ABSTRACT

Title of Thesis: Vertical Resource Partitioning and Sexuality of Three Sympatric Species of Red Sea Sandfishes (Xyrichtys melanopus, Labridae; Trichonotus nikii, Trichonotidae; Gorgasia sp., Congridae)

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Three species of marine sandfishes were studied from 1984 to 1986. Their inter- and intraspecific behavior was monitored during the daylight hours to examine interactions that could result in the vertical stratification of the species over the sandy bottom within the fringing and patch reefs in the north Red Sea. Horizontal plankton tows were taken at three heights and three times a day. These samples were compared to stomach contents of the fishes to determine the trophic relationships in the community and their affects on spatial relations between the species. Prey specificities of the fishes were determined by using an electivity measure. Using paraffin histology, Xyrichtys melanopus was determined to be a monandric protogynous hermaphrodite and Trichonotus nikii, a gonochorist. Previous work on the mating systems and territoriality of all three sandfish species helped in part to explain the vertical spatial arrangement of the sandfish species within the community. Effects of pollution on the biota of the Northern Gulf of Aqaba are noted.

VERTICAL RESOURCE PARTITIONING AND SEXUALITY OF THREE SYMPATRIC SPECIES OF RED SEA SANDFISHES (*XYRICHTYS MELANOPUS*, LABRIDAE; *TRICHONOTUS NIKII*, TRICHONOTIDAE; *GORGASIA* SP., CONGRIDAE)

BY

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INTRODUCTION

Early research of tropical marine fishes focused on those species which inhabit coral reefs (e.g. Bardach, 1958; Randall, 1961, 1963, 1965; Wainwright, 1965). The reef community is extremely diverse in comparison to temperate marine communities, thus, studies to delineate the basis of productivity, interspecific interactions of fishes and resource relationships were first attempted on the coral reef ecosystem (e.g. Randall, 1961, 1963, 1965, 1967). Competition theory stemming from work by Gause (1934), Hutchinson (1959), MacArthur (1970), Diamond (1975) and others, was examined by ecologists, in the context of fish communities and was primarily well accepted. Space and food resource limitations were the basis for the competitive interactions being described by most researchers investigating fish community structure (e.g. Molles, 1978; Anderson et al., 1981).

Tropical fishes on reefs were thought to be part of a "climax community", a biological community that persists and changes little from year to year (Odum and Odum, 1955; Hiatt and Strasburg, 1960; Goldman and Talbot, 1976). In the mid- 1970's, other researchers began questioning the existence of space limitations and the existence of climax assemblages of fishes. Their small scale studies (testing hypotheses on a few small coral head replicates) tended to find conspicuous changes in fish assemblages from year to year and season to

season (Sale, 1972, 1975, 1977, 1978a, 1978b, 1980, 1982; Sale and Dybdahl, 1975,; Sale and Williams, 1982; Williams, 1980). Opponents to Sale's ideas argued that the scale of his studies were too fine and if one examined larger ranges, stability of the assemblages overwhelms the small scale fluctuations (Gladfelter and Gladfelter, 1978; Anderson et al., 1981; Ogden and Ebersole, 1981). The movement away from explanations of community structure based primarily on competition between species had begun. Deemphasis of competition structured communities allowed other researchers to present their ideas of how communities are structured.

Among these ideas, Connell (1961) and Paine (1966) spearheaded the concept of the keystone predator. The keystone predation theory states that, predation on the dominant species in the community allows less dominant species to exist and thrive where they might not be able to if the dominant species numbers were not being cropped by the predator. Thus, by cropping the numbers of the dominant species, the predator disengages competition between the species and allows a higher diversity to exist.

Other factors such as environmental disturbances allow increased diversity in coral reef communities (Connell, 1975, 1978). Connell's hypothesis states that if enviromental disturbances occur at an intermediate frequency and intensity, competitive exclusion by

dominant species over less dominant species does not occur. The periods of quiesescence (reestablishing of species ranges after destruction from the disturbance) is not long enough to allow for exclusion of subordinant species by dominant species. Therefore, according to Connell (1978), intermediate disturbance does not allow the establishment of a climax community. High diversity is maintained by environmental disturbance.

