THE TROPHIC ECOLOGY OF PELAGIC FISH SPECIES IN MTWAPA CREEK AND SHIMONI CHANNEL, KENYAN COAST.

BY

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT FOR THE AWARD OF THE DEGREE OF MASTER OF SCIENCE IN ZOOLOGY (HYDROBIOLOGY) OF THE UNIVERSITY OF NAIROBI.

DECLARATION

I, Adhiambo Judith Nyunja, declare that the work presented in this thesis is my original work and has neither been accepted nor submitted for any other degree.

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DEDICATION

To my daughter Nicole Wasala

*

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ABSTRACT

This study explores the trophic status of pelagic fishes in Mtwapa creek and Shimoni channel on the Kenyan coast. Both qualitative and quantitative spectra of the diets of these fish were investigated in relation to the biotic and abiotic conditions in the study areas. In- depth trophic analyses were undertaken on *Sardinella gibbosa* and *Atherinomorous lacunosus*. Mtwapa (3° 55'S, 39° 45' E) is estuarine, surrounded by extensive mangrove swamps and mudbanks with freshwater input from a seasonal river. The creek is relatively eutrophic due to raw sewage disposed from the Shimo la Tewa GK prison. Shimoni channel on the other hand (4° 37'S, 39° 41' E) is more open oceanic with no freshwater input, and has few patches of mangrove vegetation along the rocky shoreline.

Samples were taken at 3 sites from each study area between January and August 2001. Fish were collected using a beach seine net of 20m long and 20mm stretched mesh. All fish were immediately preserved in 10% formaldehyde in seawater solution. Diets of the 8 most abundant fish from Mtwapa creek: Sardinella gibbosa, Pellona ditchella, Spratelloides delicatilus, Atherinomorous lacunosus, Selar crumenophthalmus, Gerres oyena, Secutor insidiator and Leiognathus equulus were studied. Since S. gibbosa and A. lacunosus were found to be common and abundant in both study areas, they were given an in-depth treatment to investigate the spatial and temporal differences in their diet.

This study established a clear spatial separation of Mtwapa creek from Shimoni channel in terms of the abiotic and biotic data. Highly significant differences (t-test, P<0.05) were observed between the two study areas in temperature, salinity, transparency, conductivity, chlorophyll *a* and in zooplankton abundance and diversity. There were however, no differences in pH and dissolved oxygen (DO) values between the two areas (t-test, P>0.05). It is suggested that the observed differences in the abiotic environment and the habitat heterogeneity, i.e. presence or absence of mangrove swamps and the nature of the substratum, may have caused the observed habitat difference between the two areas. This observation was further reflected by the differences in the diets of *S. gibbosa* and *A. lacunosus* collected from the two study areas. There

was a significant difference (t-test, P<0.05) in monthly abundance of zooplankton between Mtwapa creek and Shimoni channel. Mtwapa creek had lower mean densities than Shimoni channel. Diversity of zooplankton species was however, higher in Mtwapa creek (H' = 0.92 ± 0.48 SE) than in Shimoni channel (H' = 0.89 ± 0.02 SE).

Temporal pattern was observed in dissolved oxygen, transparency, temperature and salinity between the two monsoon seasons. Higher values were recorded during the Northeast monsoon (January – March) as compared to the lower values of the Southeast monsoon (April – August). This pattern was dictated by the reversing monsoon winds and the rainfall regime.

Total fish catch from the experimental fishing was higher in Shimoni channel (11 270 specimens) than in Mtwapa creek (7 179 specimens). While diversity of fish species and evenness of species distribution in the study areas were higher in Mtwapa creek (H' = 0.97, J = 0.63) than in Shimoni channel (H' = 0.42, J = 0.62). The size range for most of the fish caught from the two areas was much lower compared to their adult sizes at maturity which suggests that the majority were juveniles.

Copepods were the principal food item in the diets of studied fish species with the exception of *Selar crumenophthalmus*, which fed mainly on fish scales. Polychaetes were an important diet for *Gerres oyena* and *Leiognathus equula*. Two trophic categories, i.e. carnivores and omnivores, were identified among the studied fishes. *Spratelloides delicatilus* was basically a carnivore having fed only on zooplankton and zoobenthos with the lowest diet (H' = 0.40). The rest were omnivores. *S. gibbosa, P. ditchella, L. equula, S. insidiator, G. oyena* and *S. crumenophthalmus* fed on phytoplankton, zooplankton, zoobenthos and detritus with a relatively higher diet diversity (H' = 0.68 - H' = 0.96). *A. lacunosus* did not take detritus in their diet and had a lower diet diversity compared to the other omnivores (H' = 0.47).

The examined species highly overlapped each other in the feeding niche. The Morisita feeding niche overlap values ranged between 0.84 and 1.00. Most of them were generalised opportunistic feeders except for *S. dilicatilus*, which exhibited a specialised feeding strategy.

The in-depth analyses on spatial and temporal variation in diets of *S. gibbosa* and *A. lacunosus* showed that the two species took a greater number of prey categories in Mtwapa creek than in Shimoni channel (χ^2 – test, P<0.05). Copepods were important prey items for both species in Mtwapa creek for both the NE and SE monsoons. However, *S. gibbosa* from Shimoni fed mostly on copepods during the NE monsoon but took more nematodes and brachyuran megalopas during the SE monsoon. *A. lacunosus* from Shimoni channel fed mostly on lemellibranch larvae during the NE monsoon and on nematodes during the SE monsoon. No pattern was discernible in their feeding strategies. On the other hand, *S. gibbosa* from Mtwapa creek highly selected sergestids in their diets, and nematodes in Shimoni channel. *A. lacunosus* selectively took brachyurans in Mtwapa creek, and nematodes in Shimoni channel. The size of copepods eaten by *S. gibbosa* and *A. lacunosus* differed significantly (ANOVA, P<0.05; Tukey HSD, P<0.05) with *S. gibbosa* eating larger and wider copepods than *A. lacunosus*. However, there was no significant difference in the size of nematodes eaten by the two species (ANOVA, P<0.05; Tukey HSD, P<0.05). No significant ontogenetic changes were observed in prey sizes eaten by either species (P>0.05).

The spatial variation in feeding intensities of *S. gibbosa* and *A. lacunosus* shows that, the two species fed with higher intensities in Mtwapa creek than in Shimoni channel. *A. lacunosus* fed with a higher intensity at dawn and dusk, and lower activity during the day. The number of prey categories was also higher at 0600 hours and 1800 hours. At these hours, copepods constituted the highest percentage of prey items in the stomachs of these fishes. Overall, this study has shown that the small pelagic fishes in the studied inshore waters had a flexible diet, which relied greatly on the prevailing biotic and abiotic conditions in their habitats.

CHAPTER 1: INTRODUCTION, JUSTIFICATION AND LITERATURE REVIEW

1.1 INTRODUCTION

Different studies have been carried out on food and feeding habits of fish. In these studies, an attempt has been made at understanding the feeding regimes, food preference, migrations, growth and breeding patterns of fish. In most of these studies, food is found to be an important factor in the biology of fishes especially in governing their growth, condition, fecundity and migration patterns (Rao, 1974).

Food habits of fishes provide essential information for bionomic studies of single species, for comparing related or coexisting species, for describing assemblages and for the analysis of ecosystem energetics and regulation (Sheldon & Meffe, 1993). The analysis of stomach contents in fish is a common method for investigating the dietary composition and feeding habits of fish and hence making it possible to describe food chain, and food webs. Such studies also shed light on interactions among species i.e. among potential competitors and between predator and prey (Rice, 1988). Composition of food items in the guts of fish provides information about the habitat from which the fish fed. The nature of this ingested food depends primarily on the mode of feeding, morphology of the feeding apparatus and the time of feeding. Furthermore, the composition and amounts taken depend on selectivity and availability of the prey organisms (Pillay, 1952). Therefore, to obtain comprehensive information about the feeding habits of a fish species and about its role in the community, both gut contents and the potential food sources need

to be investigated. Analysis of the potential food sources provides the basis on which trophic interrelationships can be assessed in different fish species. It is in this regard, that studies on zooplankton communities were undertaken to establish their diversity and abundance at the two study sites, which are ecologically different. These sites were Mtwapa Creek, which is an estuarine ecosystem, and Shimoni channel which is an open system with more oceanic influence.

Studies on the ecological role and community structure of zooplankton in marine ecosystems provide fundamental information on the productivity in the given ecosystems. Zooplankton are an important link in energy transfer between the primary producers and secondary consumers. They are important food for both juveniles and adults of most pelagic fishes, e.g. the diets of clupeids (sardines, herrings), atherinids (silversides) and engraulids (anchovies) are restricted to planktonic organisms. Most fish rely on plankton for food during their larval and juvenile stages.

Data on food and feeding ecology of pelagic fishes is not readily available in the East African region. Some biological studies have however been reported on Carangids and Sphyreanids (Williams, 1965), the dolphin fish *Corypheana hippurus* (William & Newell, 1957) and Istiophorids (Merrett, 1968). Also notable are studies by Losse (1968) and Kamanyi (1975) on the elopoid and clupeid fishes and on the scrombrids respectively. It is not very clear from these studies, the outline of the natural history, food habits, behaviour and distribution of these pelagic fish. The biology of sardines has

comparatively received a wider coverage, though most of the studies were outside the East African waters (Blaxter and Holliday, 1965).

Exploitation of fisheries resources in Kenya has been carried out in the absence of adequate ecological knowledge of fish food (Mavuti, 1990). This study therefore, investigates the trophic ecology of pelagic fishes on the Kenyan coastline in relation to available food in their environment. Various methods have been adopted in this study to analyse the stomach contents of fish.

1.2 JUSTIFICATION

While investigating food relationships in the sea and the rate of metabolism from the lower to the higher levels in the food web, basic information may be gathered from studying the biomass of the main groups of organisms which build up this system of energy transfer in the ocean. Investigations on zooplankton abundance and species diversity provide an insight on the effects of environmental factors and the effects of fish predation on zooplankton. Regarded in this way, studies on zooplankton are important for gaining an insight into fish production.

The commercial importance of planktivorous fish in East African waters calls for more research on their trophic ecology. Since seasonal fluctuations of planktivorous fish catches have been reported (Wakwabi, 1981), there is need to investigate further the relationship between changes in environmental variables and their food and feeding habits. Small sized pelagic fish, e.g. sardines, are an important source of food to man and

other fish. Understanding their food habits may increase our knowledge on their seasonal abundance. Hence, various methods can be employed of improving their fishery and causing an increase in the amount landed which finally give rise to a commercial activity. Their stock may also be used to improve the fisheries of predator fish and of those fish, which coexist with them, e.g. mackerels, carangids and scrombriods.

Previous studies on stomach content analysis of planktivorous fishes employed the occurrence and points methods (Hynes, 1950). These methods do not provide in-depth analysis of the food habits of these species. Therefore, this study will employ other elaborate methods of determining the food and feeding habits of these commercially important fish.

1.3 LITERATURE REVIEW

1.3.1 The general nature of interactions within the marine ecosystem

Initial production of organic compounds in the ocean is confined to the photic zone where, through photosynthesis, carbondioxide and nutrients are fixed and incorporated into living tissues. The dominant organisms achieving this primary production are phytoplankton and related benthic flora (Barnes and Hughes, 1988). This primary production provides a direct source of food for herbivores. Detritus also provide another direct source of food through the detritus food chain. Major trophic interactions in marine ecosystems are summarised in Figs. 1 and 2.

1.3.2 The structure and function of pelagic ecosystems

The structure of the pelagic ecosystem is characterised by three factors. The first concerns the nature of primary production with reference to phytoplankton. The second concerns the nature of zooplankton that forms the first trophic link, and finally the relationship between higher trophic levels and lower trophic levels. The pelagic zone is characterised by a complex plankton based food web (Bougis, 1976; Mann, 1982). Phytoplankton is situated at the lowest level of production since they provide the basis for the food chain in the marine environment. Phytoplankton forms the first trophic level as photosynthesising primary producers. Despite their small biomass, they have very high rates of turnover, and hence they are able to sustain and drive productivity of higher trophic levels. Zooplankton relies on phytoplankton production and constitutes the next step in the food chain as secondary producers. Juvenile fish and other small pelagic fishes feed on phytoplankton and zooplankton. These small pelagic fishes are in turn fed on by other larger carnivorous fishes (Bryceson, 1984). Zooplankton in themselves constitutes a complete community consisting of herbivores, carnivores and omnivores. However, the major component of zooplankton are herbivores, which play an important role in marine pelagic food webs by transferring energy derived from phytoplankton and possibly from dissolved and particulate organic matter to subsequent higher trophic levels (Raymont, 1963 & Wickstead, 1965).

Studies on the relationship between the structure and function of marine ecosystems have become one of the principal tasks in marine biology. Trophic relationships between species determine the functioning of any given ecosystem and therefore, the metabolism

of the organic matter in that ecosystem. Organic matter produced by one organism is transferred and utilised by others through the food webs. Thus, the analysis of trophic relationships between organisms and populations is of considerable importance in studying the functioning of pelagic ecosystems.

Two types of trophic interrelationship may be distinguished in the pelagic ecosystem. These include predator prey relationships and non-predatory relationships based on external metabolites excreted into the environment by one organism and consumed by others. The first type, comprises direct relationships between organisms and prevails at higher trophic levels whereas the second type dominates at lower levels (bacteria, algae, some lower invertebrates) (Khailov, 1971). However, most studies on the trophic ecology of planktivorous fish mainly focus on the predator-prey interrelationship.



Fig. 1. A simplified diagram showing the major interrelations of the four semi-isolated subsystems into which the aquatic systems can be divided. (After Barnes 1980.)



Fig. 2. A food web for the neritic/shelf marine system with only the energetically more important links shown. Omitted, are imports from the littoral system and interchange with the oceanic/abyssal region; in reality all organisms will contribute to the dead organisms category, and some benthic carnivores will also be taken by bentho-pelagic nekton. (After Pomeroy 1979.)

1.3.3 Composition of ichthyofauna in tropical inshore waters

Fish fauna in inshore waters, which include coral reefs, seagrass beds and mangrove swamps overlap considerably with the greatest species diversity associated with coral reefs (Johannes, 1978). High proportions of reef - associated fish species have been collected from lagoons and mangrove swamps in Kenya (Little *et al.*, 1988; Kimani *et al.*,

1996: De Troch et al., 1996). Gazi estuary is inhabited on a temporary or permanent basis by at least 128 fish species belonging to 50 families. These include first - order consumers like Gerreidae, Clupeidae, Atherinidae, Teraponidae, Acroponidae and Gobiidae (Kimani et al., 1996). First-order consumers have also been noted to dominate estuarine fish communities in California and in the tropical Indo - Pacific region (Allen & Horn, 1975 & Blaber, 1980). These first-order consumers (including Gerreidae, Clupeidae, Atherinidae, and Gobiidae) were similarly found to dominate the Gazi fish community with members of the Clupeidae and Atherinidae occurring occasionally in large schools (Kimani et al., 1996). Eighty-three species of teleost fish belonging to 38 families have also been recorded in Tudor creek (Little et al., 1988). This was found to be similar to other mangrove systems and estuaries that have been studied since it was dominated by a small number of species. Seasonality in reproductive activity and recruitment of juveniles has been recorded for a large number of tropical marine fish. Ouinn and Kojis (1985) found that most abundant fish species in Labu estuary, Papua New Guinea, demonstrated an annual cycle of abundance, which coincided with seasonality in reproductive activity and recruitment of juveniles.

Diversity indices have been successfully used to analyze temporal patterns in fish populations of tropical and temperate estuaries (Bell *et al.*, 1984). Mean number of species and diversity indices varied with peaks during certain months of the year suggesting seasonality in the population structure. Higher Shannon-Weiner diversity indices were recorded during the Northeast monsoon in Tudor creek (Little *et al.*, 1988).

These observations might be attributed to migration of small pelagic species (Day, 1974) into the creek from offshore waters.

1.3.4 Ecological and economic importance of small sized pelagic fish

Although bait fisheries have received much less emphasis than primary fisheries, bait fish e.g. sardines, anchovies, silversides and herrings comprise a large portion of the diets of most larger pelagic species such as scrombrids and carangids. Fishermen readily recognise the importance of sustaining abundance of bait species and they are often knowledgeable of their movements and migrations patterns (Friedlander & Beets, 1997). Most studies on the biology of tropical bait fisheries have been conducted in the Indo-Pacific region (Williams and Clarke, 1983; Clarke, 1987; Milton *et al.*, 1993; Dalzell, 1993). Most of the information pertaining to the life history, food habits and distribution of these small pelagic fishes has been obtained from the South Pacific. This is because of their importance as traditional food source, and more recently, as a source of live bait by pole and line tuna fishing vessels (Dalzell, 1993). But also important for fish meal production.

Biological information on forage bases is essential for improved fisheries management of larger migrating pelagic species (tunas and jacks) since they are dependent on the abundance and movement of a few bait species. Observations of stomach contents of Virgin Island pelagic species revealed selective feeding on *Sardinella* spp. (Friedlander & Beets, 1997). These baitfishes are also an important component of the diets of most seabirds whose migrations tend to coincide with baitfish migrations (Milton *et al.*, 1990). Large numbers of baitfishes are still observed in a few inshore areas, such as protected bays, mangrove areas and offshore aggregation sites.

Sardines, and particularly the Clupeids *Sardinella* spp. and Atherinids *Atherinomorous* spp., are the most common bait fish used along the Kenyan coast. These small pelagic fishes are important in the artisanal fishery as baitfish, and there is lack of adequate biological information on their trophic ecology. It is therefore important to investigate the trophic ecology of these fishes in relation to available food in the environment.

1.3.5 Migration and schooling patterns of clupeids

Sardines are small sized fish rarely reaching 20cm in length. They are characteristically migratory, forming heterogeneous migratory shoals of varying sizes and densities. The shoals are only formed during migration but break up during active foraging, spawning and at night. The shoaling has protective advantages for these most preyed on fishes (Wakwabi, 1981). Large shoals of sardines and other Clupeids migrate inshore into shallow water during the day and migrate offshore at night presumably to feed (Milton *et al.*, 1991; Boulon, 1992; Coblentz, 1995). Inshore migrations into shallow water have been suggested to be antipredatory behaviour (Major, 1977, 1978).

Variation in abundance of clupeids is strongly determined by their migratory patterns. Clupeids migrate to the shallow waters when food is abundant in these waters, followed by migration to coastal waters during the spawning of mature fish and finally return to deep waters after spawning. This migration pattern has been fully described for Sardinella aurita, off the coast of Ghana (Longhurst and Pauly, 1987) and Sardinella longiceps in the Bali strait (Soerjodinoto, 1960). The most extensive reports on the seasonal migration of *S. longiceps* are from the West Coast of India (Raja, 1969), where shoals appear in the coastal waters during the rainy season, which coincides with the upwelling season. At the end of the rainy season, fish start relocating into deep waters (Raja, 1969; Longhurst & Pauly, 1987). Clupeid stocks are mostly found near continental shelves. These productive fishing grounds are at places were nutrient rich water from great depths is pushed up against a continental shelf, enriching the water layers in the euphotic zone (Longhurst and Pauly, 1987).

Schooling behaviour in planktivorous fishes has relevant ecological implications since it affects the rate of prey consumption. Intuitively, it is expected that the amount of food ingested be less for schooled planktivores, because of competition between individual members of the school whose visual field overlap. This mutual sharing of the visual field results in a lower rate of prey encounter per unit time for schooled fish than for non schooled fish, which possess an identical stationary visual field (Eggers, 1976). This scenario is a disadvantage to schooling planktivores. A second consequence of fish schooling is that prey density relative to individual members is not constant over the length of the school. Rather, prey density decreases as one progresses from the anterior to the posterior end of the school (relative to the direction of school movement) owing to - removal of zooplankton from the water column, which are encountered first by fish at the front of the school (O' Connell, 1972).

