required validation in future

studies. In this study, growth rates of larvae and juveniles varied temporally, with highest growth coinciding with months of high temperature and zooplankton abundance during the NE monsoon season, and low growth rates experienced in the months of May to July during the SEM season. Data derived on growth in this study are important for modeling population dynamics of the species and should form useful reference for future studies on the engraulid species in the Western Indian Ocean.

Larval supply to Malindi Marine Park was influenced by lunar cycles with larvae arriving in the park in cycles of 30 days within a short term period. Larval supply during diel cycles was found to peak during spring tides at 2400 hours likely indicating behavioral component to larval replenishment. These results have some significant implications for modeling larval transport and recruitment and will help understand the scale of processes regulating larval supply to reef sites.

The performance of the locally assembled light trap in this study was comparable to other traps. A greater challenge would be to assess its performance and endurance in deeper offshore waters in the range of 50 m. The traps with appropriate modifications, can find applications in other habitats like mangrove swamps, within creeks, estuaries and lakes. They can also be useful in sampling crustacean and juveniles of pelagic fishes for qualitative ecological and taxonomic work, apart from catching ornamental fish for aquarium fish trade.

6.2 Recommendations

Following the results of this study and the encountered constraints, the following recommendations are advanced for future directions.

- 1. Future studies should investigate taxonomy and distribution of larval assemblages from offshore waters in order to determine the magnitude of inshore-offshore larval flux.
- 2. The use of DNA techniques in validating fish larvae identification will be useful in consolidating taxonomic databases in the WIO in addition to developing a photographic larval identification guide for fish larvae and juveniles from Kenya
- 3. There is need for further studies on levels of fish recruitment in different habitats this will have important implications in selecting the range of habitat to include in Marine Protected Areas. Additionally, complimentary studies on physical oceanography will be useful in modeling the factors that influence larval supply at different scales.
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APPENDICES

Appendix 1.0 Monthly age-length relationship of *Stolephorus commersonii* larvae in Malindi Marine Park determined by linear growth curves for the period, March 2005 to June 2006