Other basic environmental variation can cause changes in community structure of marine animals. Variation and change of current strength can cause shifts in ranges of planktivorous fishes. Also, movement of sand patches and depth variation of sand deposits by disturbances can force sand inhabitants to shift their home ranges (Clark, pers. comm.).

Therefore, in the context of marine fish communities, many factors may be involved in structuring the species ranges and associations. Space and resource limitations may cause competition-based community structure. Predation may limit a species abundance or the plasticity of the ranges of prey species. Other environmental factors such as disturbance intensity and frequency, currents, topography, temperature, light intensity can influence the assemblage structure of marine coral reef fishes.

The main emphasis of the community ecology of fishes has been within coral reef systems. But, within the last

decade, researchers have begun describing the factors involved in structuring fish populations and communities that inhabit the sand environment bordering the reefs (e.g. Clark, 1971a, 1971b, 1972, 1975, 1980, 1983a, 1983b; Clark et al., 1968; Clark et al., in press; Clark and Shen, 1986; Clark and von Schmidt, 1966; Nemtzov, 1985). The processes of predation and competition for food and space resources are also being examined in the context of sand fish ecology.

In the Red Sea, fringing and patch coral reefs are numerous. Bordering all of the reef environments, large sand patches exist that are inhabited by many invertebrates and fishes. Field research on the fishes of the Red Sea's sand environments have illuminated species abundances, intraspecific social systems, and sexual life histories (e.g. Clark, 1968, 1971a, 1971b, 1972, 1975, 1980, 1983; Clark and Shen, 1986; Nemtzov, 1985). Interspecific interactions between species of sandfishes have been mentioned in passing, but no research focusing on the interactions themselves has been completed.

The structure of assemblages of marine sandfishes can be influenced by intraspecific and interspecific competition, predation, and environmental variations. Examination of all of the factors involved in structuring a community can be overwhelming. Most research on communities have isolated one to a few factors which

influence structure and then manipulate them to see changes in community structure subsequent to the manipulations (e.g. Paine, 1966; Connell, 1961, Brock, 1979). To begin to investigate a community of sandfishes that inhabit the sand patches bordering coral reefs, I focused on three species of sandfishes and their spatial, trophic and interspecific relationships. Although many more factors are probably intertwined in influencing the community structure of these fishes, this study focused on the diet and food resource availability in the sand environment and its influence on community structure of the sandfishes.

Investigation of these species of fishes has been a continuing goal of Clark and others (Clark and von Schmidt, 1966; Clark, 1971a, 1971b, 1972, 1980, 1983a, 1983b; Randall, 1965, 1981; Nemtzov, 1985; Shimada and Yoshino, 1984). Within the scope of the investigation of factors that may influence community structure of the three species of sandfishes, further characterization of sex change within the genus Xyrichtys (Xyrichtys melanopus) was also investigated and determined.

Within the Red Sea sand environment, the genus Xyrichtys is represented by X. pentadactylus, X. melanopus, X. pavo, and X. niger. Both X. melanopus and X. pavo exhibit haremic territoriality (Clark, 1983b; Clark and Shen, 1986). This social system is similar to X. pentadactylus (Nemtzov, 1985). An investigation of

hermaphroditism in other species of Xyrichtys in the Red Sea, aside from X. pentadactylus, has not been attempted. X. melanopus and X. pavo are rare species in comparison to X. pentadactylus. Completion of the analysis of hermaphroditism in this genus is hampered by the lack of sufficient specimens. However, over two summers, enough X. melanopus specimens were collected to complete a histological analysis of the male and female gonads of this species.

The goals of the present study were to (1) observe several sympatric species of sandfishes within a community, noting interspecific and intraspecific interactions; (2) describe the community structure of the sandfishes within the sand environment and possible structuring forces; (3) examine behavioral limitations to the species ranges; (4) relate diet and food resource availability from the plankton to the community structure of the sandfishes; (5) continue investigation of the sexuality of the genus Xyrichtys by histologically examining the gonads from X. melanopus for evidence of hermaphroditism; and (6) examine T. nikii for evidence of hermaphroditism that is theorized by Shimada and Yoshino (1984), but has never been experimentally determined.