Zooplankton is assumed to occur in patches characterised by uniform density of prey, where there is gradual transition between patches so that a fish predator cannot recognise the patches (Eggers, 1976). Schooled predators have a greater chance than individual fish of encountering a patch of prey because the total visual field of the school is certainly greater than that of an individual fish. However, schooling behaviour occurs at the expense of foraging efficiency; since for schooling to be an advantage in foraging, the patches of prey items must be large enough so that the entire school can get adequate ration. This theory also shows that it would be advantageous for schooling fishes to disperse while feeding to minimise lateral visual field overlap.

1.3.6 Food and feeding habits of planktivorous fishes

Planktivorous fishes are very flexible in their feeding behavior and possess two feeding modes, namely: filter and particulate feeding. In filter-feeding mode, fish swim in a tight school with their mouths wide open and their opercula flared as they collect food particles on their gill rakers. However, in particulate feeding mode, fish do not school, but independently align themselves towards specific food particles, which they then engulf.

Filter feeding is the principal feeding mode among sardines (Van der Lingen & Hutchings, 1988). Particle size is the prime determinant of fish feeding mode. It is believed that food particles of less than 1.2mm elicit a filtering response, whilst larger particles elicit particulate feeding at low concentrations but filter-feeding at high concentrations (Van Der Lingen, 1994). Field based research on sardines in southern

Benguela, indicated that they were primarily filter feeders showing an apparent preference for phytoplankton, and having a mean ratio of 2:1 by volume of phytoplankton to zooplankton in their stomachs (Davies, 1957). King and Macleod (1976), working in Namibia found juvenile sardines to be zooplanktophagous, feeding predominantly on calanoid copepods, but switching to phytoplankton at approximately 100mm-standard length. Adult sardines were regarded as essentially non-selective filter feeders. The change from selective zooplanktivory to non-selective phytoplanktivory is attributed to reduction in gill rakers gap and increased ability to retain small particles (King & Macleod, 1976).

Preliminary studies on the diet of sardines from the Southern Benguela (Van Der Lingen pers. comm.) showed that sardine ingest both phytoplankton and zooplankton, and that while phytoplankton appeared to be more important volumetrically, the relative dominance of each fraction appears to be influenced by location. However, the size frequency distribution of ingested zooplankton closely matched that of ambient prey size distribution, indicating non-selective feeding. Substantial quantities of microzooplankton, including copepod eggs, nauplii, copepodites as well as adult copepods are frequently found in sardine stomach contents, thus confirming non selective feeding.

Sardines do not appear to be obligate vertical migrators, though they are known to form small scattered schools at night and dense schools by day while generally remaining in the top 20-30m of the water column (Hampton *et. al.*, 1979; Thomas & Schulein, 1988).

However, at times they have been observed to undertake significant diel vertical migration (Van Der Lingen pers. comm.). In addition, no obvious feeding periodicity cycle has otherwise been observed in sardines.

1.3.7 Relationship between the environment and food availability for planktivorous fishes

Spatial and temporal variations in prey size range and concentrations typify pelagic food environments (James, 1988). The size range and biomass of phytoplankton population are closely related to environmental conditions resulting from physical forcing mechanisms (Mitchell-innes & Pitcher, 1992). Nutrient enrichment in inshore waters due to surface runoff during the rainy seasons or intermittent mixing during upwelling promotes the development of phytoplankton populations of high biomass dominated by diatoms. In turn, the structure of zooplankton communities in such areas is shown to be affected by these phytoplankton community and size structures (Verheye *et al.*, 1993). Large copepods (e.g. *Calanoides* and *Rhincalanus*) display enhanced growth rates under diatom dominated conditions, whereas small species (e.g. *Oithona*) show elevated growth rate where small cells dominate (Verheye *et al.*, 1993). Different physical scenarios can therefore lead to varied food_environments dominated by either large or small particles (plankters).

An important feature of clupeid fisheries is the high variability of clupeid stocks (Longhurst & Pauly, 1987; Csirke, 1988). This unpredictable variability is caused by the direct link between environment and fish, since clupeids feed on zooplankton or phytoplankton whose productivity are determined by environmental conditions (Csirke, 1988). Changes in upwelling areas can greatly influence their abundance, as much as

rainfall and the presence of predators are also important factors affecting their recruitment (Raja, 1969, 1973).

1.3.8 Zooplankton Communities in tropical inshore waters

Studies on zooplankton biomass and distribution in the Indian Ocean show that areas with greater zooplankton stock correspond with high phytoplankton production. Present knowledge of Systematics and spatial distribution of copepods in the Indian Ocean is based on the report of plankton collections during the Siboga (Scott, 1909) and Siboga and John Murray expeditions (Sewell, 1929, 1932, 1948). Many studies of zooplankton ecology have been conducted in the inshore waters of Kenya especially in creeks around Mombasa Island (Grove et al., 1986; Okemwa, 1989; Mwaluma et al., 1998; Osore et al., 1997: Anyango, 2000). All these studies revealed that zooplankton is abundant and diverse in this region. The community structure of zooplankton is affected by the presence of predatory organisms. In the absence of significant predation by fish, larger zooplankton species normally dorminate, either because they have higher grazing and processing efficiency or because of selective predation on smaller zooplankton species. Whereas, when there is heavy fish predation on large zooplankters, small zooplankters become dominant (Brooks & Dodson, 1965). However, the effects of intermediate levels of predation are not clear

Preliminary studies on the ecology of the zooplankton in Gazi Bay, Tudor Creek and Port Reitz (Kenya), also revealed the existence of abundant and diverse zooplankton groups.

Copepods (Oithona spp. and Acertia spp.) chaetognthans (Sagitta spp.) and various developmental stages of Brachyura and Mollusca dominated these areas.

Kimaro (1986) demonstrated the possibility of seasonal, lunar and tidal influences on the abundance and composition of zooplankton at the mouth of Tudor creek. High proportions of meroplankton characterized the zooplankton of Tudor Creek. The most abundant meroplanktonic forms were larvae and post-larvae of crustacean decapods including those of Caridae, Anomura, Penaeidae and Brachyura. Occasionally the phyllosoma larvae of Scyllaridae and Palinuridae were encountered. Molluscan larvae mainly of gastropod larvae and a few bivalve larvae formed a small component of the meroplankton. Fish eggs and fish larvae were also common. Other encountered meroplankton included annelid larvae, which occurred mostly in night samples. The common holoplanktonic forms were the Copepoda, Calanoid copepods being the most important component, followed by the cyclopoid and lastly by the harpacticoid copepods. The most commonly encountered calanoid families were Calanidae, Ecalanidae, Paracalanidae, Euchaetidae, Temoridae, Metriidae, Centropagidae, Candaciidae, Pontellidae and Acartiidae. Common cyclopoid families were Oithonidae, Oncaeidae, Sapphirinidae and Corycaeidae. Occasionally, copepods of the order Monstrilloida were also found. The other important holoplanktonic group was the Chaetognatha with Sagitta being the most common genus. On a lesser scale, siphonophores, ctenophores, planktonic polychaetes and molluscs, stomatopods, euphausids, sergestids, salps and doliolids were also encountered among holoplankton. Ostracods, amphipods, isopods, mysids, cumaceans and the cephalochordate (Branchiostoma) occurred mostly in night samples.

Mwaluma (1993) compared the zooplankton in mangrove, seagrass and coral reef systems in Gazi bay, Kenya. He identified a total of 30 different taxa, with the important groups being, Copepoda, Brachyuran larvae, Medusae, Molluscan larvae and Caridea. There was marked localisation of zooplankters in the different niches, which was attributed to hydrographic conditions and their feeding habits. However, some species were found scattered in all the three zones due to tidal action. The highest zooplankton abundance was recorded in April, which was at the peak of rainy season.

Osore (1994) also studied the zooplankton of Gazi Bay and the adjacent waters and identified 37 main taxonomic groups. Rainfall, tidal regime and transparency were the most important factors that were found to affect the zooplankton community structure in the bay. Higher abundance and diversity of zooplankton communities were found in waters closer to the shore than those offshore. On further analysis on the effects of rainfall and tidal rhythm on the community structure and abundance of zooplankton in this bay, highest zooplankton abundance were found during the wet period (March, April, May) for both neap and spring tides (Osore *et al.*, 1997). The peaks in zooplankton biomass exhibited a pattern closely related to the rainfall pattern. This was associated to increased nutrient input into the creek via increased rivers inflow loaded with land derived nutrients. This increased nutrient enhanced phytoplankton production which inturn led to increased zooplankton biomass.

Okera (1974) reported the presence of *Rhincalanus cornutus*, *Acartia danae*, *Centropages gracilis* and *Temora discaudata* in the inshore waters around Dar-es-salam, Tanzania. He also observed higher zooplankton diversity in waters around Mombasa than in Dar-es-salaam. This was attributed to the differences in productivity around these areas.

CHAPTER 2: HYPOTHESIS, OBJECTIVES AND STUDY AREA.

2.1 HYPOTHESIS

Trophic status of pelagic fishes is influenced by habitat variability in coastal inshore ecosystems.

2.2 OBJECTIVES.

2.2.1 General Objective

To establish the trophic and feeding interelationships of pelagic fishes in relation to zooplankton abundance and diversity in Mtwapa Creek and Shimoni channel.

2.2.2 Specific Objectives

1. Determine the diets of abundant pelagic fish species.

2. Determine inter- and intraspecific differences in the diets of the abundant fish species in Mtwapa creek and Shimoni channel.

3. Investigate prey selectivity between the most dominant fish species i.e Atherinomorus lacunosus and Sardinella gibbosa.

4. Investigate zooplankton abundance and diversity in both study areas and their effects on the diet composition of *A. lacunosus* and *S. gibbosa..*

2.3 STUDY AREAS

2.3.1 Overview of Mtwapa Creek and Shimoni channel

This study was carried out in two sites: Mtwapa creek and Shimoni channel of the Kenyan coast. These two sites were selected for comparative purpose since they are physically seperated by distance and have different ecological characteristics. Mtwapa

creek and Shimoni channel are situated approximately 85 Km apart. as shown in Fig. 3. In each study area, three sampling sites were established as shown in Fig. 4 (stations MT1, MT2 and MT3 for Mtwapa creek) and Fig. 5 (stations SH1, SH2 and SH3 for Shimoni channel). The stations were located about 2 km apart. Mtwapa creek (Fig. 4) is situated 25 km north of Mombasa (3° 55' S, 39° 45' E). Shallow waters at the entrance and towards the inner parts characterise the creek. The middle part of the creek especially near the bridge is narrower and deeper. The creek receives fresh water from a seasonal river (River Mto Mkuu/ River Luadani) whose annual mean discharge is 0.3 m³ s⁻¹ (Magori, 1997). A dense mangrove cover of mainly Rhizophora mucronata on extensive mud banks lines the edges of the creek. There is little obvious industrial development around Mtwapa creek except for the intensive boating activities. The creek is relatively eutrophic (Mwangi et al., 2001) with evidence of seasonal water contamination. The seasonal river discharge, surface water runoff and raw sewage disposal especially near Shimo la Tewa government prison are the possible causes of the reported eutrophication.

Shimoni channel (Fig. 5) is situated 90 km south of Mombasa (4° 37' S, 39° 22' E). It is characterised by a deep channel approximately 5 km long. The channel is protected to the north by Wasini Island and to the south by a fringing reef. There is a patchily developed fringe mangrove formation along the channel. These few solitary mangroves growing at the bases of rocky cliffs are rooted on coral substrate with superficial sediments that can hardly cover the root system. The channel is characterised by welldeveloped seagrass beds. There is no fresh water input into the channel and the water mass is characteristically oceanic due to the open nature of the channel. However, during the rainy season, the channel receives freshwater from surface runoff and direct precipitation. There is no industrial development around Shimoni except for the extensive boating activities carried out due to the large numbers of tourists visiting the Kisite marine national park.

2.3.2 Tides

The tides on the Kenya coast are semi-diurnal with 2 low and 2 high waters every 24 hours and 2 springs and 2 neaps after every 28 days. There is a strong tidal influence from the sea with an average tidal range of 1.0 meter at neap tide to over 2.5 meters at spring tide.

2.3.3 Ocean Currents

The main oceanic and coastal circulation along the Eastern African coast are driven by the interplay between the South Equatorial Current (SEC) and the East African Coastal Current (EACC); on one hand and the South East Monsoon Winds (SEMW) and the North East Monsoon Wind (NEMW) on the other hand. With a fetch across the expansive Indian Ocean, the SEC on approaching the coast just north of Madagascar splits into the EACC northwards and the Mozambique and Madagascar currents southwards (Fig. 6). The north flowing EACC washes the East African coast for most of the year with an average current velocity of between 2-4 knots. The Mozambique Current flows southwards from the northern coast of Mozambique to join the Madagascar and becomes the Agulhas stream.
A general feature of water circulation on the East African coast is the seasonal change in direction of flow caused by the monsoon trade winds. From November to March, the Northeast Monsoon (NEM) winds are dominant while from May to October the Southeast Monsoon (SEM) winds dominates. During the later, the EACC flows northward continuing into the Northerly Somali Current. The NEM force a reverse direction of the Somali Current souththwards. During the Northeast monsoon, therefore, the southward Somali current and the northward EACC meet off the North Kenyan coast and veer eastward as the Equatorial Counter Current (Newell, 1957) causing a temporary upwelling.

2.3.4 Water circulation

Tidal forces drive the exchange of water between the creek and the ocean. However, due to the creeks restricted entrances, the tidal force is reduced as it progresses inward. In Mtwapa creek, ebb current is stronger than flooding currents. The hydrodynamics at the restricted creek-ocean entrances favours the dispersion of nutrient enriched creek waters into the adjacent lagoon especially during the wet seasons. The materials transported with the ebb currents from the creek are dispersed northwards by the near shore coastal current (Mwangi *et al.*, 2001). The creek-ocean water exchange rate is low compared to the exchange between the creek and the lagoon waters with an estimate of 3 to 12 days (Magori, 1997). Exchange between open lagoon waters and the ocean is higher resulting in high flushing rates (Magori, 1997). Therefore, Shimoni channel being an open ecosystem experiences strong tidal forces with strong ebb and flooding currents. The detrital materials deposited in the channel are therefore constantly washed off.



Fig. 3. Map of the Kenyan coast showing locations of Mtwapa creek and Shimoni channel



Fig. 4. Map of Mtwapa creek showing sampling stations MT1, MT2 and MT3. (Source: Survey of Kenya, 1998).



Fig. 5. Map of Shimoni channel showing the sampling stations SH1, SH2 and SH3. (Source: Survey of Kenya, 1998).



Fig. 6a Major currents of the Western Indian Ocean region (After Richmond, 1997). NB: The study areas are under the East African Coastal Current.



Fig. 6b & 6c. Current patterns (solid lines) and wind directions (dashed lines) during (b) the Southeast monsoon and (c) the Northeast monsoon in the East African region

2.2.5 Climate

Climate along the Kenya coast is different from that experienced in the hinterland because of the low altitude, coastal location and the continuous effects of the monsoon winds (McClanahan, 1988). Figure 6 shows the average rainfall for Mtwapa and Shimoni areas for the period between September 2000 and August 2001 (Meteorological department headquarters, Nairobi). Rainfall is bi-modal with the long rains usually starting from March/April and continues until June, while the short rains occur towards the end of October and lasts until December. It is hot and dry from January to February while June to August are cool months. The hot and dry period coincides with the Northeast monsoon when the winds are mainly northeasterly and light. The Southeast monsoon characterises the cool and wet season when the winds are southeasterly and strong. The short periods (March - April and October - November), when the winds may be blowing from either direction are known as the inter -monsoons. Short rains in November and long rains characterise the inter-monsoon period in April - May. Average annual temperatures range from 26.3° C to 26.6° C in the coastal lowlands.



Fig. 7. The average monthly rainfall (mm) for Mtwapa and Shimoni areas covering the entire study period. (Source: Meteorological Department Headquaters.)

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CHAPTER 3: MATERIALS AND METHODS

3.1 FIELD SAMPLING AND LABORATORY ANALYSIS

This research was carried out from January to August 2001. This research period is representative of the NE and SE monsoons. The months of January to March represents the NE monsoon while May to August represents the SE monsoon. A preliminary survey of the study areas was carried out in December 2000 to set out the appropriate sampling strategy. Three stations were selected for each study area. All samples were taken at about mid ebb tide. In order to get the fish species composition in the study areas and to establish the most abundant planktivorous species; it was necessary to undertake a survey of the fish species found in the two study areas. Individuals in the dominant size-classes of the abundant and characteristic planktivorous species were gutted for diet analysis. Alongside fishing, zooplankton samples were collected at each fishing site and environmental variables were also determined.

3.2 PHYSICAL AND CHEMICAL PARAMETERS

3.2.1 pH

A digital pH -meter (Orion Research Model 231 pH/ temperature meter) was used to determine the pH of collected water samples. Each sample was allowed to stabilize for 5 minutes before the final pH reading was recorded.

3.2.2 Dissolved oxygen

Seawater from each sampling station was carefully collected in a 10-liters container after which a plastic tube was used to transfer about 250 ml to each BOD bottle. This was done inorder to avoid introduction of air bubbles into the sample bottles. The samples

were fixed by adding 0.2 ml of manganese sulfate followed by 0.2 ml of potassium iodide and shaken thoroughly.

In the laboratory, 0.2 ml of concentrated sulfuric acid was added to each sample bottle and the contents shaken until all the precipitate was dissolved. Using a pipette, subsamples of 50 ml were transferred into different Erlenmeyer flasks. The samples were then titrated using 0.01N Sodium thiosulphate upto the end point. The volume of sodium thiosulphate used for the titration was recorded and the concentration of dissolved oxygen calculated as follows:

$$O_2 mgl^{-1} = \frac{Normality Na_2S_2O_3 \times 0.25 \times 32 \times 1000 \times volume \text{ of } Na_2S_2O_3 \text{ added (ml)}}{volume \text{ titrated}}$$

3.2.3 Secchi Disc Transparency

A Secchi Disk with 40 cm diameter was used to measure the transparency of water at each sampling site. The disc was lowered into the water and the depth of disappearance recorded, it was then gradually lifted and the depth of appearance noted. The mean of the two readings was determined and taken as the correct level of transparency.

3.2.4 Temperature

An ordinary mercury thermometer with 0.5° C graduations was used to determine surface water temperature. Water was drawn in a bucket and temperature reading taken within 30 seconds by lowering the thermometer into the water and letting it to stabilize.

3.2.5 Salinity

Salinity readings were made using a Stago Salinity refractometer (S / mill) calibrated for salinity range of 0 % - 100 %.

3.2.6 Conductivity

A conductivity meter was used to determine the conductivity of surface water.

3.3 BIOLOGICAL PARAMETERS

3.3.1 Chlorophyll a Analysis

Surface water was collected using five litres black jerry cans at each sampling station. In the laboratory, two litres of seawater was filtered on a GF/C -filter under low suction pressure. The filters were put into 10ml of 90% acetone in a centrifuge tube and immediately placed in the fridge, as chlorophyll is very unstable in light. This was left for a period of 24 hours for the chlorophyll pigments to be extracted out of the phytoplankton by the acetone. Samples were then centrifuged for 10 minutes at 3000 rpm. The supernatants of the centrifuged samples were filled into cuvettes and their extinction measured at 630, 647, 664 and 750nm against a blank cuvette filled with 90% acetone. The readings obtained at 750nm were subtracted from all other readings.