HABITAT DESCRIPTION

The Red Sea is a geologically young, flooded rift valley created by the past division of the African and Asian continents (Kennett, 1982; Morley, 1975). The

basin is connected with the Indian Ocean at the straits of Bab-el-Mandab in the south and with the Mediterranean Sea by the man-made Suez canal in the north. The Northern Red Sea is split into two gulfs that surround the Sinai peninsula. To the west of the peninsula is the Gulf of Suez, which is fairly shallow (avg. 40m). To the east of the Sinai peninsula is the Gulf of Aqaba. This gulf is the site of active ocean spreading, thus, the trough is very deep (in excess of 1800m) (Kennett, 1982). The Gulf of Aqaba is bordered by fringing reefs in the south and patch reefs and coral heads in the north. The salinity of the Northern Red Sea is approximately 41ppt (Morley, 1975). The salinity is much higher than the Pacific, Atlantic, or the Indian Oceans which average between 33-35ppt (Morley, 1975). The presence of an elevated salinity in the Red Sea can in part be contributed to comparatively little water runoff into the sea from bordering land masses and the lack of major rivers flowing into the sea. Interspersed between and along side of the reefs are three types of sand formations described by El Baz (Clark, 1983a).

The sands of the Red Sea are derived from different sources and exhibit different characteristics. The first of the sand types is wadi sand. It is derived from flash flood runoff from desert mountains of the bordering land masses. The grains are very angular and loosely compacted (Clark, 1983a). The second type is "current

deposit" sand. It is carried great distances by nearshore currents and deposited in depressions on the fringing and patch reefs and between coral heads. These current deposits contain few skeletal or coral fragments and thus, appear darker than the other sand types. Along the Gulf of Aqaba, at Ras Mohammed, these "current deposit" sands are overlapping and to a degree intermixed with other sands, (especially coral sand) (Clark, 1983a). The grains of "current deposit" sand are rounded from erosion during travel in the currents. The third type of sand is coral sand. It is angular and less well-sorted than the other types of sand. Coral sand contains many foraminifera and other complete and incomplete shells in addition to tabular and branching coral skeleta (Clark, 1983a). The coral sands are produced by fishes, (especially parrot fish, Scaridae; Coris angulata, C. lunula, and triggerfishes of the genera Rhinecanthus and Balistes) which ingest stony coral while feeding on the symbiotic algae of the corals (Fishelson, 1968). The carbonate material is ingested by the fish and is passed through its intestinal tract. The ground coral fragments are defecated into the water column where they sink and collect in depressions on the reef structure. Another important source of coral sand is from sponges and other boring organisms. The importance of the sand type in an organism's habitat selection has not been thoroughly investigated.

Many species of marine animals are residents or visitors in the sand environment. In comparison to reef dwelling organisms, sand dwelling organisms are dull in coloration. Most of the sand dwelling species are cryptically colored to blend into the sand environment. Cryptic coloration is a preventative measure to avoid predation (Clark, 1983a).

Within the north Red Sea, three study sites were chosen within which to study sandfish community interactions. The three sites are (1) Ras Mohammed, (2) Marsa el Mukibela (= Muqabila), and (3) Aquasport (a dive center in the Gulf of Aqaba, Eilat, Israel) (Figure 1). The sites were chosen according to the following criteria: (A) At least two of the three sandfish species in the study were present in the sand environment, and (B) we could obtain access to the area.

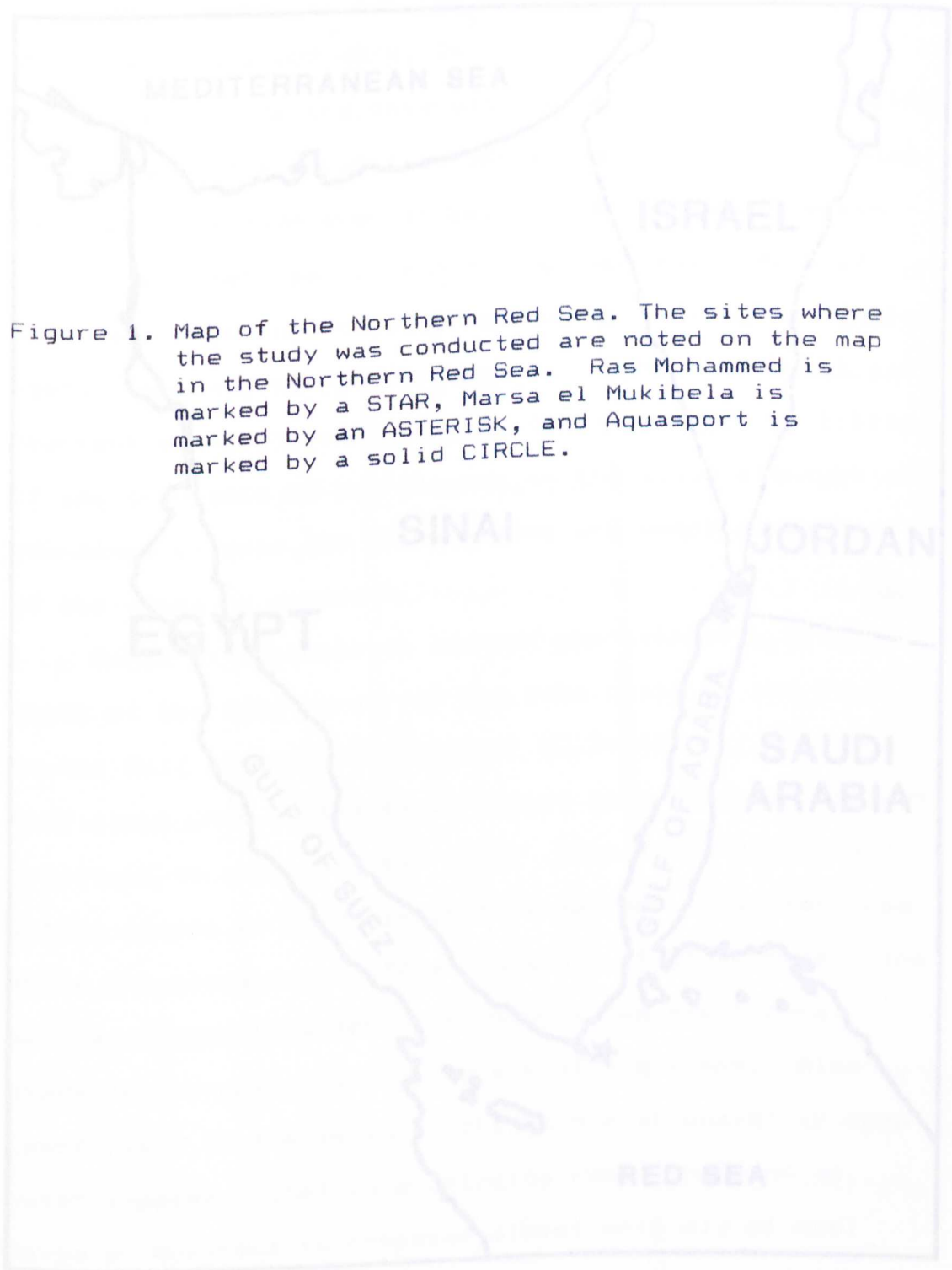
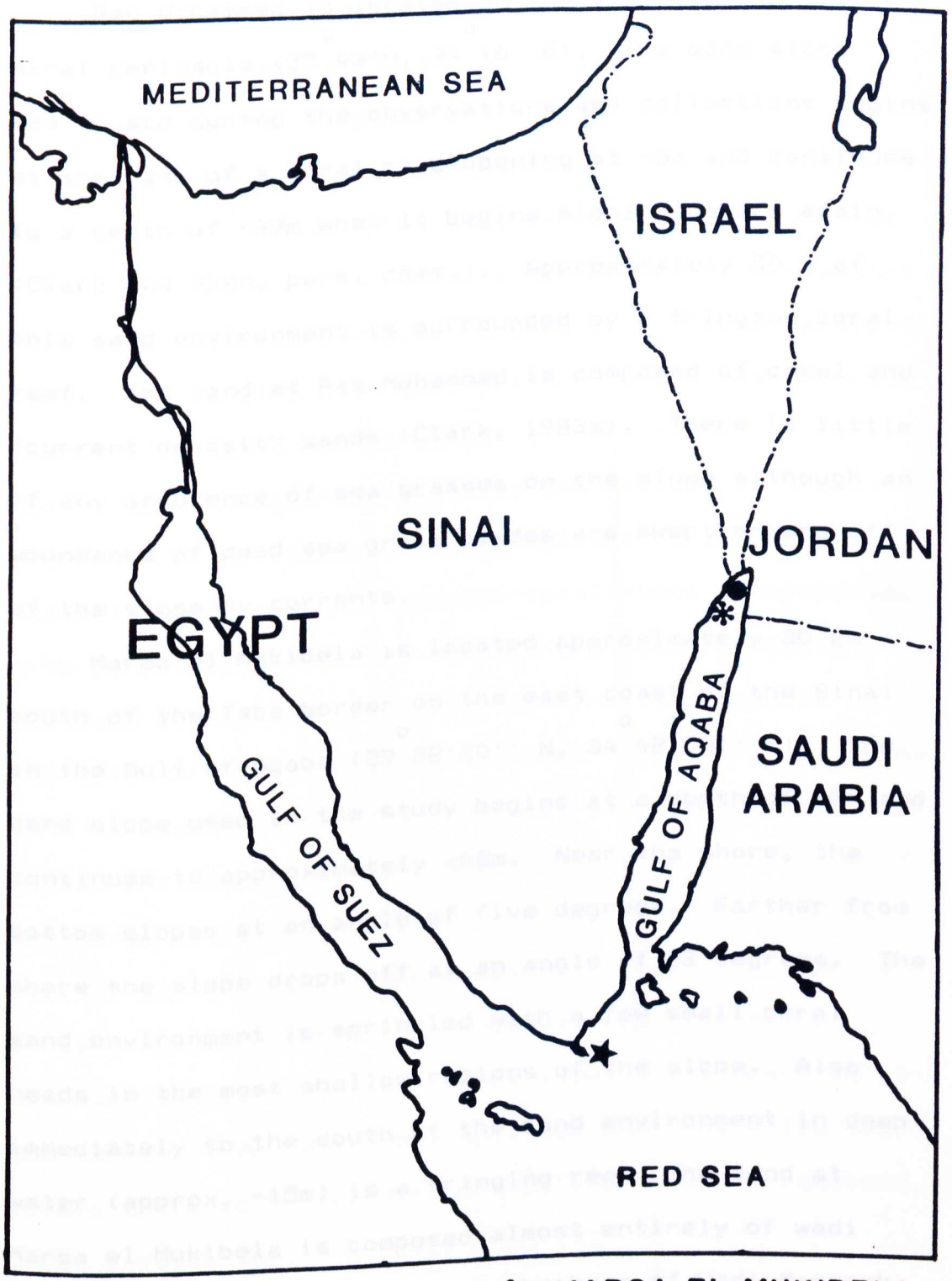