The chlorophyll *a* values were estimated using the Parsons-Strickland formula (Parsons *et al.*, 1984) expressed as follows:

C (Chl a) =11.6E₆₆₄ -1.31E₆₄₇ -0.14E₆₃₀

Where

C (Chl a) = Concentration of chlorophyll a

E = Extinction at 664nm, 647nm and 630nm.

Values in the equation = Constants.

The results obtained from this formula were multiplied by a factor of F, in order to obtain the chlorophyll concentrations in mg/m³. The values obtained were converted into μ g/l.

 $F = V_a / 1 \times V_b$

Where

1= Length of cuvette (cm)

 $V_a = ml$ of acetone used for extraction

 $V_{\rm b}$ = volume of sea water filtered (in litres)

3.3.2 Zooplankton Sampling and Analysis

Zooplankton samples were obtained from every fishing site immediately after the fish were caught. A 1.5 meter long Bongo net with a mouth radius of 45cm and a mesh size of 335μ m was used throughout the study. The Bongo net was towed horizontally at 0.5m depth behind an outboard engine powered boat for five minutes at a constant speed of 0.5m/s. The volume of water filtered during each haul was measured by a flowmeter. Three hauls were made at each station. After each haul, the catch was washed into the cod end of the Bongo net and transferred immediately into labeled sample bottles in which they were fixed in buffered 5% formaldehyde solution for further analysis at the lab.

*

In the laboratory, the fixed samples were filtered through a 50µm-mesh size sieve. The fixative was washed off under running water. The samples were then placed in petri dishes and observed under Wild (Heerbrugg) M3C stereomicroscope. This initial step of scanning through the whole sample was to ensure that all the possible zooplankton groups present were exposed and accounted for qualitatively. Identification was based on

keys and identification references in Tregouboff and Rose (1957), Wickstead (1965) and Newell and Newell (1978).

Each sample was diluted to 200ml and agitated gently. Four subsamples of 5ml each were pipetted from each sample into a Bogorov tray. The total subsample volume being 1/10 of the total sample i.e. $(5 \times 4)/200 = 1/10$. Zooplankton counts were made using a Bogorov tray under a stereomicroscope at a magnification of 10 x10 for bigger organisms and 10 x 40 for smaller ones. The number of individuals in each taxon was counted and *in situ* abundance calculated as numbers per cubic meter of filtered water (no /m³). Measurements of zooplankton species diversity were calculated using Shannon-Wiener diversity index (H') (Washington, 1984) expressed as:

 $H = n \log n - \sum (\emptyset \log \emptyset) / N$

Where n = The number of species in a sample

 \emptyset = The number of individuals in a species

N = Total number of individuals in a sample

3.4 FISH PARAMETERS

3.4.1 Fishing

Fish samples were collected at low water, in the daytime, mid between spring and neap udes. Fish were caught at a uniform depth of 2m using a simple beach seine-net of 30-m long, 2-m wide and 6-mm stretched mesh size. With the help of an outboard powered boat, the net was laid perpendicular to the shore starting from the shoreline into the waters. It was then dragged in a semi-circular manner shoreward and hauled onto the beach. In total, it took 10 fishers to accomplish the fishing. Three tows were made at each station. The catches from the three stations at each study area were pooled to constitute the fish community in the study area. All the fish caught were immediately preserved in 10% formaldehyde in seawater solution.

After the initial survey of fish species composition, subsequent fishing for Sardinella gibbosa, and Atherinomorous lacunosus was done with a standard cast net of 20mmmesh size.

3.4.2 Fish species composition in the study areas

All collected fish were brought to the laboratory where they were sorted and identified to species level using identification keys from Bock (1978), Fischer and Bianchi (1984) and Smith (1986). The number of individuals per species was established. The standard length of every individual fish was also measured to the nearest millimeter using a graduated fish measuring board. The fish were also weighed to the nearest gram on an electronic weighing balance. The generated data were used to calculate the species richness index from the Shannon-Wiener diversity index (H[']) (Washington, 1984) and expressed as shown in section 3.3.2 above. An attempt was made to measure "eveness / homogeneity" of fish species caught from the two study areas using the Pielou evenness index (J[']) (Washington, 1984) expressed as:

J' = H' / H' max.

Where H = The Shannon-Weaver diversity index

H' max = The maximum possible diversity of sample consisting of K taxa. H' max. = Log K

3.4.3 Diet Analysis

The 8 most abundant fish species in Mtwapa creek were selected for stomach contents analysis. These included three clupeids: Sardinella gibbossa, Pellona ditchella and Spratelloides delicatulus; one atherinid: Atherinomorous lacunosus; two leiognathids: Secutor insidiator and Leiognathus equulus; one gerreid: Gerres oyena; and one carangid: Selar crumenopthalmus were examined (Plate 1 - 7). The examined fish specimen included both juveniles and mature fish. To determine any spatial differences in diets between the two areas, a detailed analysis of trophic status was carried on Sardinella gibbossa and Atherinomorous lacunosus from both Mtwapa creek and Shimoni channel. These two species were most abundant in the beach seine catch from two study areas.

Fish for gut analysis were weighed and later dissected to open the viscera. The guts were carefully severed from the esophagus to the last portion of the intestine. Each gut was opened and the contents removed carefully and weighed to the nearest 0.0001g, after which they were emptied into 4% ethanol in a petri dish and examined under a binocular microscope. The gut contents-were sorted through and identified as much as possible to a high taxonomic level and counted. For the partially digested food items, only the undigested portion of the organisms, usually the head were used for identification and counts.

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Various mathematical indices decribed below were applied to the weights and counts data to determine the food habits of these fishes. The feeding intensity (F.I) was determined from the degree of stomach fullness expressed in Hureau (1969) as:

 $F.I = \frac{\text{Weight of ingested food x 100\%}}{\text{Weight of fish}}$

Where F.I = Fullness index or feeding intensity

The numerical abundance and frequency of occurrence methods have been used to examine the diet of fish population with a iew to assess the species nutritional standing in the context of the fish community (Hyslop, 1980). Such studies also consider seasonal variation in the diet and /or dietary comparison either between different sub-groups of the same species, e.g year classes or different species living in the same or comparable habitats. In both instances, the aim is to discern whether there is competition for food. This category also includes studies, which monitor the feeding intensity of fish population throughout the day to discern the diel rhythm or feeding periodicity (Hyslop, 1980). The numerical abundance method is:

- (i) Relatively fast and simple to operate provided identification of prey items is feasible (Hyslop, 1980).
- Most appropriate when prey items of different species are in the same size range
 e.g planktivorous fishes (Guma'a, 1978).
- (iii) It gives a better indication of the amount of effort exerted in selecting and capturing different organisms (Ball, 1961).

Other factors that prevent the use of this method in isolation as an index of dietary importance are:

- (i) Numerical estimates overemphasize the importance of small prey items taken in large numbers (Hyne 1950).
- (ii) For many fish stomachs, it is difficult to estimate the numbers in each category because of mastication of food before it reaches the stomach, and /or the effects of the digestive process (Crisp *et al.*, 1978).
- (iii) Fish size is not taken into account (Hyslop, 1980).
- (iv) The method is not suitable for dealing with food items such as macroalgae and detritus, which do not occur, in discrete units (Arawomo, 1976).

The simplest way of recording data obtained from stomach contents is to record the number of stomachs containing one or more individuals of each food category (Hyslop, 1980). The advantages of the frequency of occurrence method are:

- (i) It is quick and requires minimum apparatus provided food items are readily identifiable (Hyslop, 1980).
- (ii) It provides a crude qualitative picture of the food spectrum (Fagade & Olaniyan, 1972).

(iii) It can be used to illustrate seasonal changes in diet composition (Frost, 1977).
 However, the frequency of occurrence method gives little indication of the relative amount of each food category present in the stomach (Hyslop, 1980).

The numerical abundance (%N) of each prey item encountered in the stomach contents was obtained by recording the number of individuals in each prey category for all the stomachs examined. The total of each prey category was expressed as a percentage of the

total individuals in all prey categories (Berge, 1979). The formula used is expressed below.

$$\%N = \underline{n}_{i} \times 100$$

N tot

Where $n_i =$ number of individuals of prey item *i*

 N_{int} = total number of prey items encountered in the stomach contents

The frequency of occurrence of prey items (%F) was obtained by calculating the percentage of fish in a sample, which contained that prey item in their stomach contents (Berge, 1979). This is expressed as:

$$\%F = \underline{n}_{fi} \times 100$$

N_f

Where n_{ij} = number of fish with prey item *i* in the stomach contents

 N_{f} = total number of fish examined

Diet diversity of fish was determined by using Shannon – Weiner diversity index as described in section 3.3.2. One step of understanding community organization is to measure the overlap in resource use among the different species in a community. The most common resources measured in order to calculate overlap are food and space (or microhabitat). The simplified Morisita index proposed by Horn (1966) as a similarity index was used to measure the feeding niche overlap between the eight fish species that were selected for diet analysis in this study i.e.

 $C_{\rm H} = 2 \sum P_{ij} P_{ik} / \sum P^2_{ij} + \sum P^2_{ik}$

Where:

 C_{H} = Simplified Morisita index of overlap between species *j* and species *k*.

 $P_{ij}P_{ik}$ = Proportions of resource *i* is of the total resources used by the two species (*i*= 1, 2 ... n)

n = Total number of resource states.

The feeding strategies of each species was determined by Tokeshi analysis (Tokeshi, 1991) as shown in Fig. 8. The figure graphically represents the generalist/ specialist feeding strategies in fish. The mean individual feeding diversity (D_1) is used as an indication of how diverse a diet an individual predator takes on average. The population feeding diversity (D_P) indicates the diversity of prey types consumed by the predator population as a whole. A population with low D_1 and low D_P corresponds to a specialist, whereas one with high D_1 and high D_P corresponds to a generalist with homogeneous feeding regime. The combination of low D_1 and high D_P indicates a generalist with heterogeneous feeding regime, while high D_1 and low D_P is considered a rare occurrence (Tokeshi, 1991).

The species mean individual feeding diversity (D_I) was plotted against its population feeding diversity (D_P) to indicate the feeding strategy of the species. D_I and D_P are determined using the following equations.

 $D_{I=} \left(-\sum P_{ij} \ln P_{ij}\right) / N$

$$D_P = \sum P_I \ln P_I$$

Where N = the total number fish examined.

 P_{ij} = the proportion of prey type *i* in the *j*th fish.

 \mathbf{P}_{i} = the proportion of prey type *i* in the entire fish population.



DD

Fig. 8. Guide to the interpretation of the Tokeshi graphical method. (After Tokeshi, 1991).

The numerical method and the frequency of occurrence methods take into account only food items in the gut. To gain some insight into the possibility of the species having preference for certain food items over the others, the number of prey consumed was compared to the prey available using the Strauss electivity index (L) (Strauss, 1979):

$$L = r_i - p_i$$

Where r_i = the proportions of the *i* th prey category in the diet.

 p_i = the proportions of the *i* th prey category in the environment.

The Strauss electivity values ranges between +1 and -1. Prey items with +ve values are those that are actively selected and are preferred by the fish, -ve values indicates invoidance, inaccessibility of prey or lack of preference while zero value indicates random selection. The numerical percentages of various zooplankton species obtained from zooplankton analysis were used to represent the potentially available food from the environment.

The sizes of common prey were measured using an ocular micrometer and a dissecting microscope.

3.5 STATISTICAL ANALYSIS

Whenever possible, t-tests, ANOVA and post-hoc multiple comparisons of means (Tukey HSD test) were used to analyze the collected data. If ANOVA assumptions were not met and no appropriate transformation could be found, a non - parametric two way Analysis of Variance (Friedman ANOVA) was used.

CHAPTER 4: RESULTS AND DISCUSSIONS

4.1 PHYSICAL - CHEMICAL FACTORS

The physical-chemical variables investigated during the study period are summarised in Table 1 and depicted in figures 9 - 14. Also provided in appendix 1, is a summary of mean data for the entire study period, for each sampled station (MT1, MT2, MT3, SH1, SH2 and SH3).

4.1.1 pH

The mean pH values for surface water ranged from 8.04 ± 0.06 SE - 8.91 ± 0.01 SE with a mean of 8.34 ± 0.10 SE in Mtwapa creek; while in Shimoni channel, the values ranged from 8.2 ± 0.04 SE - 8.75 ± 0.04 SE with an overall mean of 8.38 ± 0.06 SE (Table 1). Note that with the exception of April, pH values were relatively constant around normal marine levels at all the stations during the entire study period (ANOVA, df = 132, P>0.05) (Fig. 9). There was a slight rise in pH in April (Fig. 9). No significant difference in pH was observed between the two studied sites: Mtwapa creek and Shimoni channel (t = 0.75, P>0.05) (Table 1).



Fig. 9. Monthly variation in surface water p H (Mean $\pm SE$).

4.1.2 Dissolved Oxygen (D.O)

The concentration of D.O in Mtwapa creek varied between 3.35 mg/l \pm 0.06 SE - 7.68 mg/l \pm 0.09 SE with a mean value of 5.62 mg/l \pm 0.5 SE. For Shimoni channel, recorded D O ranged from 2.71 mg/l \pm 0.06 SE to 7.19 mg/l \pm 0.11 SE with an overall mean of 5.01 mg/l \pm 0.62 SE (Table 1). There was no significant difference in D.O values between stations at the two sites (ANOVA, df = 132, P>0.05) and between the two study sites (t = 0.99, P>0.05) (Table1). Higher D.O values were recorded during the SE monsoon (April - July). D.O was relatively lower during the NE monsoon (January – March) (Fig. 10).



Fig. 10. Monthly variation surface water dissolved oxygen (mg/l) (Mean \pm SE).

4.1.3 Transparency / Secchi Disk reading

Throughout the study period Shimoni channel had relatively higher transparency than Mtwapa creek (Fig 11). The monthly mean values ranged from $1.41m \pm 0.06$ SE - 3.38

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m \pm 0.09 SE in Mtwapa creek with an overall mean value of 2.19m \pm 0.24 SE (Table1), while in Shimoni channel it ranged from 5.22m \pm 0.21 SE - 6.29m \pm 0.41 SE with an overall mean value of 5.94m \pm 0.16 SE. There was highly significant difference in transparency between the sampled stations in the two sites (ANOVA, df = 132, P<0.05). Transparency was significantly different between the two study sites (t = 22.92, P<0.05) (Table 1). Fig. 11 shows that transparency was higher during the NE monsoon (January – March) and declined with the onset of the SE monsoon especially in April – May.



Fig. 11. Monthly variation in water transparency (m) (Mean \pm SE).

4.1.4 Temperature

The mean monthly surface water temperature in Mtwapa creek ranged from 26.10°C \pm 0.23 SE to 31.50°C \pm 0.11 SE with an overall mean of 28.31°C \pm 0.65 SE (Table 1). The mean monthly surface water temperature in the Shimoni channel ranged from 25.53°C \pm 0.10 SE to 29.99°C \pm 0.04 SE and a mean of 27.56°C \pm 0.58 SE (Table 1). The

maximum and minimum temperature values from both sites were observed in March and July - August respectively (Fig. 12). There was no significant difference in temperature readings in all the sampled stations in the two sites (ANOVA, df =132, P>0.05, Tukey HDS test, P>0.05). However, there was a significant difference in mean temperature value between the two study sites (t = 2.73, P<0.05) (Table 1).



Fig. 12. Monthly variation in surface water temperature ($^{\circ}$ C) (Mean ± SE).

4.1.5 Salinity

Typically, marine water salinities were recorded from both Mtwapa creek and Shimoni channel (Table 1 & Fig. 13). However, a slight seasonal variation is likely responsible for the observed difference in salinity between the sampled stations (ANOVA, df = 132, P<0.05). The highest and lowest salinity was recorded during the months of February and April – May respectively (Fig. 13). During the study period, there was also a significant difference in salinity between Mtwapa creek and Shimoni channel (t = 4.70, P<0.05) (Table 1).



Fig. 13. Monthly variation in surface water salinity (‰) (Mean ± SE).

4.1.6 Conductivity

The conductivity values in Mtwapa creek ranged from 50.70 mS/cm \pm 0.06 SE to 51.6 mS/cm \pm 0.06 SE with a mean value of 51.58 mS/cm \pm 0.17 SE. The values in Shimoni channel ranged from 50.64 mS/cm \pm 0.06 to 52.68 mS/cm \pm 0.1 SE with a mean of 52.10 mS/cm \pm 0.22 SE (Table 1). Λ significant difference in conductivity values was observed between stations (ANOVA, df = 132, P<0.05) and between study sites (t = 8.31, P<0.05). Figure 14 shows that conductivity was relatively constant from January to April but dropped remarkably in May and June in Shimoni channel and Mtwapa creek respectively. However, conductivity values increased again towards August.



Fig. 14. Monthly variation in surface water conductivity (mS/cm) (Mean \pm SE).

	Mtwapa creek	ς.	Shimoni chann	el	
	Min Max. Mear	$a \pm SE$ Min Max.	Mean ± SE	t-test	
рН	8.10 - 8.91	8.34 ± 0.10	8.20 - 8.80	8.348 ± 0.06	P>0.05
Dissolved oxygen (n	ng/l) 3.40 - 7.71	5.62 ± 0.50	2.71 - 7.19	5.01 ± 0.62	P>0.05
Transparency (m)	1.41 - 3.40	2.19 ± 0.24	5.22 - 6.29	5.94 ± 0.16	P<0.05
Temperature (°C)	26.10 - 31.50	28.31 ± 0.65	25.53 – 29.99.	27.56 ± 0.58	P<0.05
Salinity (%)	34.00 - 34.80	34.40 ± 0.10	34.00 - 35.30	34.70 ± 0.20	P<0.05
Conductivity mS/cm	50.70 - 51.60	51.58 ± 0.17	50.64 - 52.68	52.10 ± 0.20	P<0.05

Table 1. Summary of Physical-chemical Variables.

4.1.7 DISCUSSION

Environmental parameters monitored during this study were dictated by the reversing monsoon winds that are experienced along the East African coast. The pH values that were observed in Mtwapa creek and Shimoni channel ranged within those recorded from

adjacent open seawater. Osore *et al.* (1997) also observed pH values ranging between 7.5 and 8.5 in Gazi bay. Compounds leaching from mangrove detritus and causing a drop in pH as they are oxidised (Osore *et al.*, 1997) could possibly contribute to the lower pH values in Mtwapa creek. Osore *et al.* (1997) reported that, lower pH values were frequently observed in the inner parts of Gazi bay, which were characterised by dense mangrove vegetation and lower dissolved oxygen. In this regard, high pH values in Mtwapa creek and Shimoni channel during the month of April can be explained on the basis of the higher dissolved oxygen values and lower leaching rates from detritus. The month of April coincides with the start of long rains (Fig. 7) and the onset of the SE monsoon. During this period, there was increased water turbulence, dissolved oxygen and amount of allochthonous input as a result of surface runoff. The high turbulence, higher flushing rates and increased dissolved oxygen depressed leaching processes and subsequent oxidation of detritus; hence favouring alkaline conditions in these ecosystems.

Dissolved oxygen is important in water since most organisms require it for survival. The high dissolved oxygen during-the SE monsoon is attributed to higher water turbulence and lower temperatures characteristic of this season. The observed D.O values in this study are comparable to those recorded in Kasyi (1993), Osore *et al.* (1997) and Mwangi *et al.* (2001) and fall within the reasonable ranges of seawater (4 – 10 mg/l)

Water transparency is an important factor in biological processes of aquatic ecosystems. The higher transparency value in Shimoni channel implies lesser suspended particulate matter in Shimoni channel than in Mtwapa creek. Due to the constricted nature of the Mtwapa creek, water circulation between ebb and flood tides causes high turbulence that leads to re-suspension of organic detritus and mud (Mwangi *et al.*, 2001). Riverine discharge during the wet season carries large amounts of suspended particles into the creek. These factors must have caused the reduced transparency in the creek. Shimoni channel has no river discharge or extensive mangroves on the banks that would increase detritus load. The coastal current also constantly wash through the Shimoni channel due to its open nature. There is therefore very little organic detritus re-suspended into the water column. It is however apparent that, during the wet seasons, surface runoff into the channel contributed to the reduced values of transparency in Shimoni channel. In overall, lower transparency readings were observed in the SE monsoon due to increased turbulence, resuspension of particles and increased input of allochthonous materials from surface runoff.

Surface water in Mtwapa creek was slightly warmer than Shimoni channel implying reduced exchange between the creek and open sea. Mwangi *et al.* (2001) also observed higher temperatures in a creek ecosystem than in an open lagoon ecosystem. The surface water temperatures were relatively high during the NE and low during the SE monsoon. This observation conforms to the characteristics of the two distinct coastal seasons experienced in this region. High cloud cover, rains, increased wind energy and decreased temperatures and light characterises the SE monsoon (April-October). This is in contrast to the situation during the NE monsoon when these variables are reversed (McClanahan, 1988).

The monthly variation in surface water salinity was small (<1.1%) at all stations. However, during the wet seasons, direct precipitation and storm waters slightly lowered the salinity. The lowest salinity measurements were recorded in April – May in both Mtwapa creek and Shimoni channel. This coincided with the onset of rainfall when large quantities of freshwater were discharged into these ecosystems from surface runoff and river discharge. Mean monthly salinity values for Mtwapa creek were lower than that of Shimoni channel due the continuous influence of river input into the creek. Mtwapa creek therefore exhibited an estuarine ecosystem while salinity values in Shimon channel exhibited more stable marine conditions subject to open coastal water influences.

Shimoni had significant influence of oceanic waters since it is more of an open channel. Mtwapa creek, which is an enclosed estuarine ecosystem, had lower conductivity values especially during the wet seasons. The drop in conductivity in May – June at both study areas may have been as a result of increased freshwater input. Therefore, conductivity fluctuation was tied to the rainfall regime with values as low as 51.60 mS/cm being observed in Mtwapa creek during the rainy period.

4.2 **BIOLOGICAL PARAMETERS**

A summary of the results obtained for chlorophyll *a* analysis, zooplankton abundance and diversity is presented in Table 2.

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4.2.1 Chlorophyll a

The concentration of chlorophyll *a* (Chl *a*) in a given water sample is an indication of the phytoplankton biomass in the sampled water. Chlorophyll *a* values in Mtwapa creek ranged between $0.55\mu g/l \pm 0.05$ SE and $2.24\mu g/l \pm 0.27$ SE with an overall mean value of 1.10 ± 0.19 SE. The values for Shimoni channel ranged between $0.75\mu g/l \pm 0.04$ SE and $2.77\mu g/l \pm 0.17$ SE with a mean of $1.50\mu g/l \pm 0.23$ SE. A peak of Chl *a* concentration was observed in Mtwapa creek in June; while in Shimoni channel, the highest Chl *a* concentration was also observed in Shimoni channel in June (Fig. 15). Further, a significant difference in Chl *a* concentrations was recorded between the sampled stations (ANOVA, df = 132, P<0.05) at the two sites and between the two study areas (t = 3.58, P<0.05) (Table 2).



Fig. 15. Monthly variation in chlorophyll *a* concentrations ($\mu g/l$) (Mean \pm SE).

4.2.2 Zooplankton taxonomic composition and abundance.

The full list of zooplankton taxonomic groups and species composition identified from collected samples is presented in Table 3 and Appendix 2. Table 3 shows that there was a difference in the distribution of most of the zooplankton groups. Mtwapa creek had a greater percentage composition of meroplankton (crustacean decapods, osteichthyes and mollusca). Mtwapa creek may therefore be an important nursery area for meroplankton including those of commercial importance like brachyurans. Conversely, Shimoni channel had a percentage composition of appendicularians. There was a high proportion of meroplanktonic forms from both study sites. Larvae of crustacean decapods (sergestids, carideans, anomurans, pangurids, brachyuran zoea / larvae and megalopas), molluscan larvae (gastropods and lemellibranchs), fish, polychaetes and nematodes were the commonly encountered meroplanktonic groups. The common holopanktonic forms were the copepods, siphonophores, ostracods, chaetognaths and ctenophores. Throughout the study period, copepods had the highest percentage composition from both study areas; followed by brachyuran zoea/larvae (Table 3). Brachyuran zoeas were however more abundant in Mtwapa creek than in Shimoni channel. The temporal variation in zooplankton abundance is depicted in Fig. 16. The highest density in Mtwapa creek (329 individuals / m³) and in Shimoni (628 ind./ m³) were recorded in May; while the lowest density in Mtwapa creek (20 ind./ m³) and in Shimoni (23 ind./ m³) were recorded in January (Fig. 16). Overall, zooplankton abundance was lower during the NE monsoon but higher during the SE monsoon. There was a significant nonthly difference in zooplankton abundance between the two study sites (t-test, df = 9, P < 0.05) (Table 2). Mean zooplankton density at the stations in Mtwapa creek was

lower than that recorded for Shimoni (Fig. 17). Stations SH3 and SH2 located in Shimoni had the highest zooplankton densities while MT3 in Mtwapa creek had the lowest density (Fig. 17).

Zooplankton species diversity was highest in Mtwapa creek ($H' = 0.92 \pm 0.48$ SE) and low in Shimoni ($H' = 0.89 \pm 0.07$ SE) (Table 2). The highest species diversity in both Mtwapa creek and Shimoni was observed during the NE monsoon (January - March). The lowest species diversity was recorded in April for Mtwapa creek and between April and June for Shimoni (Fig. 18). This period April – June coincided with the SE monsoon when zooplankton abundance was highest. Between station variations shows that station MT3 in Mtwapa creek had the highest zooplankton species diversity (Fig. 19). Note that this station was located in the inner part of the creek and it also had relatively lower zooplankton density compared to other stations as depicted in Fig. 17.

	Range	Mean ± SE	t-test					
Chlorophyll a (• g/l)							
Mtwapa creek	0.55 - 2.24	1.11 ± 0.19	P<0.05					
Shimoni channel	0.75 - 2.77	1.50 ± 0.23						
Zooplankton abundance (no/m ³)								
Mtwapa creek	20-329	122 ± 36	P<0.05					
Shimoni channel	20 - 628	186 ± 82						
Zooplankton species diversity (H')								
Mtwapa creek	0.77 - 1.04	0.92 ± 0.48	P<0.05					
Shimoni	0.72 - 1.26	0.89 ± 0.07						

 Table 2. Summary of biological variables investigated during the study period.

GROUPS	SITE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
Copepoda	MT	51.2	53.67	48.86	23.84	57.13	15.06	34.18	64.52
	SH	34.19	38.34	48.74	16.14	43.16	48.97	77.04	59.91
Cirripedia	MT	3.55	3.79	2.64	1.9	0.77	0.26	1.02	0.38
	SH	5.96	3.21	8.69	1.37	1.91	2.04	0.42	6.45
Malacostraca									
Stomatopoda	MT	-	-	-	-	-	-	-	0.07
	SH	-	0.13	-	-	-	-	0.13	
Mysidacea	MT	-	0.11	1.78	2.06	0.67	0.28	1.06	0.47
	SH	3.85	1.32	0.36	1.54	1.7	1.08	1.6	4.17
Cumacea	MT	1.2	1.27	0.71	7.31		0.08	0.88	0.02
	SH	0.7	1.16	2.5	1.15	0.09	2.07	0.11	0.76
Isopoda	MT	-	-	-	0.1	0.13	1.2	0.05	-
	SH	-	-	-	1.59	-	0.05	-	-
Amphipoda	MT	5.61	2.51	0.99	2.79	0.1	0.36	1.81	0.16
	SH	3.62	1.24	3.67	2.32	0.95	1.33	0.14	2.08
Euphausiacea	MT	-	0.03	-	-	0.64	0.21	0.06	0.9
	SH	1.27	1.15	-	-	0.91	0.31	2.51	1.37
DECAPODA									
Sergestids	MT	2.54	2.59	0.58	2.25	1.19	1.69	1.62	0.09
	SH	0.58	0.95	2.12	1.54	1.44	2.46	0.47	1.63
Carideans	MT	4.37	4.11	2.58	22.49	1.5	7.11	3.57	1.54
	SH	1.39	1.38	1.58	17.46	6.37	2.94	3.29	1.51
Anomurans	MT	1.06	0.02	0.1		0.37	0.23	3.36	0.09
	SH	-	0.68	1.33	1.83	0.25	2.63	0.05	-
Pangurids	MT	-	1.08	-	1.49	0.14	0.53	1.73	-
	SH	-	1.8	-	1.55	1.45	4.18	0.16	-
Brachyuran	MT	15.52	27.88	6.29	8.83	7.81	63.8	30.8	0.77
zoea	SH	7.87	7.8	4.86	2.62	1.79	5.58	-	
Brachyuran megalopa	MT	1.1	0.88	1.32	4.12	0.23	0.77	1.35	0.31
	SH	0.58	1.53	0.12	3.26	2.19	2.12	-	0.63
USTRACODA	MT	2.88	3.17	1.42	3.35	1.03	0.34	0.84	16.59
	SH	12.48	2.95	1.88	3.26	2.31	2.43	1.66	
Branchiopoda	MT	-	-	-	-	-	0.04	-	0.05
	SH	-	0.21	0.6	-	-	-	1.42	-

Table 3. Percentage composition of zooplankton taxa as average from monthly samples at the three sampling stations in Mtwapa creek (MT) and Shimoni Chchannel (SH).

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Thaliacea	MT	-	-	0.3		0.05	0.45	0.14	-
	SH	-	-	-	-		0.62	-	
Appendiculata	MT	2.5	0.05	2.44	0.97	5.27	0.06	0.01	0.08
	SH	2.62	1.85	2.18	4.6	5.34	1.45	2.08	2.84
Ascidiacea	MT	-	-	-	-	0.03	-	-	-
	SH	-	0.01	-	-	0.14	0.31	-	-
Osteichthyes	MT	3.22	3.69	11.76	0.97	5.27	2.34	3.25	0.07
	SH	2.55	2.23	2.18	4.6	5.34	4.91	3.82	2.76
Mollusca								,	
Gastropod	MT	5.22	4.26	2.39	4.31	3.55	0.89	3.62	9.25
larvae	SH	1.28	1.64	1.22	14.89	3.91	2.51	1.95	1.39
Lemellibranch	MT	1.77	1.69	0.86	0.94	2.92	0.45	1.9	0.11
larvae	SH	1.05	1.72	0.85	1.37	1.51	1.42	0.27	1.13
ECHINODERM	MT	-	-		-	-	-	-	0.28
ATA	SH	-	-		-	-	-	0.47	-
Cnidaria			,					·	
MEDUSAE	MT	-	0.61	0.56	-	1.39	0.8	0.69	0.05
	SH	-	1.95	0.66	4.41	0.33	0.15	0.05	-
Siphonophore	MT	0.89	2.37	6.14	4.93	0.43	0.72	0.33	0.5
	SH	3.85	3.24	5.22	1.31	-	0.26	0.29	4.17
CHAETOGNAT	MT	1.29	1.37	3.92	1.98	4.12	0.3	0.57	0.75
HA	SH	1.05	1.39	1.22	1.11	1.26	1.91	1.04	1.13
Polychaeta	MT	1.53	1.28	0.66	1.78	0.95	0.26	1.06	0.43
	SH	1.64	0.67	0.24	2.29	0.84	1.65	0.08	1.77
Nematoda	MT	-	-	0.3	0.77	-	-	0.02	0.13
	SH	-	0.11	2.73	0.7	-	-	0.11	-
Protozoa	MT	-	0.32	2.08	6.57	7.21	0.53	1.85	2.35
	SH	5.48	1.21	5.78	0.96	8.93	1.09	0.4	5.93
Ctenophora	MT	r .44	1.51	1.32	2.46	1.88	0.58	1.4	0.04
	SH	0.23	0.5	0.97	0.96	0.77	3.2	-	0.25
Insecta	MT	0.38	-	-	-	-	0.17	0.08	-
	SH	0.11	0.17	0.3	0.96	0.05	-	-	0.12
Others	MT	0.38	0.02	-	-	1.24	0.49	2.75	-
	SH	-	1.18	-	-	1.04	2.33	0.44	-
	1	l							



Fig. 16. Monthly variation in zooplankton abundance (no/m^3) (Mean ± SE). Samples pooled for stations in Mtwapa creek and Shimoni channel.



Fig. 17. Stations variation in zooplankton abundance (no/m^3) (Mean ± SE). Samples pooled for all months.



Fig. 18. Monthly variation in zooplankton species diversity (H') (Mean \pm SE). Samples pooled for stations in Mtwapa creek and Shimoni channel.


Fig. 19. Stations variation in zooplankton species diversity (H') (Mean ± SE). Samples pooled for all months.

4.2.3 DISCUSSION

chlorophyll a (Chl. a) concentrations in the two study areas indicate the levels of phytoplankton production. Chl a concentrations were quite variable over the study period. In Mtwapa creek, the Chl a concentrations were low during the NE monsoon (January - March) but increased considerably between April and June (SE monsoon). The low levels of Chl a observed in Mtwapa creek during the NE monsoon was probably as a result of nutrient limitation during this warm season. In areas with seasonal climates, nutrients are depleted during the presence of warm season thermocline and production also decreases; both nutrient levels and production increases again when the thermocline disappears (Barnes and Hughes, 1988). Increased nutrients from river input and surface runoff during the wet season seemed to have caused the increased phytoplankton production in the creek. This observation corroborates earlier reports, which indicated evidence of eutrophication and seasonal water contamination in Mtwapa creek (Mwangi et al., 2001). In addition, Krey (1973) associated enhanced phytoplankton production in river discharge, estuarine and upwelling areas during the SE monsoon to increased nitrogen availability from terrestrial sources and upwelling. Finally, when seawater is enriched artificially with nutrients, as when sewage is discharged into semi-enclosed bays, primary production is stimulated, suggesting that nutrients were limiting hitherto (Barnes and Hughes, 1988).

A different scenario was observed in Shimoni channel in which the maximums Chl *a* concentration were obtained in March. This was as a result of an algal bloom, which was ^{observed} in Shimoni channel in March. This bloom resulted from very high transparency

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levels, high temperatures and increased proliferation of blue – green algae. Barnes and Hughes (1988) also reported that the most successful algae in areas or at times of extreme nutrient poverty are the moneran blue-greens since some of them are capable of obtaining nitrogen from dissolved nitrogen gas, of which there is no shortage in the sea. In overall, mean Chl *a* values were higher in Shimoni channel than in Mtwapa creek. This was attributed to very low transparency levels in Mtwapa creek, as a result of high suspended particles in the water. This inhibited light penetration and hence caused low phytoplankto production.

Zooplankton abundance was significantly higher in Shimoni channel than in Mtwapa creek, while the reverse was true for zooplankton diversity (t-test, P< 0.05). The two indices however were inversely related to one another. In many comparative studies of diversity, a homogeneous habitat with few resources or microhabitats will support fewer species than one with more resources (Washington, 1984). Mtwapa creek therefore, being a complex mangrove ecosystem with more resources and microhabitats had high zooplankton species diversity than Shimoni channel which is a more stable marine environment with low habitat-complexity due to lack of extensive mangrove vegetation along its banks. Zooplankton in productive waters is also typically species poor and has relatively low community biomass (abundance) supported by each unit of primary production. In contrast, zooplankton species in unproductive waters are typically small, efficient and each unit of primary production supports a relatively large community biomass (Barnes and Hughes, 1988). These observations explain the inverse relationship between zooplankton abundance and diversity. Also, as zooplankton diversity increases,

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the number of trophic levels increases resulting in a greater incidence of predatory depression of competion in lower trophic levels which eventually leads to decrease in zooplankton abundance (Barnes and Hughes, 1988). It is worth noting that lower salinity values discouraged zooplankton production in Gazi Bay (Osore, 1997). Therefore, lower zooplankton abundance in Mtwapa creek is attributed to lower salinity values in the system compared to Shimoni channel. High zooplankton abundance in Shimoni channel was due to high chlorophyll a values as observed in this study, since zooplankton production highly depends on phytoplankton production. Habitat characteristics such as the degree of oceanic versus terrestrial influence, depth of the water column and substrate type play a major role in the distribution, abundance and diversity of zooplankton. Holoplankton, especially copepods and appendicularians are more associated with marine conditions than meroplankton. Shimoni channel having more holoplankton than Mtwapa creek, which conversely had a higher number of meroplankton (decapod larvae and brachyuran larvae) denotes two different environmental ecotones. The extensive mangrove vegetation and mudbanks forms a complex ecosystem that favoured meroplankters in Mtwapa creek while the open marine conditions at Shimoni favour holoplankton. The observed seasonal cycle of zooplankton abundance between January and March (NEM), and between April and August (SEM) was influenced by differences in phytoplankton production between the two seasons, since zooplankton production tends to lag behind phytoplankton peaks.

The seasonality on the East African coast seems to influence zooplankton abundance and diversity. In both Mtwapa creek and Shimoni channel, the maximum zooplankton abundance occurred during the NE monsoon and declined with the approach of the SE

monsoon. It is worth noting that lower salinity values tend to discourage zooplankton production (Osore, 1997). Previous studies along the East African coast in the general area of this work show that zooplankton abundance is highest during the NE monsoon and early SE monsoon (Kimaro, 1986; Osore, 1994; Osore *et al.*, 1997; Mwaluma *et al.*, 1998) and probably lags behind phytoplankton peaks (Bryceson, 1982). Zooplankton diversity and abundance have a reciprocal relationship as observed in this study. Since when zooplankton abundance was high, species diversity was lowered. Higher zooplankton diversity in Mtwapa creek than Shimoni channel was a result of habitat complexity in the creek.

4.3 SPECIES DIVERSITY AND ABUNDANCE OF FISH IN MTWAPA CREEK AND SHIMONI CHANNEL

In total, 18449 fish specimens comprising 55 teleost species in 29 families was identified from the two study sites. Of these, 7 179 specimens in 38 species were caught from Mtwapa creek and 11 270 specimens in 32 species from Shimoni channel (Table 4). Three species: *Leptoscarus vaigiensis, Sardinella gibbosa* and *Atherinomorous lacunosus* made up 70% of the total catch, while, *Sardinella gibbosa, Spratelloides delicatilus* and *Pellona ditchella* were the dominant clupeids and together accounted for 30% of the catch collected from Mtwapa creek. Ten species constituted 96% of the total catch the creek. The rest (others) of the 28 species constituted only 4% (Fig. 20). The catch from this creek was always dominated by small sized fish species of the families: Atherinidae, Clupeidae and Stelophoridae. In Shimoni channel, two species (*S. gibbosa* and *A. lacunosus*) formed 95% of the total catch (Fig. 21). Thirty species accounted for the rest of the 5%. The bulk of the species from both study sites were very rare in the catch. At family level, Haemulidae, Lethrinidae and Mullidae contributed the highest numbers of species from both study sites i.e. 4, 5 and 4 species respectively. Clupeidae, Leiognathidae, Scaridae and Siganidae had 3 species each.

The size range (mm SL) for all the fish species was low compared to the recorded size at maturity; this suggests that only juveniles were caught. Details on size range are depicted in appendix 3. There was spatial variation in diversity of fish caught from the two study sites. The ecological diversity indices calculated for both sites are represented in Table 4. Mtwapa creek had higher fish diversity (H' = 0.98) with more evenly distributed species (J' = 0.62) than Shimoni (H' = 0.42 and J' = 0.28). The catch from Shimoni was mainly dominated by *S. gibbosa* and *A. lacunosus*, hence resulting in a less even distribution.