Figure 1. Map of the Northern Red Sea. The sites where the study was conducted are noted on the map in the Northern Red Sea. Ras Mohammed is marked by a STAR, Marsa el Mukibela is marked by an ASTERISK, and Aquasport is marked by a solid CIRCLE.


MEDITERRANEAN SEA
ISRAEL
SINAI
JORDAN
EGYPT
GULF OF AQABA
SAUDI ARABIA
GULF OF SUEZ
RED SEA
★-RAS MOHAMMED
✱-MARSA EL MUKIBELA
●-AQUASPORT (CORAL SEA)

PHYSICAL CHARACTERISTICS OF THE STUDY SITES

Ras Mohammed is located on the southern tip of the Sinai peninsula (27° 43'N, 34° 16' E). The sand slope (20°) used during the observations and collections begins at the base of a coral cave opening at -8m and continues to a depth of -47m when it begins sloping upward again (Clark and Shen, pers. comm.). Approximately 50 % of this sand environment is surrounded by a fringing coral reef. The sand at Ras Mohammed is composed of coral and "current deposit" sands (Clark, 1983a). There is little if any occurence of sea grasses on the slope although an abundance of dead sea grass blades are swept on and off of the slope by currents.

Marsa el Mukibela is located approximately 30 km south of the Taba border on the east coast of the Sinai in the Gulf of Aqaba (29° 22'20'' N, 34° 42'50'' E). The sand slope used in the study begins at a depth of -2m and continues to approximately -48m. Near the shore, the bottom slopes at an angle of five degrees. Farther from shore the slope drops off at an angle of 22 degrees. The sand environment is sprinkled with a few small coral heads in the most shallow regions of the slope. Also immediately to the south of the sand environment in deep water (approx. -15m) is a fringing reef. The sand at Marsa el Mukibela is composed almost entirely of wadi sand. The slope is located at the base of Wadi Magresh. During winter storms, wadi sand washes down into the bay

onto the site. The slope is well populated with sea grasses of the genera Halophila and Cymodocea, which stabilize the sand surface.

Aquasport is located in the Gulf of Aqaba approximately 6 km north of the Taba border in Israel (34° 56' E, 29° 30' N). The site is immediately north of the "Coral Sea Reserve" in an area used by the Aquasport dive shop. The sand slope, ranging from approximately -2m to -30m, begins just beyond a rock and algae covered shore. The sandy bottom slopes at an angle of approximately eight degrees. Beyond the slope, the bottom drops off steeply toward the Gulf's shipping channel. The site has numerous coral heads interspersed with sand expanses in the shallow and deeper regions. The sand at the site is variable. The top layer is silty and below are coarse sand grains and rocks mixed in. The sand is dominated by coral and wadi sand mixed with small rocks from the shore. The grain is the most coarse of the three sites in this study. There is a conspicuous lack of sea grasses at the Aquasport site. The absence of seagrasses, which were previously reported to be abundant by Clark (1971a, 1971b, 1980), is thought to be due in part from recent oil spillage and record low sea levels suffered by the Northern Gulf of Aqaba (Fishelson, 1973; Loya, 1975).

BIOTIC CHARACTERISTICS OF THE STUDY SITES

During the summer of 1984, survey of the fishes that were resident and visitors near the sites was begun and was finished in the summer of 1985 (Table 1). The fishes recorded in the survey are either resident or visitors in the sand environment or on coral heads located in intimate contact with the sand environment. Residence status was given when the fish species was observed on or near the sand environment during the majority of the observation periods. In no way can this survey be considered a complete listing. Rather, the fishes listed are the most conspicuous to the researchers. Cryptic species and those that hide within the reef are probably underrepresented. All of the survey periods were done during the daylight hours.

The following biotic descriptions of the three study sites focus on the three species of sandfishes which are the basis of the study. The three sandfishes were chosen because their territories within the sand environment were sympatric, although during daylight they seemed to be vertically separated in the water column. The sandfishes that were the focus of this study were easy to observe because they remained in nearly the same place in the sand environment day after day. Also, all of the fishes could be observed by SCUBA divers without disturbing their natural behavior. If the divers laid quietly on the bottom near the reef, the animals would

Table 1. Fishes seen in the sand environment at the three study sites in the north Red Sea. The fishes are listed by family, genus, and species, where possible.
V = Visitor species (seen occasionally)
R = Resident species (seen during the majority of observation periods)

FAMILY	GENUS AND SPECIES
Acanthuridae	*Acanthurus* spp. (V)
	Naso unicornus (V)
	Zebrasoma xanthurum (V)
Atherinidae	*Atherinomorus lacunosus* (V)
Balistidae	*Balistapus undulatus* (V)
	Sufflamen albicaudatus (V)
	Rhinecanthus assasi (V)
Belonidae	*Tylosurus choram* (V)
Bothidae	*Bothus pantherinus* (R)
Caranidae	*Caranx sexfasciatus* (V)
Caseionidae	*Caseio lunaris* (V)
Chaetodontidae	*Chaetodon auriga* (V)
	Chaetodon austriacus (V)
	Chaetodon fasciatus (V)
	Chaetodon lineolatus (V)
	Chaetodon melannotus (V)
	Chaetodon semilarvtus (V)
	Heniochus intermedius (V)
	Pomacanthus imperator (V)
	Pygoplites diacanthus (V)
Cirrhitidae	*Oxycirrhites typus* (R)
Congridae	*Gorgasia* sp. (R)
Fistulariidae	*Fistularia commersonii* (V)
Gobidae	*Amblyeleotris steinitzi* (R)
Haemulidae	*Plectorhynchus gaterinus* (V)
Hemiramphidae	*Hyporhamphus gambarur* (V)
Holocentroidae	*Holocentrus diadema* (R)
Kyphosidae	*Kyphosus cinerascens* (V)
Labridae	*Cheilinus undulatus* (V)
	Coris angulata (R)
	Gomphosus coeruleus (V)
	Thallasoma klunzingeri (R)
	Xyrichtys melanopus (R)
	Xyrichtys niger (R)
	Xyrichtys pavo (R)
	Xyrichtys pentadactylus (R)
Lutjanidae	*Lutjanus bohar* (V)
Mullidae	*Pseudupeneus forsskali* (V)
Muraenidae	*Siderea grisea* (V)
Ostraciidae	*Ostracion cubicus* (V)

(Families of Fishes, cont.)