Table 4.	Summary of the fish species composition in Mtwapa creek and Shimoni
channel.	

	Mtwapa creek	Shimoni channel	
Total number of individuals	7 179	11 270	
Number of taxa / species	38	32	
Shannon - weiner diversity (H')	0.98	0.42	
Peilou (J')	0.62	0.28	



Fig. 20. Percentage composition of fish species caught by a beach seine and a cast net in Mtwapa creek. Full names of abbreviations are in the key below.



Fig. 21. Percentage composition of fish species caught by a beach seine and a cast net in Shimoni. Full names of abbreviations are in the Key below.

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Abbreviations used in figure 20 and figure 21.

h species from Mtwapa creek.	Abb.	Fish species from Shimoni.	Abb.
moscarus vaigiensis	L. vai.	Atherinomorous lacunosus	A.lac.
dinella gibbosa	S. gibb.	Sardinella gibbosa	S.gibb.
prinomorus lacunosus	A. lac.	Siganus oramin	S.ora.
notosus anguillaris	P. ang.	Leptoscarus vaigiensis	L.vai.
Gerres oyena	G. oye.	OTHER FISH SPECIES	Others
pratelloides delicatilus	Sp.del.	Pellona ditchella	
cutor insidiator	S. ins.	Cheilio inermis	
siognathus equulus	L. eq.	Lethrinus sp.	
ellona ditchella	P. dit.	Scolopsis bimaculatus	
dar crumenopthalmus	S.cru.	Lethrinus nebulosus	
THER FISH SPECIES	Others	Pomadasys multimaculatum	
atjanus fulviflammus		Plectorhincus flavomaculatus	
selophorus delicatilus		Sphyraena jello	
plephorus indicus		Plectorhincus sordidus	
Anampses caeruleopunctatus		Parupeneus barberinus	
hryssa malabarica		Lethrinus mahsena	
enza minuta		Lutjanus fulviflammus	
Caranx ignobilis		Lethrinus miniatus	
ethrinus mahsena		Siganus stellatus	
lectorhincus gaterinus		Calatomus spinidens	
lago sihama		Thryssa malabarica	
pogon hyalosoma		Lutjanus sp.	
urres filamentosus		Scarus ghobban	
Oligolepis keiensis		Scomberomorus sp.	
hrinus harak		Gerres oyena	
Upeneus vittatus		Plectorhincus gaterinus	
Dyraena jello		Lethrinus harak	
tus pantherinus		Scolopsis ghanam	
ahrinus nebulosus		Dinoperca petersi	
omberoides tol		Anampses caeruleopunctatus	
heliodipterus sp.		Upeneus tragula	
pioscarus sp.		Abudefduf sp.	
unupeneus barberinus		Saurida undosquamis	
undosquamis			

ax pinnatus		
heilio inermis		
hctorhincus flavomaculatus		
arascorpaena mossambica		
anus canaliculatus		
rothron immaculatus		

14 DISCUSSION

The fish community in Mtwapa creek was more diverse and evenly distributed than those of Shimoni channel. The spatial difference in abundance and diversity of fish species from Mtwapa creek and Shimoni channel was due to variation in the abiotic environment and habitat heterogeneity. Mangrove ecosystems are often characterised by diverse habitats, including open water channels, seagrass beds, small creeks and inlets, intertidal mudflats, sandy-mud beaches and mangrove prop root habitats (Little *et al.*, 1988; De Troch *et al.*, 1998; Coene, 2000). This contributes significantly to high fish species diversity (Blaber *et al.*, 1989; Van der Velde *et al.*, 1995). Therefore, high fish species diversity in Mtwapa creek is due to the complexity of the habitat as a result of extensive mangrove vegetation and mud banks surrounding the creek. On the other hand, reduced habitat complexity in Shimoni channel due to its physical characteristics explains the observed low fish species diversity.

Water clarity and salinity differences also played an important role in explaining the variation in fish species diversity between these two study areas. Blaber and Blaber (1980) argued that water ^{clarity} has a major influence on habitat choice by juvenile fish in inshore waters. Turbid waters ^{provide} greater protection from potential predators. In addition, water clarity influences the ^{habitat} preference of certain fish species especially visual predators. It has also been suggested ^{that} low salinity's provide cues, which guide juvenile prawns and fish to inshore nursery grounds

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(Hughes, 1969). High water turbidity due to re-suspension of materials in creeks and the effect of river input reduced predation risk by visual predators in Mtwapa creek. The reverse is true for Shimoni channel with low turbidity, which resulted in avoidance behaviour among juvenile fish since they would tend to keep away from predation, and therefore predators also searching for food elsewhere.

Leptoscarus vaigiensis, Sardinella gibbosa and *Atherinomorous lacunosus* were the most dominant species in the catches from Mtwapa creek having constituted in total 70% of the total catches from the creek. On the other hand, only 2 species made up 95% of the catch from Shimoni channel. The higher abundance, low species diversity and uneven distribution of dominant species in Shimoni channel was therefore because of this highly skewed dominance. Water carity in Shimoni channel would have caused the high abundance of small pelagic fishes, which are mainly visual feeders.

The high proportion of juveniles in the catches from both study areas is typical of inshore lagoons and mangrove estuaries since these areas act as fish nursery sites. Occurrence of large schools of juveniles and adults of Clupeidae and Atherinidae indicates residence in the creek and inshore lagoon waters. Beach seining, although frequently used in shallow water fish studies, is ^{not} suitable for catching the larger pelagic and fast swimming fish (Potter *et al.*, 1990). It is therefore likely that larger fish species were underrepresented in this study. In addition, the use of a small, fine-mesh seine and cast nets in the shallow waters may have strongly targeted these ^{\$12es} of fish resulting into over selection of juveniles. Little *et al.* (1988) having used a beach ^{\$eine} in Tudor creek, Kenya also observed that pelagic and schooling species such as Clupeidae

and Atherinidae formed an important part of the catch. The same was observed from studies conducted in Gazi bay, Kenya where families of small-sized fish with a wide distribution in shallow waters (Gerreidae, Clupeidae and Atherinidae) were found to have dominated the fish community (Kimani *et al.* 1996). In this study Kimani *et al.* (1996), *Gerres oyena* was the most abundant, while members of Clupeidae and Atherinidae occurred occasionally in large schools in the bay. Investigations elsewhere have also revealed that, although many species are represented in mangrove ecosystems, the catches are always dominated by very few species (Quinn, 1980; Robertson and Duke, 1987).

4.5 TROPHIC STATUS OF ABUNDANT PELAGIC FISH SPECIES FROM MTWAPA CREEK

4.5.1 Diet Composition

The dominant fish species caught from Mtwapa creek are shown in plates 1 - 7. The dietary status of these dominant species is summarised in Table 5 and figure 22. More detailed data is presented in appendix 3 for further reference. All prey items which accounted for less than 5 %N in the diet of were grouped together and categorised as "others". Comparison of the dietary distribution of the prey across all the eight species by Friedman's ANOVA showed a significant difference among all species in the proportions of each eaten prey (P<0.05). The frequency of occurrence of each prey type were all significantly different among the eight species (P<0.05). There was a positive correlation between the frequency of occurrence (%F) and the percentage abundance (%N) contributed by each eaten prey item by all the eight species (r = 0.57, P<0.05).

sardinella gibbosa

An average of 26 prey categories was present in the stomach contents of the analysed fish (Table 5). Numerically, copepods were the most important prey item (41.6%N). Other important prey items were the hyperrids, mysids and cladocerans which accounted for 33.5%N, 10.3%N and 5 3%N respectively (Fig. 22). Prey items which were encountered with the highest frequency of occurrence (%F) in the examined stomachs were the phytoplankton, detritus, copepods, mysids, and brachyuran megalopas having occurred in 100%, 100%, 100%, 73.3%, and 63.3% respectively.

Spratelloides delicatilus

In overall, 20 prey categories were identified in the stomach contents (Table 5). Copepods (51.8% N) and brachyuran larvae (44.2% N) dominated their diet (Fig. 22). Copepods, brachyuran larvae and gastropod larvae were encountered in 100%F, 100%F and 87.2%F respectively of all examined stomachs for this species. The absence of phytoplankton and detritus in the diets of this species was noted.

Pellona ditchella

On average, 25 prey categories were identified from the examined guts of this species (Table 5). Copepods (29.7%N), anomuran larvae (28%N), and mysids (10%N) were the most important prey items (Fig 22). Phytoplankton and copepods occurred in 100% of the examined stomachs while mysids occurred in 85% these two having been the most frequently taken prey by the species.

Atherinomorous lacunosus

Nine prey categories were identified (Table 5) where Copepods (63.4% N) and hyperrids (24.6% N) dominated the diet (Fig. 22). Phytoplankton, copepods and hyperrids had been taken with the highest frequency of occurrence, i.e. 100%F, 100%F and 85.7%F respectively.

Gerres oyena

Twenty-two prey categories were identified from the examined guts of *G. oyena* (Table 5). Numerically, copepods (25.8%N), polychaete larvae (25.8%N), nematodes (18.4%N), ostracods (6.4%N), foraminifera (5.7%N) and invertebrate eggs (5.5%N) were the important preys in that order (Fig. 22). Phytoplankton and copepods occurred in 100% of the examined stomachs; polychaete larvae and nematodes occurred in 77.8%.

Selar crumenophthalmus

An average of 20 prey categories were encountered (Table 5) in the diets taken by *S. crumenophthalmus.* This species mainly fed on fish spales (49.3%N), nematodes (21.1%N) and rotiferas (7.3%N) (Fig. 22). Other prey items were eaten but in very low quantities. Phytoplankton and fish scales occurred in 100% of the examined stomachs while rotifers occurred in 55.5%.

Secutor insidiator

¹⁸ prey categories were found in the stomach contents (Table 5). Chaetognaths (39.3%N) and ^{copepods} (32.2%N) were the important prey in their diet (Fig. 22). Items taken with the highest ^{frequency} of occurrence were phytoplankton, detritus, copepods (each 100%F), rotifera and ^{cladocerans} (each 46.7%F).

Leiognathus equula

A total of 16 prey categories were identified (Table 5). The important prey items were polychaete larvae (28.7% N), foraminifera (15.2% N), nemertea and lemellibranch larvae (each 13.5% N), copepods (7.2% N) and mysids (5.5% N) (Fig. 22). Phytoplankton and detritus occurred in 100% of the examined stomachs, while polychaete larvae, copepods and nemerteans occurred in 92.4%, 84.6% and 76.9% of the stomachs respectively.





Plate 1: Sardinella gibbosa. (Family: Clupeidae)



Plate 2: Pellona ditchella. (Family: Clupeidae)



Plate 3: Atherinomorous lacunosus. (Family: Atherinidae)



Plate 4: Gerres oyena. (Family: Gerreidae)



Plate 5: Selar crumenophthalmus (Family: Carangidae)



Plate 6: Secutor insidiator. (Family: Leiognathidae)



Plate 7: Leiognathus equula. (Family: Leionathidae)

Table 5. Summary of the dietary data from Stomach contents analysis of 8 fish species mught from Mtwapa creek. N = sample size. * Denote absence of phytoplankton and ** denote absence of detritus in the stomach contents.

Fish species	N	Size	Mean no. of	Diet diversity	Mean fullness index
		(mmSL)	preys	(H')	$(F.I \pm SE)$
	123	57 - 94	26	0.68	4.96 ± 1.24
s gibbosa					
S. delicatilus */ **	78	38 - 55	20	0.40	0.84 ± 0.20
P. ditchella	102	55 - 130	25	0.97	2.18 ± 0.46
A. lacunosus **	95	49 - 71	9	0.47	1.26 ± 0.51
G. oyena	35	43 - 73	22	0.88	4.50 ± 0.10
S.	38	120 - 150	20	0.74	0.50 ± 0.09
crumenophthalmus					
S. insidiator	64	45 - 55	18	0.74	2.50 ± 0.36
L. equula	44	48 - 90	16	0.92	4.77 ± 0.24



Fig 22. The numerical composition (%N) of important prey items in the stomach contents of fish species from Mtwapa creek..Detailed data is presented in appendix 4

15.2 Diet diversity and feeding niche overlap among fish species in Mtwapa Creek

From the results of the analysis on diet diversity (Table 5) *P. ditchella* was found to have the most diverse diet (H' = 0.97), followed by *L. equula* (H' = 0.92) and *G. oyena* (H' = 0.88). These fish fed mostly on hyper-benthos: hyperrids, mysids, polychaetes, nematodes and gastropod larvae. The next group with intermediate diet diversity were *S. crumenopthalmus* (H' = 0.74), *S. insidiator* (H' = 0.74) and *S. gibbosa* (H' = 0.68). This group mainly fed on holoplanktonic copepods and chaetognaths except *S. crumenopthalmus*, ate more fish scales and nematodes. Species with the lowest feeding niche breadth (i.e. with lowest diet diversity) were, *A. lacunosus* (H' = 0.47) and *S. delicatilus* (H' = 0.40). Their diets were characterised by the absence of detritus in the stomach contents of *A. lacunosus* and absence of both phytoplankton and detritus in *S. delicatilus* (Table 5). Differences in feeding intensity among the species were assessed by comparing the mean stomach fullness indices. Species that did not include detritus in their diet had lower fullness indices. Consequently, their diet diversity was lower as observed in *S. delicatilus* and *A. lacunosus* (Table 5).

The results on feeding niche overlap between the 8 fish species are shown in Fig. 23, in which three fish groups are depicted. More details are depicted in appendix 5. There were considerably high values of feeding niche overlap between the 8 investigated species. Feeding niche overlap was highest within the groups than between the groups. The highest values were recorded between *A. lacunosus* and *S. delicatilus*, *S. crumenophthalmus* and *S. gibbosa*, *S. insidiator* and *S. gibbosa* and finally between *S. insidiator* and *S. crumenophthalmus*. However, lowest values were recorded between G. oyena and S. delicatilus, G. oyena and A. lacunosus, L.



Fig 23. Cluster diagram showing diet overlap between fish species in Mtwapa Creek. Details of Morisita diet overlap values are in appendix 5.

4.5.3 Feeding strategies of fish species from Mtwapa creek

Using the Tokeshi graphical analysis method on feeding strategies, *S. delicatilus* was clearly separated from the other 7 species (Fig 24). It was noted that for *S. delicatilus*, both individual and population feeding diversities were low, indicating a specialised feeding strategy. All the other 7 species were characterised by high individual and population feeding diversities, ^{Suggesting} a more generalist and opportunistic feeding strategy.



Fig. 24. The feeding stategies of 8 fish species from Mtwapa creek as determined by Tokeshi graphical analysis.

4.5.4 DISCUSSION

Planktivores are separated based on whether they feed on holoplankton or meroplankton (Parrish, 1989). In this present study, two trophic categories were identified among the eight species of fish that were examined. *S. delicatilus* was exclusively carnivorous feeding mainly on ²⁰oplankton and zoobenthos. It was characterised by a very low diet diversity / feeding niche breadth of (H' = 0.40) and low fullness index (F.I = 0.84), while *S. gibbosa*, *P. ditchella*, *L.* ^{equula}, *S. insidiator*, *G. oyena* and *S. crumenopthalmus* belonged to the omnivorous category having also taken plant material in their diets. This later group fed on phytoplankton, ²⁰oplankton, detritus and zoobenthos with a relatively higher feeding niche breadth ranging

between H' = 0.68 for *S. gibbosa* and H' = 0.96 for *P. ditchella*. This group also had higher stomach fullness indices except for *S. crumenophthalmus*. A third which consisted of *A. lacunosus* was found to have fed on phytoplankton, zooplankton and zoobenthos only, and had a narrower feeding niche (H' = 0.47) as compared to the other omnivores. Low stomach fullness index and very low diet diversity are characteristic planktivorous species, while benthivores tend to have intermediate fullness index with very diverse diets (De Troch *et al.*, 1998 and Wakwabi, 1999). Therefore, from this study *S. delicatilus* and *A. lacunosus* can be considered to be exclusively planktivorous, while the other 6 species are both planktivorous and benthivorous.

James (1988) reviewed the diet of some commercially important clupeids and found that most of them were omnivorous microphagists that derived the bulk of their energy from zooplankton. Their feeding modes have also been described from laboratory and field studies (Blaxter and Holliday, 1958). In addition to filter and particulate feeding, some species display a tendency towards iliophagy and are capable of capturing floating prey (James, 1987). Many filter- feeders display tendencies towards detritivory and iliophagy, utilising high detrital loads and large biomass of unicellular benthic algae present in shallow coastal and estuarine waters they inhabit (Darnell, 1958). The diets of *S.-gibbosa* and *P. dichella* examined in this study support this view. Flexibility in the feeding behaviour of these species enables them to adequately use the available food.

The diet diversity of omnivorous fishes was high compared to that of the carnivorous fish. This was because the omnivores fed on a wide range of food items than the carnivore (*S. delicatilus*). Note that carnivores had mostly fed on zooplankton and zoobenthos. *A. lacunosus* that did not

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feed on detritus also had relatively low diet diversity. The high diversity of prey items found in the diets of omnivorous group suggests that they are more generalist predators.

This study also shows that the investigated fish species foraged on a wide variety of prey organisms with a high level of interspecific dietary overlap. The high degree of niche overlap does not however lead to conclusion on the importance or intensity of competition (Abrams, 1980) as indeed, high niche overlap does not need to result in competition unless food resources are in short supply (Coene, 2000). Therefore, the ratio of demand to supply is of vital concern in the relationship between ecological overlap and competition (Pianka, 1994). A high niche overlap may actually be an indication of a strong ongoing competition between species, which are unable to develop resource partitioning due to evolutionary, developmental constraints or ecological needs. Therefore, low niche overlap values in *G. oyena* vs *S. delicatilus*, *G. oyena* vs *A. lacunosus*, *L. equula* vs *S. delicatilus* and *L. equula* vs *A. lacunosus* was because *G. oyena* and *L. equula* utilised more food resources including endobenthos, which *A. lacunosus* and *S. delicatilus* did not ingest.

Comparatively, the diet diversity in *G. oyena* and *L. equula* was higher than in *A. lacunosus* and *S. delicatilus*. This may further explain the low feeding niche overlap observed between these species. Therefore, there was either no competition or minimal competition for the available food resource between *G. oyena* and *A. lacunosus*, *G. oyena* and *S. delicatilus*, *L. equula* and *A. lacunosus* and finally between *L. equula* and *S. delicatilus*. The higher feeding niche overlap observed among the remaining species was seen as an indication of existing competition for food since they had similar ecological needs.

Seven of the examined fish species exhibited a generalised feeding strategy, against *S. delicatilus*, which had a specialised diet. *S. delicatilus* specialised on feeding on copepods and brachyuran larvae and had lowest mean individual and population diet diversity as shown by the Tokeshi's method. Again, although *A. lacunosus* exhibited a generalist feeding strategy, it had a relatively low individual and population diet diversity compared to the other generalists. This was because *A. lacunosus* did not take detritus in its diet as opposed to the other species. The high feeding niche overlap among these species as observed in this study may also be attributed to having a similar feeding strategy on the same food resource. Their generalist feeding strategy also contributed to the high feeding niche overlap as observed in this study.

4.6 COMPARATIVE DIETARY ANALYSIS FOR S. GIBBOSA AND A. LACUNOSUS

4.6.1 The food composition and feeding strategies of S. gibbosa and A. lacunosus during the northeast and southeast monsoon.