FAMILY	GENUS AND SPECIES
Pegasidae	Eurypegasus draconis (V)
Pomacentridae	Abudefduf saxatilis (R)
	Amphiprion bicinctus (R)
	Chromis caerulea (R)
	Chromis dimidiatus (R)
	Chromis trialpha (R)
	Dascyllus trimaculatus (R)
	Dascyllus marginatus (R)
Pseudochromidae	Pseudochromis fridmani (R)
Scaridae	Cetoscarus bicolor (R)
Scaridae	Scarus spp. (R)
Scorpaenidae	Pterois volitans (V)
	Pterois radiata (V)
	Scorpaenopsis barbatus (V)
	Synanceia verrucosa (R)
Serranidae	Anthias squamipinnis (R)
	Cephalopholis argus (V)
	Cephalopholis miniata (V)
	Plectropomus truncatus (V)
	Variola louti (V)
Sphyraenidae	Sphyraena flavicauda (V)
Sygnathidae	Corythoicthys schultzi (R)
Synodontidae	Synodus variegatus (R)
Tetradontidae	Arthron diadematus (V)
	Arthron hispidus (V)
	Canthigaster corinatus (V)
Trichonotidae	Trichonotus nikii (R)

surface from the sand and feed, mate, etc. Another factor used in selecting the focus species was that each of the fish species only surfaces from the sand in the daylight hours. Thus, when studying the behavior of these fishes, one did not have to worry about missing any critical feeding and interspecific behaviors during the night.

On the Ras Mohammed site, the sand slope is covered with a "garden of eels." The eels, Gorgasia sp., are represented on the site by what may be in excess of 9,000 individuals. The eel colony ranges from a depth of -7m to -47m and then up a slight rise ending before dropping into deep water. The eels thin out as one approaches the coral structures surrounding the sand. The lack of eels near the coral is thought to be due in part by the lack of current (therefore, a plankton supply) and the topography of the reef structure itself. The adult eels are most abundant toward the center of the colony and the immature eels are sometimes seen within the adult community but, most often near the outer edges of the adult community (Clark, pers. comm.)

A swarm of Trichonotus nikii with approximately 200 individuals is present on the site. They inhabit a portion of the sand environment at a depth ranging from approximately -15m to -28m.

A pair of Xyrichtys melanopus is also present at Ras Mohammed. The razorfishes cruise over the sand bottom

and hold territories at a depth range of -31m to -40m. A close relative of X. melanopus, X. pavo, is also an inhabitant of Ras Mohammed. A harem comprising five individuals (1 male, 4 females) ranges from a depth of -29m to -37m.

At the Marsa el Mukibela site, a colony of Gorgasia sp. that was previously noted in the literature by Nemtzov (1985) and Clark (1983a) had disappeared by the summer of 1985. A huge swarm of Trichonotus nikii of over 500,000 individuals (Clark, 1983a) dominates the water column from a depth of -3m to -15m.

Xyrichtys melanopus is present with approximately 50 individuals in the depth ranges of -6m to -14m. Individuals of the Xyrichtys genus, X. pentadactylus, the focus of Nemtzov's (1985) work on sex change and social behavior, is highly abundant. X. pavo, which is also a haremic fish species (Clark and Shen, 1986), is also present at Marsa el Mukibela. X. niger, a solitary razorfish, has territories which are widely spread out over the sand environment at Marsa el Mukibela.

Aquasport supports a colony of approximately 120 Gorgasia sp. individuals. The colony was first documented by Clark (1971a) as containing over 1,500 eels. The sharp decrease in numbers of garden eels could be tied to the loss of seagrasses and the general poor condition of the sea life in this area, but a direct tie between these observations has not been clearly

established. The colony of eels ranges from a depth of -4m to -9m.

A small swarm of Trichonotus nikii with approximately 20 individuals is present on the northern boundary of the eel colony. The T. nikii swarm hovers between -6m and -8m. There were no Xyrichtys melanopus present at the Aquasport site but, X. pavo adults and immatures were present at the site. The razorfish were never seen diving within the eel colony limits, but they were frequently seen cruising through the colony during the observation periods.