A further analysis of the diets of *S. gibbosa* and *A. lacunosus* with respect to mean number of prey items consumed using the χ^2 test for independence is presented in (Table 6). It is observed that the stomachs of *S. gibbosa* and *A. lacunosus* from Mtwapa creek had a greater number of prey items than those from Shimoni (P < 0.05) (Table 6). For both *S. gibbosa* and *A. lacunosus*, the mean number of prey items consumed was higher during the NE monsoon than in the SE monsoon due to favourable conditions in the environment which facilitated feeding activities during this period.

The spatial and temporal variation in the diet composition of these two species is illustrated in figure 25. Copepods were the most important prey items for *S. gibbosa* from both sites: Mtwapa

creek during the NE monsoon (37.1%N) and SE monsoon (24.8%N), and in Shimoni NE monsoon (48.6%N). Copepods were also important for *A. lacunosus* in Mtwapa creek during the NE monsoon (63.4%N) and SE monsoon (33.2%N). In addition to copepods, sergestids (19.1%N) were important prey items for *S. gibbosa* (Mtwapa) during the SE monsoon; while nematodes and brachyuran megalopas constituted the important food for *S. gibbosa* (Shimoni) SE with 35.4%N and 24.6%N respectively. Lemellibranch larvae (22.6%N) were the important prey for *A. lacunosus* (Shimoni) NE followed by foraminiferans (18.3%N). During the SE monsoon *A. lacunosus* (Shimoni) fed mainly on nematodes (36.26%N) and copepods (16.4%N).

Figure 26 shows the feeding strategies of *S. gibbosa* and *A. lacunosus* during the two monsoon periods. Both species exhibited a generalised feeding behaviour. There were no spatial or temporal differences in their feeding strategies since all points in the Tokeshi's graph tended to cluster together.

Table 6. A	seasonal	comparison o	of mean nu	mber of p	prey items	in the	stomach	contents of
Sardinella	<i>gibbosa</i> ai	nd Atherinom	orous lacu	nosus. N	= mean nu	mber o	of preys.	

Species/ Site	NE monsoon	SE monsoon	χ^2	P value
	N	N		
S. gibbosa (Mtwapa)	142	16	4.86	0.03
S. gibbosa (Shimoni)	21	7		
A lacunosus (Mtwapa)	189	53	4.92	0.02
A. lacunosus (Shimoni)	39	3		



Fig. 25. The numerical composition (%N) of the important food items in the stomach contents of *S. gibbosa* and *A. lacunosus* from Mtwapa creek (MT) and Shimoni channel (SH) during the NE and SE monsoons. Detailed data is presented in appendix 5.



Fig. 26. The feeding strategies of *S. gibbosa* and *A. lacunosus* during the northeast and southeast monsoons as determined by Tokeshi graphical analysis.

4.6.2 Prey Selectivity

There were clear spatial differences in prey selectivity by *S. gibbosa* and *A. lacunosus* depending on changes in prey abundance and availability as depicted in figures 27 A - H. No clear temporal pattern was observed in prey selectivity. A spatial pattern was observed in which, there was a tendency of *S. gibbosa* from Mtwapa creek selecting sergestids during both the NE and SE monsoons (Fig. 27 A & B), while *S. gibbosa* from Shimoni channel selected hyperrids and nematodes (Fig. 27 C & D). On the other hand, *A. lacunosus* from Mtwapa creek highly selected brachyurans (Fig. 27 E & F), while those of Shimoni channel selected nematodes (Fig. 27 G & H). It is notable that, the highly selected prey items were rare (i.e. very low quantities) in the samples of zooplankton collected in the same areas fished. These differences in prey selectivity confirm the trophic flexibility exhibited by these species in their generalised and opportunistic feeding behaviour. The prey items with positive values were actively selected from the environment, while those with negative values were either not preferred by the fish, were inaccessible or were avoided. Most of the prey items especially those found to be abundant in the environment e.g. copepods were randomly selected by the fish (Fig. 27 A – H).

The above observations show that *S. gibbosa* and *A. lacunosus* from Mtwapa creek and Shimoni channel did not actively select similar prey items at any particular season or site. The difference in the type of prey selected could be an adaptive behaviour minimising competition for food resource and hence allowing coexistence of the two species in similar habitats.

Fig. 27 A - H. Strauss selectivity indices showing prey selection by *S. gibbosa* and *A. lacunosus* during the NE and SE monsoons. +Ve denote active selection, -Ve denotes either avoidance, prey inaccessibility or lack of preference and zero denotes random selection on the vertical scale. Appendix 7 shows proportions of prey in the stomach and in the environment used to derive the figures.





Sardinella gibbosa (Shimoni) SE monsoon.

D

-0.1 -0.2 -0.2 -0.2 -0.3 -0.5 Rotifera Hyperrids Nemertea Nematodes Sardinella gibbosa Invertebrate eggs Cladocerans Unident. crustaceans Brachyuran megalopa Crustacean nauplii Insect (Shimoni) NE monsoon. Pangurids Copepods Brachyuran larvae Anomuran larvae Foraminiferans Siphonophores Lemellibranch larvae **Mysids** Chaetognaths Ostracods Gastropod larvae Acantharians Fish eggs

0

90



(F)



2

E



(H)
-0.2 -0.2 -0.3 -0.5 Foraminiferans Nematodes Nemertea Flat worms Atherinomorous lacunosus Invert. eggs Ostracods **Hyperrids** Pangurids Brachyuran megalopa Gammarids Unident. crustacean Sipunculids Insecta Anomurans (Shimoni) NE monsoon Fish scales Polychaete larvae Fish larvae Caprellidae Medusae Rotifera Siphonophores Brachyuran larvae **Mysids** Echinoderm larvae Gastropod larvae Acantharians Fish eggs

14.5

G

92

4.6.3 Prey size

Since copepods and nematodes were the most common prey items eaten by *S. gibbosa* and *A. lacunosus*; the results presented in Table 7 & 8 shows the variation in these prey sizes eaten by the two species. The mean carapace length of copepods eaten by the two species ranged between 311 μ m and 665 μ m, and the mean carapace width varied from 134.8 μ m to 293.7 μ m (Table 7). Note that smaller copepods were taken by *A. lacunosus* as *S. gibbosa* consumed larger sized copepods (ANOVA, P<0.05, Tukey HSD, P<0.05) (Table 7). *A. lacunosus* ate slightly larger nematodes than *S. gibbosa*, though there was no significant difference in the body length of nematodes eaten by the two species (ANOVA, P>0.05, Tukey HSD, P>0.05) (Table 7).

There was no significant ontogenetic change in prey sizes for both *A. lacunosus* and *S. gibbosa* (Table 8). The mean copepods carapace length and width, and nematodes body length were not significantly different between the size classes of *S. gibbosa* (ANOVA, P>0.05, Tukey HSD, P>0.05), but there was a difference in nematodes body width (ANOVA, P<0.05, Tukey HSD, P<0.05). Neither did the prey sizes (copepods carapace length and width, and nematodes body width) eaten by *A. lacunosus* differ within the size classes (ANOVA, P>0.05, Tukey HSD, P>0.05) (Table 8). However, there existed a significant difference in the nematodes body width eaten by the different size classes (ANOVA, P<0.05, Tukey HSD, P<0.05) (Table 8). However, there existed a significant difference in the nematodes body width eaten by the different size classes (ANOVA, P<0.05, Tukey HSD, P<0.05). In all comparisons, nematodes body length contributed to interspecific differences in size of prey eaten, while nematodes body width contributed to ontogenetic differences in prey size eaten by the two species.

_	Copepods		Nematodes			
	Carapace length (µm)	Carapace width (µm)	Body length (µm)	Body width (µm)		
Species	P<0.05	P<0.05	P>0.05	P<0.05		
S. gibbosa	665 ± 17 (587)	294 ± 9 (587)	391 ± 15 (250)	103 ± 5 (250)		
A. lacunosus	311 ± 4 (65)	135 ± 8 (65)	422 ± 25 (436)	137 ± 5 (436)		

Table 7. Interspecific differences in prey size eaten by Sardinella gibbosa and Atherinomorous lacunosus (\pm SE). Sample sizes in parenthesis.

Table 8. Ontogenetic changes in prey sizes eaten by Sardinella gibbosa and Atherinomorous lacunosus (\pm SE). Sample sizes in parenthesis.

	Copepods		Nematodes			
Size classes	Carapace length	Carapace width	Body length	Body width		
(mmSL)	(µm)	(µm)	(µm)	(μm)		
S. gibbosa	P>0.05	P>0.05	.05 P>0.05 P<0			
80 - 90	661 ± 27 (143)	311 ± 17 (143)	469 ± 15 (94)	125 ± 31 (94)		
91 - 100	697 ± 26 (159)	359 ± 64 (159)	500 ± 16 (67)	164 ± 27 (67)		
101 - 110	683 ± 23 (124)	289 ± 12 (124)	380 ± 7 (56)	98±5 (56)		
111 - 120	611±14 (98)	273 ± 22 (98)	354 ± 21 (33)	94 ± 1 (33)		
121 - 130	516 ± 22 (63)	- 164 ± 24 (63)	-	-		
A. lacunosus	P>0.05	P>0.05	P>0.05	P<0.05		
70 - 80	328 ± 14 (44)	138 ± 9 (44)	356 ± 18 (133)	135 ± 7 (133)		
81 - 90	188 ± 1 (21)	109 ± 16 (21)	521 ± 25 (154)	167±13 (154)		
91 - 100	-	-	432 ± 33 (88)	130 ± 7 (88)		
101 - 110	-	-	281 ± 1 (61)	109 ± 16 (61)		

4.6.4 Spatial difference in feeding intensities of S. gibbosa and A. lacunosus

The spatial and temporal variation in feeding intensities of *S. gibbosa* and *A. lacunosus* as measured using the stomach fullness indices are depicted in figure 28. The feeding intensities for *S. gibbosa* and *A. lacunosus* from Mtwapa creek were higher compared to those of Shimoni channel (Fig. 28). There was a significant difference in the feeding intensity of *S. gibbosa* from Mtwapa creek and those from Shimoni channel (ANOVA, P < 0.05). However, there was no significant difference in the feeding intensity of *A. lacunosus* between the two study sites (ANOVA, P > 0.05).



Fig. 28. Stomach fullness indices (Mean ± SE) for A. lacunosus (ALM & ALS) and S. gibbosa (SGM & SGS). M = Mtwapa creek, S = Shimoni channel. The last letters in the legend refers to study areas.

4.6.5 DISCUSSION

An apparent temporal and spatial separation in the diet composition of *S. gibbosa* and *A. lacunosus* was observed. The diets of the two species were separated during the two monsoon periods based on prey availability. During the NE monsoon, copepods seemed to be the most abundant prey in the environment. It was thus observed to have dominated in their diet. However, during the SE monsoon, nematodes were more abundant in the environment especially in Shimoni channel. It was therefore noted that the diets of the two species in Shimoni channel was dominated by nematodes during the SE monsoon while copepods and sergestids were important preys for *S. gibbosa* in Mtwapa creek during the same season.

The overall dominance of copepods in the stomach contents of *S. gibbosa* and *A. lacunosus* during the NE monsoon than in the SE monsoon was apparently due to the relative abundance of copepods in the environment. This period was also associated with high water transparency that made it easier for both species, which are mainly visual feeders (Major, 1977) to locate their prey. During the SE monsoon when transparency was lowered due to increased turbidity as a result of increased turbulence and river / runoff inputs from terrestrial environment, there was relatively low visibility for the two fish species thus restraining their activities in this season.

Any attempt at generalising the feeding ecology of fish confronts the problem posed by the ^{trophic} flexibility that many species show (Wootton, 1990). Ontogenetic, seasonal and diel ^{chan}ges in diet are examples of this flexibility. Fish may also change its feeding behaviour ^{depending} on food availability and environmental conditions prevailing. *S. gibbosa* and *A.*

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lacunosus from Mtwapa creek and Shimoni exhibited a generalised feeding strategy during both the NE and SE monsoons. From the foregoing, both *S. gibbosa* and *A. lacunosus* responded to seasonal changes in food availability, since they reflected an opportunistic behavior and trophic adaptability.

Tropical fish in coastal water are acknowledged to be generalists, as they have to cope with a seasonally changing environment (Lowe-McConnell, 1991). The reversing monsoons along the East African coast is for example the main overriding feature affecting the local climate in this area (Richmond, 1997). These monsoon winds, together with the changes in the major coastal and oceanic currents in the region control many ecological processes (McClanahan, 1988).

Clupeids have long been recognised as opportunistic foragers that feed on suitable food as encountered (Koslow, 1981 and James, 1988). These habit results in flexible feeding cycles that depend on local conditions. Laboratory and field data indicate that intermediate microphages (*S. gibbosa* and *A. lacunosus*) display a high degree of opportunism in fulfilling their dietary requirements (Koslow, 1981). They are energy maximisers, capable of alternating their feeding strategies to use the available trophic spectrum efficiently. It has been commonly recognised that the diets of these fish reflect the composition of the ambient plankton communities (King and Macleod, 1976, Koslow, 1981, James, 1987). Therefore, the observed spatial difference in the diet composition of these two species is indicative of their generalist and opportunistic feeding behaviour. Copepods were the most important prey item for both *S. gibbosa* and *A lacunosus* in Mtwapa creek during the NE monsoon. However, nematodes were more important ^{In} their diets during the SE monsoon in Shimoni channel. These show how fish may switch from One type of prey to another as the relative abundance of the prey changes. The above

observations clearly show that habitat variability can affect predator behaviour as well as prey availability, resulting in habitat specific foraging strategies. *S. gibbosa* and *A lacunosus* exhibited a flexible feeding strategy that could be contributing to their success in this seasonal environment.

planktivorous fish can be highly selective feeders (Milton *et al.*, 1990) and their impact on the community structure of zooplankton can have an important influence on the distribution and abundance of both zooplankton and fish. Comparatively, *S. gibbosa* and *A. lacunosus* selected different prey items at the two study sites. This observation indicates the spatial difference in prey selection by the two species.

Although copepods were the most abundant prey items in the two study areas, *S. gibbosa* and *A. lacunosus* did not actively select them. According to the optimal foraging theory, high prey capture probability is a function of prey density, size, total visibility and motion (Lazzaro, 1987). In this regard, when copepods are considered against other highly selected prey items in this study; copepods were usually smaller and this decreased their capture probability. Consequently, *S. gibbosa* and *A. lacunosus* were better at catching larger prey since they were more conspicuous and easy to catch. This may explain the high positive selection of larger prey items (sergestids, hyperrids and brachyurans) by these two species. Wootton (1990) also reported that ²⁰oplanktivorous fish are better at catching larger prey than smaller prey items. *S. gibbosa* and *A. lacunosus* did not select similar prey items at any of the study areas or during the two monsoon seasons.

visual predators pursue the prev item that appears largest at the start of the search (O' Brien et al., 1976). Based on prey size, S. gibbosa consistently ate larger individuals of copepods than A. *lacunosus*. This could suggest that it is a visual predator. The high proportion of phytoplankton and small-sized copepods in the diet of A. lacunosus suggests that its feeding mode may be mainly through filter feeding. The position of the mouth also plays an important role in determining the kind of prey items eaten by fish (Wooton, 1990). S. gibbosa have a superior mouth while A. lacunosus have a terminal mouth (Smith, 1986). Surface feeding fish usually have superior mouth while fish that feed in midwater have terminal mouth. The difference in copepod sizes eaten by these two co-existing species is probably a strategy to reduce interspecific competition for this prey, since larger copepods tend to aggregate at the water surface and small sized copepods aggregate at the midwater column or at the bottom. From this study, the prey sizes (copepods) did not differ significantly with increase in size of the fish. However, other studies have shown that the range of prey size increased with increase in fish body size (Morato et al., 2000). Similarly, larger predators were found to utilise all food resources ranging from smaller prey items to larger ones, thus giving them a competitive advantage (Brooks & Dobson, 1965).

The spatial differences observed in feeding intensities of *S. gibbosa* and *A. lacunosus* is a result of spatial niche differences between Mtwapa creek and Shimoni channel. The stomach fullness index closely reflects these spatial differences. Differences in productivity and food availability between habitats as a result of presence or absence of mangrove vegetation, influences the distribution and feeding activities of fish (Robertson & Duke, 1987). Extensive mangrove vegetation and mud banks surround Mtwapa creek creating microhabitats that support dense populations of micro- and macrofauna at both benthic (Ruwa, 1990) and planktonic levels (Osore, 1994). One notable attribute of mangroves is their high net primary productivity compared to other aquatic ecosystems. This production results in high leaf and litter fall that forms the basis for the detritus food web for microbes, molluscs, crabs and fish. They also bind roots and sediments creating a stable habitat for burrowing organisms. In this regard, Mtwapa Creek therefore, is considered rich in planktonic and benthic food supply. *S. gibbosa* and *A. lacunosus* are both planktivores and benthivores, hence they were able to utilise the available food resource adequately resulting in very high fullness indices in the creek ecosystem as compared to Shimoni channel.

Although primary production in the form of Chlorophyll *a* and zooplankton production was high in Shimoni channel than Mtwapa creek, the benthic zone in Shimoni channel seem to have supported a very low population of micro- and macrofauna. Production in Shimoni channel relies mainly on photosynthetic processes unlike Mtwapa creek where detritus also play a major role in energy flow. Hence, low stomach fullness indices that was observed in *S. gibbosa* and *A. lacunosus* from Shimoni channel was a result of lack of adequate food resource in the benthic zone. In addition, benthic organisms tend to be larger in size than planktonic organisms. Therefore, fish feeding on a larger proportion of benthic organisms tend to have a higher fullness index than those feeding mostly on planktonic organism

4.7 DIEL VARIATION IN FEEDING PERIODICITY AND FOOD COMPOSITION OF *A. LACUNOSUS* IN SHIMONI CHANNEL

4.7.1 Feeding periodicity of A lacunosus

Variation in feeding periodicity in *A. lacunosus* as measured by using stomach fullness indices is depicted in Fig. 29. *A. lacunosus* had the highest fullness index at 0600 hrs and the lowest at 1200 hrs. After mid day, the feeding intensity increased gradually again with a higher fullness index of 0.92 ± 0.12 SE at 1800 hrs. This gradual increase in feeding intensity may suggest that feeding intensity in *A. lacunosus* increased with decreasing light intensity. This species exhibited negative phototrophic behaviour via diel vertical migration, seemingly controlling their feeding chronology.

Daytime feeding pattern shows that their feeding intensity was remarkably reduced at higher light intensity. Changes in light intensity affect the daily rhythm of zooplankton and hence affect the availability of different food organisms to the fish. Field observation showed that at dawn, the fish schools were concentrated in the surface waters with optimal light intensity. As light intensity increased, they migrated downwards to the bottom following the daily migration pattern of zooplankton.



Fig. 29. The diel stomach fullness indices (F.I) in A. lacunosus (mean \pm SE).

4.7.2 Day time variation in food composition of *A. lacunosus*

The food composition in *A. lacunosus* guts between 0600 hours and 1800 hours is depicted in Table 9. More prey categories were found in the stomach contents of *A. lacunosus* caught at 0600 hours than the rest of the day. The number of prey categories decreased with time of day, but again appeared to have increased at 1800 hours (Table 9). At 0600 hours, the fish fed mostly on copepods (28 %N) and some unidentified crustaceans (28 %N). At 1000 hours and 1600 hours, nematodes were the main prey items in their stomach contents. At 1200 hours, the dominant prey items were copepods (45 %N) and lemellibranch larvae (24 %N). The number of prey categories increased towards dusk (1800 hours) with copepods again constituting the highest percentage of prey in the stomach contents. Copepods were the dominant prey items at dawn (0600 hrs) and at dusk (1800 hrs) coinciding with the time when feeding intensity was highest.

Table 9. Diel changes in food composition for A. lacunosus. Present (+), absent (-), numbers (% N).

N: Sample size.	30	27	22	30	19 1800	
Time (Hours)	0600	1000	1200	1600		
Phytoplankton	+++	+++	+++	+++	+++	
Copepods	27.61	1.45	45.24	1.28	33.24	
Brachyuran larvae	-	-	3.38	-	1.47	
Brachyuran megalopa	4.48	-	-	-	-	
Hyperrids	5.22	1.45	-	-	3.11	
Gammarids	5.22	-	-	-	-	
Mysids	0.75	-	-	-	7.48	
Pangurids	6.72	-	-	-	-	
Ostracods	5.97	8.69	10.52	2.56	5.39	
Unidentified crustaceans	27.61	1.45	-	-	6.84	
Nermertea	0.75	-	-	-	-	
Nematodes	1.49	39.13	-	29.49	20.7	
Fish eggs	11.19	-	7.9	-	-	
Fish larvae	0.75	-	-	-	3.18	
Foraminifera	1.49	2.9	8.14	-	-	
Anomuran larvae	0.75	-	-	-	0.92	
Invertebrate eggs	-	10.14	-	7.69	-	
Lemellibranch larvae	-	26.09	23.81	55.13	16.05	
Gastropod larvae	-	8.7	-	1.28	-	
Medusae	-	-	-	1.28	-	
Polychaete larvae	-	-	-	1.28	1.59	
Total number of prey categories	14	9	6	8	11	
Mean stomach fullness index ± SE	1.14 ± 0.10	1.09 ± 0.06	0.48 ± 0.05	0.76 ± 0.06	0.92 ± 0.12	

4.7.3 DISCUSSION

The observed feeding periodicity in *A. lacunosus* with peak feeding activity at dawn and at dusk in the upper water layers does seem to be under the direct influence of day light intensity. There was a decrease in feeding intensity with increasing light intensity during the day. Further, direct observations in the field during this study also confirmed this since the fish formed tight shoals on the seabed as light intensity increased. Similarly, studies conducted on *Clupea herangus* (planktivorous fish) revealed that twilight foragers whose peak feeding occurs at dawn and dusk in the upper water layers, had decreased feeding intensity during the day and during the darkest hours of the night (James, 1988).

Studies carried out elsewhere show that vision is the principal sense used in feeding for most pelagic and plankton-eating fishes (Okul, 1941). Marshall (1965) observed that the eyes of fish are adapted for vision in an environment characterised by low illumination, poor visibility and monochromatic light. Light can affect prey availability by restricting the ability of visual predators to locate their food (Hunter, 1968), and by influencing vertical migration patterns of zooplankton and fish (Hutchings, 1985). Further, Protasov (1970) discovered that the eyes of atherinids and anchovies are adapted for detecting rapidly moving prey in poor light.

James (1987) observed in *Engraulis capensis* a diurnal alternation between filter feeding in the day and particulate feeding at dawn and dusk. This species makes dense feeding shoals at daytime and are solitary during the dark hours. Another factor that may affect feeding periodicity is predation pressure, which in planktivores may influence the feeding cycle (Hobson, 1968, Major, 1978). *A. lacunosus* forms dense shoals at the sea bed as an antipredatory strategy

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when light intensity is high and they are more vulnerable to predation by other larger piscivorous fishes. During this time, their feeding activity is remarkably reduced. Increase in feeding intensity after midday is a result of the progressively reducing light intensity.

Variation in food composition of A. lacunosus with time also reflects variation in prey availability. More prey categories were eaten at 0600 hours when feeding intensity was high and decreased as time progressed. The availability of food organisms to A. lacunosus alters in connection to changes in light intensity and zooplankton vertical migration. Zooplankton are known to migrate to the surface to feed during periods of low light intensity, while they migrate to the bottom as an antipredatory behaviour as light intensity increases. At dawn and dusk A. lacunosus fed mostly on copepods in the upper layers of water where copepods formed large concentrations due to their daily vertical migrations (Kozhov, 1954). At 0600 hours, copepods were the main prey item. As the day progressed, the fish moved towards the seabed, whereby nematodes and copepods became the important prey items. These changes in diet composition reflects changes in the activity of the prey and the predator, and hence the vulnerability of the prey to predation. Diel vertical migration of zooplankton especially copepods seem to coincide with the vertical migration of A. *lacunosus*. This explains the presence of copepods in their diet at dawn and at midday. Nematodes, which are mainly zoobenthos also, dominated their diet at ¹⁰⁰⁰ hours and at 1600 hours when the fish fed at the bottom where they formed tight shoals.

CHAPTER 5: GENERAL DISCUSSIONS, CONCLUSIONS AND RECOMMENDATIONS

5.1 GENERAL DISCUSSIONS

5.1.1 Inter-relationship between physical-chemical variables, biological variables and abundance of planktivorous fishes

There was a clear spatial separation of stations located in Mtwapa creek from those in Shimoni channel. This separation was based on very significant differences in environmental variables such as transparency and zooplankton abundance between the two study areas. The overriding local climatic features in the study areas are the reversing monsoons (Richmond, 1997). These winds, together with the changes in the major coastal and oceanic currents in the region, creat marked seasonality in rainfall, temperature and productivity (McClanahan, 1988). However, habitat characteristics such as the degree of terrestrial influence, presence of mangrove vegetation and mud banks also influenced the environmental variables investigated in this study. Physical-chemical and biological variables differed significantly between Mtwapa creek and Shimoni channel, with transparency and zooplankton abundance contributing highly to the differences in the two sites. To a lesser extent, the differences were due to conductivity, salinity, temperature and chlorophyll *a* concentrations. Fish species diversity, abundance and trophic status of pelagic fishes were influenced by variation in these environmental variables.

Productivity in aquatic systems varies depending on chemical and physical forces namely: light, temperature, salinity, nutrients, dissolved oxygen, pH, conductivity and water circulation (McClanahan, 1988). Nutrient shortage limits marine phytoplankton production. Marine phytoplankton production is often limited by nitrogen availability (Ryther and Dustan, 1971),

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which is normally fixed by blue green algae in tropical marine waters (Barnes and Hughes, 1988). Globally, productivity correlates well with levels of nutrients. It is always higher in nutrient - rich shelf waters and in areas of upwelling; but lower in nutrient-poor tropical ocean regions as compared to sub tropical and temperate waters (Barnes and Hughes, 1988). Bryceson (1982) reported that phytoplankton abundance, diversity and chlorophyll *a* concentration in nearshore waters in Tanzania during the NE monsoon; was attributable to a shallow stable thermocline that kept phytoplankton at optimal photosynthetic light intensities near the surface.

Habitat characteristics played an important role in determining fish abundance and species diversity in Mtwapa creek and Shimoni channel. Diverse and complex habitat in Mtwapa creek resulted in high fish species diversity than Shimoni channel which, is considered as a homogeneous habitat. Fish abundance and diversity were inversely related since as fish species diversity increases the number of trophic levels also increases. This results into higher incidence of predatory depression in lower trophic levels and hence increases abundance of higher trophic levels (Washington, 1984). This observation explains the differences in fish abundance and diversity between the two sites.

Available food resources in the environment determined the diet of abundant pelagic fish species in Mtwapa creek. Most of the fish were generalist except *S. delicatilus*, which exhibited a specialised feeding strategy. The examined fishes were therefore well adapted to the changing environment with frequent changes in food availability due to their generalist feeding strategy. Spatial and temporal analysis of the diets of *S. gibbosa* and *A. lacunosus* showed that they remained generalists. Since these two species are visual predators, they highly selected large prey items such as sergestids, hyperrids and brachyurans. Similarly, *S. gibbosa* ate larger copepods than *A. lacunosus*, which suggest that it particulate feed on the large prey. While, *A. lacunosus* filter feed on small sized copepods and a high proportion of phytoplankton. The diel variation in feeding intensity and diet composition of *A. lacunosus* was attributed to the changing light intensity / illumination, diel vertical migration of both zooplankton and *A. lacunosus* as an antipredatory behaviour. Feeding intensity was highest at dawn and dusk, which coincided with maximum zooplankton densities in the surface water. As light intensity increased, the fish migrated to the seabed following the downward migration of zooplankton. At this time, feeding activity was also minimal sinse the fish also tend to avoid predation by larger piscivorous fish species. As light intensity decreased towards dusk, *A. lacunosus* migrate to the surface water to feed on zooplankton, which also migrate to the surface during this time of the day. Jessop (1990) also observed that the feeding intensity and the choice of prey which includes benthic and planktonic organisms by opportunistic feeders seem to depend upon prey preference, time of day and synchrony in diel behaviour between predator and prey.

Livingstone (1984) observed that coastal fish assemblages are dominated by species that follow well-timed seasonal migrations from offshore areas into the shallow, highly productive inshore systems. Local habitat conditions, seasonal productivity cycles and the availability of appropriate food organisms govern the distribution and migration of such species. In this investigation, it was established that *S. gibbosa* and *A. lacunosus* migrate offshore during the SE monsoon and back inshore during the NE monsoon when they are readily caught by the artisanal fishers.

5.1.2 Plankton fish interaction

Studies on the trophic ecology of planktivorous fishes are important for understanding plankton fish interaction in any aquatic ecosystem. The biomass created by phytoplankton is passed up the food chain through a set of predator-prey interactions. These interactions depend on the quantity and quality of this biomass, which is made available to the herbivorous zooplankton and phytophagous fishes. The phytoplankton is carried passively by both horizontal and vertical motions through the water column. Zooplankton has both horizontal and vertical movements in response to diurnal changes in light and vertical variation in food concentrations. Pelagic fish, as well as exhibiting shoaling behaviour, carry out horizontal migrations over hundreds and sometimes thousands of kilometres using regular features of ocean currents. For these reasons, there will be a greater dependence of physical variability at higher trophic levels (fish); and so one would expect the effects of such variability to be passed from lower trophic levels (plankton) to higher trophic levels. Abundance of planktivorous fishes depends on the quantity and quality of plankton in the ecosystem since they utilise them as their major food component. In the present study, S. gibbosa and A. lacunosus were more abundant in the catches during the NE monsoon and early SE monsoon. This period provided optimal feeding conditions for both species. Brooks and Dobson (1965) reported that planktivorous fish selectively consume larger and more visible zooplankton prey. It could therefore, be deduced that after the peak production of zooplankton in April - May (SE monsoon), it took sometime before the peak fish production and in this case S. gibbosa and A. lacunosus. This was the lag period for zooplankton to grow into larger and more visible sizes, which are preferred by these two fish species. This

observation explains the high landing of sardines (S. gibbosa and A. lacunosus) during the NE monsoon (G.K.F.D.H., 2001).

During the NE monsoon (December – March), when sea conditions are calmer and Secchi disc transparency was high there was an increasing trend in sardine landings. The high landings extended to the early SE monsoon (April – May) when zooplankton production started increasing. Therefore, it is clear that the period of high sardine catches was after period of high plankton production (phytoplankton and zooplankton). Wakwabi (1981) also reported a synchrony between the abundance of sardines on the market during November – April when the NE monsoon prevails. Low catches during the SE monsoon was attributed to the impact of environmental conditions during that period which is characterised by strong winds and rough sea conditions. Fisheries research in Kenya indicates seasonal changes in finfish catches, with catches being low during the SE monsoon and high during the NE monsoon (McClanahan, 1988). Factors affecting observed seasonality include (1) reduced effort by fishermen during the SE monsoon due to rough sea conditions, (2) fish migrations and (3) decreased density and activity due to deeper thermocline and cooler waters in the SE monsoon. High catches of sardines during the NE monsoon is therefore due to adequate food supply in the environment, and suitable hydrographic conditions which enables them to locate their prey since they are visual predators.

5.1.3 Socio -economics and education

The small pelagic fishes normally landed by the local artisanal fishers are *S. gibbosa* and *A. lacunosus.* These fish species are grouped and referred to as "dagaa" by the coastal ^{communities.} The fishers do not have advanced technological and financial capacities to venture

into more lucrative fishing grounds, which are further offshore. They mostly use small dug out canoes and fish with small cast nets and beach seines. "Dagaa" fishing is normally curtailed during the SE monsoon when these fishes migrate offshore and the sea becomes rough due to the prevailing environmental conditions. The negative impacts of the migration of these fishes, especially on these poor fishermen, are as result of lack of alternative economic opportunities for them during the SE monsoon. During the SE monsoon fishing efforts are at minimal level due to the rough sea conditions experienced at this period (McClanahan, 1988), which also reduces the amount of sardines landed. Therefore, inorder to minimise the level of poverty in the families that depend on these resource; it is important to intensify environmental awareness programs in informal setting (media and local fishermen meetings). Through such efforts, the fishermen would understand the need to change from only relying on these marine resources but also to intensify their agricultural activities during the SE monsoon when there is adequate rainfall along the coastal region. Stapp et al. (1969) resolved that environmental education is aimed at producing citizens who are knowledgeable concerning their biophysical environment and its associated problems; aware of how to solve these problems and motivated to work toward their solution.

The "dagaa" are a cheap source of protein. A kilogram of "dagaa" is sold at only Ksh 20, while the prices of other larger fish ranges between Ksh 40 - 80 per kilogram. This means that "dagaa" is more affordable to the majority of the poor people living along the coast despite their seasonal availability. The local communities living around Mtwapa creek and Shimoni show very high dependence on marine resources. This indicates that the conservation of the environment and its natural resources is of importance to the economic well being of these coastal communities. Conservation of the existing mangroves is paramount since mangrove swamps provide complex habitats, which are inhabited by a diverse community of both benthic and planktonic organisms. This in turn increases the amount of food available to the fish communities inhabiting such areas.

5.2 CONCLUSIONS

- Although *S. gibbosa* and *A. lacunosus* shared common near-shore microhabitats and most of the times foraged together, they utilised spatial and nutritional resources of the environment differently. They minimised direct interspecific competition by differentiating their feeding niche breadth and selecting different preys. *S. gibbosa* had a higher diet breadth than *A. lacunosus* in Mtwapa creek. The utilisation of detritus as dietary component for *S. gibbosa* allowed it to take advantage of an abundant food resource in the benthic zone while minimising competition with *A. lacunosus* which did not feed on detrital materials.
- Feeding patterns in fish are more likely to be determined by site-specific features of particular habitats and their associated predator and prey assemblages.
- Both *S. gibbosa* and *A. lacunosus* use two key microhabitats as foraging grounds: the pelagic and benthic zones of the sea. They forage on holoplankton and meroplankton in the pelagic zones and on zoobenthos from near the seabed. In all the habitats, feeding strategies for the two species remained the same.

- Spatial and temporal differences in the prey items positively and negatively selected shows how habitat variability, and therefore food availability, affects the food types consumed by the fishes.
- The choice of prey by these opportunistic feeders seemed to depend upon food availability, which was determined by both the physical and chemical driving forces in the marine ecosystem.
- Species with a generalised and flexible feeding behaviour are less vulnerable to changes in abundance or availability of particular prey categories, hence giving them a competitive advantage over specialised feeders.

5.3 **RECOMMENDATIONS**

- Dietary analysis in fish provides relevant information in judging how productive an aquatic ecosystem may be. It is therefore necessary to extend such studies to dermersal fishes inorder to understand the feeding interactions among them in relation to benthic productivity.
- Mangrove ecosystems play an important role in maintaining planktonic and benthic productivity, fish production and fish species diversity in the inshore waters of our Kenyan coast. Therefore, more efforts should be geared towards conservation and restoration of this valuable resource along our coastline.

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APPENDICES

Appendix 1. Summary of the physical -chemical, and biological parameters for all stations in the sampling areas. Mtwapa creek (MT1, MT2, MT3) and Shimoni channel (SH1, SH2, SH3).

	MT1	± SE	MT2	± SE	МТ3	± SE	SH1	± SE	SH2	± SE	SH3	± SE
pH	8.39	0.05	8.39	0.05	8.37	0.06	8.38	0.05	8.37	0.05	8.45	0.04
D.O (mg/l)	4.80	0.33	5.00	0.36	4.74	0.38	4.49	0.30	4.47	0.32	4.66	0.32
Transparency (m).	2.11	0.20	2.05	0.20	1.54	0.17	5.72	0.10	5.15	0.14	6.96	0.27
Temperature (°C)	28.41	0.39	28.53	0.38	28.94	0.33	27.67	0.35	27.83	0.33	27.97	0.29
Salinity (0/00)	34.41	0.10	34.37	0.10	34.26	0.07	34.74	0.10	34.83	0.08	34.89	0.09
Conductivity (mS/cm)	51.88	0.10	51.82	0.10	51.77	0.07	51.96	0.12	51.92	0.13	51.95	0.15
Chl a µg/l	0.67	0.03	0.69	0.04	0.95	0.13	1.99	0.18	1.72	0.15	1.46	0.14
Zooplankton abundance (No/m ³)	107.20	15.73	97.32	10.20	66.55	17.52	141.45	41.50	49.65	11.09	53.19	12.29
Н	0.71	0.10	0.82	0.06	1.11	0.03	1.01	0.06	0.89	0.04	1.10	0.04

Appendix 2. Zooplankton taxonomic composition in mtwapa creek and shimoni channel.

PHYLUM: Aschelminthes Class: Rotifera Class: Nematoda PHYLUM: Rhynchocoela Nermertea PHYLUM: Mollusca Class: Gastropoda Subclass: Opisthobranchia Order: Thecosomata (Pteropoda) Suborder: Euthecosomata Family: Cavolinnidae Genus: Creseis acicula & Creseis virgula Order: Mesogastropoda Suborder: Heteropoda Family: Atlantidae Genus: Atlanta Class: Bivalvia Lemellibranch larvae PHYLUM: Chordata Subphylum: Urochordata Class: Thaliacea Order: Doliolida Family: Doliolidae Genus: Doliolum sp. Order: Salpida Family: Salpidae Genus: Thalia sp. & Salpa sp. Class: Larvacea (Appendiculata) Order: Appendicularia Family: Oikopleuridae Genus: Oikopłeura sp. Class: Ascidiacea Ascidian larvae Subphylum: Vertebrata Class: Osteichthyes (Fish eggs and larvae) PHYLUM: Arthropoda Class: Crustacea Subclass: Ostracoda Order: Myodocopida: Genus: Sarsiella sp., Conchoecia sp. & Philomedes sp. Subclass: Branchiopoda Order: Cladocera Genus: Edvane sp. Subclass: Copepoda

Order: Calanoida

Acartia sp. Calanus finmarchius, Calingus sp. & Labdiocera sp Rhincalanus sp., Eucalanus sp. Order: Cyclopoida Oithona sp., Oncaea sp., Corycaeus sp., Sapphirina sp., Copilia sp. & Centropages sp. Order: Harpacticoida Microsetella sp. & Macrosetella sp. Subclass: Cirripedia (Barnacles) Cirripede nauplii Subclass: Malacostraca Super order: Hoplocarida Order: Stomatopoda (Mantis shrimp) Stomatopod larvae Superorder: Peracarida Order: Mysidacea Order: Cumacea Order: Isopoda Order: Amphipoda Suborder: Gammaridea Suborder: Hyperridea Super order: Eucarida Order: Euphausiacea (Krill shrimp) Order: Decapoda Infraorder: Penaeidea (Penaeidean shrimp) Family: Penaeidae Genus: Penaeus sp. Family: Sergestidae Genus: Lucifer faxoni Infraorder: Caridea (Caridean shrimp) Infraorder: Anomura (Mud shrimp) Anomuran larvae Superfamily:-Panguroidea

Family: Panguroides

Pangurid larvae

Superfamily: Galatheoidea

Family: Porcellanidae

Porcellanid zoea

Infraorder: Brachyura (True crabs)

Brachyuran larvae & magalopa

PHYLUM: Echinodermata

Class: Echinoidea (Sea urchins & sand dollars) Echinopluteus larvae of sea urchins

Class: Stelleroidea

Subclass: Ophiuroidea (Brittle stars) Ophiopluteus larvae
Class: Holothuroidea (Sea cucumbers) Order: Dendrochirotida Genus: Psolus sp. PHYLUM: Cnidaria (Hydroids, anemones & medusae) Class: Hydrozoa Order: Siphonophora Siphonophores Order: Athecata Family: Corynidae Genus: Sarsia sp. PHYLUM: Chaetognatha (Arrow worms) Genus: Sagitta sp. PHYLUM: Annelida (Segmented worms) Class: Polychaeta Genus: Nereis sp. PHYLUM: Platyhelminthes (Flatworms) PHYLUM: Arthropoda (Jointed legged animals- non crustacean classes) Subphylum: Pycnogonida Class: Pantopoda (Sea spiders) Family: Pycnogonidae Genus: Pycnogonum littorale Class: Insecta Subclass: Apterygota Order: Thysanura (Bristle tails) PHYLUM: Protozoa Class: Sarcodina Radiolarians - Acanthochiasma sp., Hexacontium sp. & Lithomelisa sp. Foraminiferans - Globigerina sp. Tintinnids PHYLUM: Ctenophora Class: Tentaculata Order: Cydippida Family: Pleurobrachiidae Genus: Pleurobranchia sp. PHYLUM: Bryozoa Bryozoan larvae

Appendix 3. Percentage abundance (% N), size range in mm standard length (mmSL) and maximum recorded length (L max) in mm total length (mm TL) of fish species caught from Mtwapa creek and Shimoni channel.

	Mtwapa	Shimoni		
TAXON	%N	%N	Size (mmSL)	Lmax (mmTL)
Apogonidae				
Apogon hyalosoma (Bleeker, 1852)	0.12	-	50 - 90	170
Cheliodipterus sp.	0.05	-	70 - 80	
Atherinidae				
Atherinomorus lacunosus (Forster, 1801)	13.73	58.39	41 - 72	150
Carangidae				
Caranx ignobilis (Forsskal,1775)	0.17	-	40 - 107	170
Selar crumenopthalmus (Bloch, 1793)	0.77	-	120 - 150	600
Citharidae				
Bothus pantherinus (Ruppell, 1830)	0.06	-	110 - 140	390
Clupeidae				
Pellona ditchella (Valenciennes, 1847)	1.82	0.59	55 - 130	160
Sardinella gibbosa (Bleeker,1849)	20.74	36.09	57 - 94	170
Spratelloides delicatilus (Bennett, 1832)	7.33	-	38 - 55	70
Dinopercidae				
Dinoperca petersi (Day, 1875)	-	0.01	333	750
Engraulidae				
Stolephorus indicus (Van Hasselt, 1823)	0.28	-	56 - 92	155
Thryssa malabarica (Bloch, 1795)	0.18	0.03	68 - 120	175
Ephippidae				
Platax pinnatus (Linnaeus,1758)	0.02	-	160	450
Gerreidae				
Gerres filamentosus (Curvier, 1829)	0.11	-	31 - 47	350
Gerres oyena (Forsskal, 1775)	0.73	0.02	43 - 73	300
Gobiidae				
Oligolepis keiensis(Smith,1938)	0.09	-	24 - 32	70
Haemulidae				
Plectorhincus flavomaculatus (Erhenberg, 1893)	0.01	0.13	62 - 221	600
Plectorhincus gaterinus (Forsskal, 1775)	0.15	0.02	69	500
Plectorhincus sordidus (Klunzinger, 1870)	-	0.08	21 - 315	600
Pomadasys multimaculatum(Playfair,1867)	-	0.18	360 - 500	760
Labridae				
Anampses caeruleopunctatus (Ruppell, 1829)	0.24	0.01	150 - 264	420
Cheilio inermis (Forsskal,1775)	0.02	0.59	80 - 153	500
Leiognathidae				

Leiognathus equulus (Forsskal, 1775)	4.48	-	48 - 90		280
Secutor insidiator (Block, 1787)	6.50	-	45 - 55		113
Gazza minuta (Bloch, 1795)	0.18	-	52 - 106		210
Leptoscaridae					
Leptoscarus sp.	0.04	-	35 - 60		
Lethrinidae					
Lethrinus sp.	-	0.42	150 - 243		
Lethrinus harak (Forsskal, 1775)	0.07	0.02	136 -311		500
Lethrinus mahsena (Forsskal,1775)	0.17	0.05	249 - 292		650
Lethrinus miniatus (Foster, 1801)		0.04	245 - 360		900
Lethrinus nebulosus (Forsskal, 1775)	0.06	0.19	40 - 122		860
Lutjanidae					
Lutjanus sp.		0.03		120	
Lutjanus fulviflammus (Foster,1775)	1.47	0.05	126 -219		350
Mullidae					
Parupeneus barberinus (Lacepede, 1801)	0.04	0.07	39 - 121		600
Upeneus tragula (Richardson,1846)	-	0.01		210	300
Upeneus vittatus (Forsskal, 1775)	0.07	-	80 - 117		280
Nemipteridae					
Scolopsis bimaculatus (Ruppell, 1828)		0.35	19 - 24		310
Scolopsis ghanam (Forsskal, 1775)	-	0.02		160	300
Plotosidae					
Plotosus anguillaris (Bloch, 1794)	8.04	-	100 - 134		320
Pomacentridae					
Abudefduf sp.	-	0.01		130	
Scaridae					
Calatomus spinidens (Quoy & Gaimard, 1824)		0.04	90 - 130		190
Leptoscarus vaigiensis (Quoy & Gaimard, 1824)	24.49	1.12	163 - 245		350
Scarus ghobban(Forsskal,1775) 🛛	-	0.03	200 - 300		900
Scombridae					
Scomberomorus sp.	-	0.03	76 - 93		
Scomberoides tol (Cuvier,1832)	0.06	-			
Scorpaenidae					
Parascorpaena mossambica (Peters, 1855)	0.01	-		36	100
Stolephoridae					
Stelophorus delicatilus	7.39	-	38 - 55		120
Sillaginidae					
Sillago sihama (Forsskal,1775)	0.15	-	5 - 135		300
Siganidae					
Siganus oramin (Schneider, 1801)	-	1.27	200 - 225		320

Siganus canaliculatus (Park, 1797)	0.01	-	146	290
Siganus stellatus(Forsskal, 1775)	-	0.04	120 - 210	400
Synododontidae				
Saurida undosquamis (Richardson, 1848)	0.04	0.01	140 - 226	500
Sphyraenidae				
Sphyraena jello (Cuvier, 1829)	0.07	0.09	87 - 143	1500
Tetraodontidae				
Arothron immaculatus (Bloch & Schneider,1801)	0.01	-	150	300

Food items	S. gibbosa	S. delicatilus	P. ditchella	A. lacunosus	G. oyena	S. crumenopthalmus	S. insidiator	L. equula
Copepods	41.56	51.83	29.70	63.41	25.80	0.00	32.25	7.18
Mysids	10.25	0.00	10.15	0.00	0.00	0.00	0.00	5.52
Brachyuran larvae	0.00	44.17	0.00	0.00	0.00	0.00	0.00	0.00
Hyperrids	33.48	0.00	0.00	24.61	0.00	0.00	0.00	0.00
Lemellibranch larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.54
Polychetes	0.00	0.00	0.00	0.00	25.80	0.00	0.00	28.73
Rotifera	0.00	0.00	0.00	0.00	0.00	7.29	0.00	0.00
Anomurans	0.00	0.00	28.01	0.00	0.00	0.00	0.00	0.00
Cladocera	5.34	0.00	0.00	0.00	0.00	0.00	7.96	0.00
Gastropods	0.00	0.00	0.00	0.00	4.95	0.00	0.00	0.00
Ostracods	0.00	0.00	0.00	0.00	6.36	0.00	0.00	0.00
Chaetognaths	0.00	0.00	4.51	0.00	0.00	0.00	39.30	0.00
Foraminifera	0.00	0.00	0.00	0.00	5.65	0.00	0.00	0.00
Invetebrate eggs	0.00	0.00	0.00	0.00	5.48	0.00	0.00	0.00
Nemertea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.54
Nematodes	0.00	0.00	0.00	0.00	18.37	21.10	0.00	0.00
Unidentified crustaceans	0.00	0.00	0.00	0.00	0.00	5.41	0.00	0.00
Fish scales	0.00	0.00	0.00	0.00	0.00	49.28	0.00	0.00
Others	9.36	3.99	27.63	11.99	7.60	16.91	20.50	31.49

Appendix 4. Numerical abundance (%N) of food items in the stomach contents of fish species from Mtwapa creek.

1.3.2

Fish species	S. gib.	S. del.	P. dit.	A. lac.	G. oye	S. cru.	S. ins.	L. equ.
S. gibbosa	1.000							
S. delicatilus	0.986	1.000						
P. ditchella	0.972	0.902	1.000					
A. lacunosus	0.977	1.000**	0.904	1.000				
G. oyena	0.968	0.897*	0.999	0.837*	1.000			
S. crumenopthalmus	1.000**	0.977	0.972	0.977	0.968	1.000		
S. insidiator	1.000**	0.965	0.983	0.966	0.980	1.000**	1.000	
L. equula	0.950	0.868*	0.996	0.853*	0.997	0.949	0.964	1.000

Appendix 5. Morisita feeding niche overlap among fish species in Mtwapa creek. Highest feeding niche overlap values are marked (**) while lowest values are marked (*).

Species	Sardinella	a gibosa			Atherinom lacunos	us		
Site	Shimoni channel		Mtwap	oa creek	Shimoni channel	Mtwapa	Mtwapa creek	
Season	NEM	SEM	NEM	SEM	NEM	SEM	NEM	SEM
Prey categories								
Foraminifera	0.00	0.00	0.00	0.00	18.31	0.00	0.00	0.00
Rotifera	15.06	0.00	0.00	0.00	0.00	5.26	0.00	0.00
Nematodes	4.70	35.38	0.00	5.13	8.85	36.26	0.00	5.00
Flat worms	0.00	0.00	0.00	0.00	0.00	12.87	0.00	0.00
Nemertea	5.39	0.00	0.00	0.00	7.82	0.00	0.00	0.00
Cladocera	0.00	0.00	4.79	0.00	0.00	0.00	0.00	0.00
Copepods	48.60	10.77	37.12	24.83	10.91	16.37	63.41	33.00
Ostracods	0.00	0.00	0.00	0.00	4.53	0.00	0.00	0.00
Hyperrids	6.41	13.85	14.20	0.00	0.00	0.00	24.61	5.00
Sergestids	0.00	6.15	13.88	19.03	0.00	0.00	0.00	0.00
Carideans	0.00	0.00	8.76	0.00	0.00	0.00	0.00	0.00
Mysids	0.00	0.00	7.98	0.00	0.00	0.00	0.00	0.00
Brachyuran larvae	0.00	0.00	0.00	11.75	0.00	0.00	0.00	16.00
Brachyuran megalopa	0.00	24.62	1.64	7.21	0.00	0.00	0.00	0.00
Lamellibranch larvae	0.00	0.00	0.00	6.02	22.63	0.00	0.00	24.00
Polychaetes	0.00	0.00	0.00	0.00	0.00	5.85	0.00	0.00
Fish eggs	0.00	0.00	0.00	6.10	7.03	0.00	0.00	0.00
Others	19.84	9.23	11.64	19.93	19.93	23.39	11.99	17.00

Appendix 6. Numerical abundance (%N) of the food items in the stomach contents of *S. gibbosa* and *A. lacunosus* from the two stations during the two monsoons.

	S. gibbose	S. gibbosa			S. gibbosa					S. gibbosa			
	(Shimoni) NE monso	on	(Shimon	i) SE mons	oon	(Mtwapa) NE monsoon			(Mtwapa) SE monsoon			
	r	р		r	р	L	г	р	L	г	р	L	
Prey categories.	%N st.	%N env.	L	%N st.	%N env.		%N st.	%N env.		%N	%N env.		
Nematodes	4.70	0.00	4.70	35.38	0.15	35.24	0.58	0.19	0.40	5.13	0.02	5.11	
Invertebrate eggs	2.32	0.70	1.62	0.77	0.41	0.36	1.66	8.28	-6.61	1.34	1.10	0.24	
Lemellibranch larvae	1.70	2.23	-0.52				0.61	0.40	0.21	6.02	0.04	5.99	
Nemertea	5.39	0.00	5.39				0.67		0.67				
Gastropod larvae	1.30	3.79	-2.50				0.25	17.02	-16.77	2.75	5.97	-3.22	
Insecta	0.34	0.00	0.34										
Copepods	48.60	48.37	0.23	10.77	0.00	10.77	37.12	36.29	0.83	24.83	31.67	-6.84	
Hyperiids	6.41	0.00	6.41	13.85	0.41	13.43	14.20	1.17	13.03	2.30	0.22	2.09	
Ostracods	0.95	2.24	-1.28				0.40	11.74	-11.33	2.38	0.94	1.44	
Foraminifera Globigerina sp.	0.55	0.62	-0.08							0.07	8.26	-8.18	
Acantharians	1.57	8.22	-6.66				0.04	0.25	-0.20				
Pangurids	0.27	0.00	0.27				0.36		0.36	0.07	0.31	-0.23	
Brachyuran larvae	0.61	0.62	-0.01	2.31	3.92	-1.61	0.02	1.58	-1.55	11.75	25.92	-14.17	
Brachyuran megalopas	0.61	0.17	0.44	24.62	0.09	24.53	1.98	1.08	0.90	7.21	0.36	6.85	
Mysids	1.16	1.79	-0.63	0.77	1.03	-0.26	7.98	1.17	6.80	0.97	0.70	0.27	
Rotifera	15.06	1.03	14.04	-			0.76	0.25	0.52	1.26	0.02	1.25	
Fish eggs	0.68	15.82	-15.14	-			0.31	1.48	-1.17	6.10	5.97	0.13	
Siphonophores	1.36	1.80	-0.44	0.77	0.62	0.15	0.61	1.42	-0.81	0.74	0.41	0.33	
Unidentified crustaceans	1.84	0.69	1.16	5			0.63	0.25	0.38	1.12	0.04	1.08	
Chaetognaths Sagitta sp.	1.70	2.91	-1.21				1.53	2.75	-1.22	0.30	2.52	-2.22	
Cladocerans	2.04	0.80	1.24	-			4.79	0.12	4.66	0.22	2	0.22	

Appendix 7. Numerical abundance of prey in the fish stomach (% N st. = r) and in the environment (% N env. = p). The values were used to calculate the Strauss selectivity index (L).

Nauplii	0.75	0.34	0.41				0.09	0.93	-0.84	0.97	0.79	0.18
Anomuran larvae	0.07	0.09	-0.02				0.49	0.25	0.25			
Stomatopod				0.77		0.77						
Sergestidae: Lucifer				6.15	0.94	5.21	13.88	0.59	13.30	19.03	5.13	13.91
Caridean larvae				3.08	2.89	0.19	8.76	0.31	8.45	1.12	2.77	-1.65
Fish scales				0.77	0.24	0.53	0.02	0.06	-0.04	1.34	0.02	1.32
Polychaetes							1.64	0.59	1.05	2.30	0.63	1.68
Tinttinids							0.18		0.18			-
Doliolids							0.07		0.07			
Euphausids							0.16	0.25	-0.09	0.07	0.32	-0.25
Fish larvae			-				0.20	0.22	-0.01			
Appendicularians Oikopleura sp.	-									0.07	0.54	-0.47
Coelentrate larvae										0.22		0.22
Pteropods Creseis sp.										0.22		0.22
Medusae										0.07	0.07	0.00
Flat worms												
Echinoderm larvae												
Caprellidae												
Sipunculids												
Pycnogonid										Î		

Appendix 7 continued.

	A. lacuno (Shimoni	i) NE monse	oon	A. lacunosus (Shimoni) SE monsoon			A. lacunosus (Mtwapa) NE monsoon			A. <i>lacunosus</i> (Mtwapa) NE monsoon		
	r	р	L	r	р	L	r	р	L	r	р	L
Prey categories.	%N st.	%N env		%N st.	%N env.		% Nst.	%N env.	_	%N st.	%Nenv.	
Nematodes	8.85	0.80	8.05	36.26	0.15	36.11	2.46	0.19	2.27	3.67	0.20	3.47
Invertebrate eggs	3.50	0.70	2.80	2.34	0.41	1.93	3.34	8.28	-4.94	0.00		
Lemellibranch larvae	22.63	2.23	20.41				2.11	0.40	1.71	11.08	0.39	10.69
Nemertea	7.82		7.82				0.61		0.61	0.00		
Gastropod larvae	1.65	3.79	₹ -2.15	0.58	4.45	-3.87	1.14	17.02	-15.88	8.78	6.59	2.19
Insecta	0.62	2	0.62	1.17		1.17				0.00		
Copepods	10.91	48.37	-37.47	16.37	46.15	-29.78	61.46	36.29	25.17	45.96	39.61	6.35
Hyperiids	0.00		0.00				7.64		7.64	4.02	2.94	1.08
Ostracods	4.53	3 2.24	2.29	1.17	2.09	-0.92	2.28	11.74	-9.45	8.77	3.65	5.12
Foraminifera Globigerina sp.	18.31	0.62	17.69	0.58	6.98	-6.40	0.26	7.60	-7.33	0.00		
Acantharians	0.62	2 8.22	-7.61				0.26	0.25	0.02	2 0.00		
Pangurids	1.85	5	1.85				0.79		0.79	0.00		
Brachyuran larvae	0.00	0.62	-0.62	1.17	3.92	-2.75				15.19	5.54	9.65
Brachyuran megalopas	1.65	5 0.17	1.47				3.95	1.08	2.87	1.44	10.56	-9.13
Mysids	0.62	2 1.79	-1.17				3.07	1.17	1.90	0.00		
Rotifera	0.62	2 1.03	-0.41	5.26	0.32	4.94	2.46	0.25	2.21	4.26	0.56	3.70
Fish eggs	4.12	15.82	-11.71	4.09	4.16	-0.06	2.81	1.48	1.33	0.00		
Siphonophores	1.23	1.80	-0.57	1.17	0.62	0.55	2.19	1.42	0.77	0.62	0.84	-0.23
Unidentified crustaceans	1.44	0.69	0.76	4.09	0.03	4.06	1.76	0.25	1.51	0.00		
Chaetognaths Sagitta sp.										0.6	8 1.46	-0.78
Cladocerans				2.92	1.21	1.72	2			8.7	1 2.35	6.37
Nauplii										0.0	0	

Anomuran larvae	0.62	0.09	0.53				0.09	0.25	-0.16	0.00		
Stomatopod										0.00		
Sergestidae Lucifer sp.		_								2.30	0.98	1.33
Caridean larvae										0.43	0.96	-0.44
Fish scales	0.41	0.00	0.41	2.34	0.24	2.10	0.00	0.06	-0.06	1.36	0.36	1.00
Polychaetes	0.21		0.21	5.85	1.86	3.99	0.44	0.59	-0.15	7.76	4.11	3.65
Tinttinids							0.09		0.09	0.00		
Doliolids	1									0.00		
Euphausids							0.61	0.25	0.37	0.00		
Fish larvae	0.21		• 0.21							0.00		
Appendicularians : Oik	opleura									7.59	2.26	5.32
Coelentrate larvae							0.18	0.22	-0.04			
Pteropods Creseis sp.												
Medusae	0.21	0.34	-0.14									
Flat worms	2.88		2.88	12.87	0.24	12.63						
Echinoderm larvae	0.41	2.16	-1.75									
Caprellidae	0.21		0.21									
Sipunculids	0.62		0.62						-			
Pycnogonid				1.75		1.75						