All three sites support an abundance of marine life within and above the sandy bottom. When compared, the study sites have major differences. The depth at Ras Mohammed is significantly deeper than Marsa el Mukibela or Aquasport. The sites are similar in the presence of the focus species, but the relative abundances of the species are not similar between sites. The garden eels dominate in abundance at Ras Mohammed, T. nikii dominates in abundance at Marsa el Mukibela and at Aquasport, both T. nikii and the garden eels are present in low abundances in comparison to the other two sites.

FOCUS SPECIES OF FISHES

The following is a description of the habits and behaviors of the three focus species in this study, Xyrichtys melanopus, Trichonotus nikii, and Gorgasia sp..

Xyrichtys* melanopus, (* Briggs, 1961 points out the spelling of Xyrichtys that must be followed) a razorfish of the Family Labridae, inhabits sand environments from the Red Sea to Japan (Indopacific). It is a rare species of the genus Xyrichtys which has at least 10 Indopacific and Red Sea species (Masuda et al., 1985; Dor, 1984) and three in the Atlantic and Caribbean (Bohlke and Chaplin, 1968; Randall, 1981). Razorfishes are known for their sharp keel-like foreheads which they use to dive head first into the sandy bottom with the approach of danger (Randall, 1965). They are diurnal fishes, only surfacing from the sand during the daylight hours.

The razorfishes have prominent canine teeth in the front of the mouth, therefore it is not suprising that these are carnivorous fishes (Randall, 1967). X. melanopus has been seen to pick on the sand surface for food and also to eat small fishes.

X. melanopus is a territorial haremic labrid with dominance hierarchies within the harems (Clark and Shen, 1986). This haremic social system has been investigated by Clark (1983b) in a closely related species, X. pentadactylus shown to be a monandric protogynous hermaphrodite by Nemtzov (1985). Monandry describes hermaphroditism when only one male phase (stage) is present within the life history of a sex- changing species. Haremic territories have also been discovered in X. pavo in the Red Sea (Clark and Shen, 1986).

In each X. melanopus harem, one male controls one to five females within his territorial boundaries. All of the fish on a territory on the sand bottom, defend it from other X. melanopus individuals present. The fish cruise at a height of about one-third of a meter from the sand bottom on their territories. Within a territory the razorfish have multiple "dive sites" where they may disappear in times of danger. A dive site is a specific region in the sand used by a fish to bury itself. The sites are recognized by the fish and used repeatedly. Clark (1983b) manipulated the landmarks around many dive sites to determine if the fish were using visual cues to find the sites. By moving the objects surrounding the sites, no noticeable difference in the fish's ability to recognize the site was made. Further work was attempted to delineate the sensory cues of dive site recognition, but no clear answers have been found (Clark, pers comm).

Xyrichtys melanopus is sexually dimorphic. The males are larger than the females (SL * MALES X = 15.1 cm, SL FEMALES X = 12.7 cm) (* the lengths for all of the species were measured after the fishes had been preserved, thus some shrinkage may have occurred). Both sexes have a large, conspicuous dark red blotch on their mid-side below their dorsal fin. Males have a bright blue line along the profile of their head (almost absent in females) and a more swollen forehead that the females. The males lack a mustard yellow blotch on the mid-side,

which is characteristic of females. The location of the males, once mapped, allows for easy identification of the male during subsequent observations.

The females have a conspicuous white patch on the mid-side under the red blotch and violet triangles on the scales of the lower part of the white patch. Late in the day, during spawning season, the females develop a swollen belly region due to the large numbers of ripe eggs that they carry. Also, the females have a bright red rim around the anus opening and females show a mustard yellow blotch anterior and dorsal surrounding the white patch.

Trichonotus nikii is a sand-diving species of the Family Trichonotidae. The species is endemic to the sand environment of the Red Sea. T. nikii is one of five little known species in the genus Trichonotus, whose distribution is limited to the Indo-Pacific. T. nikii individuals dive into the sand bottom at the hint of danger. The fish do not dive into specific "dive sites" (as does X. melanopus), but, rather into dive "areas" (Clark, pers. comm.). This species is also diurnal, surfacing from the sand only in the daylight hours. Feeding by T. nikii is thought to be by selecting plankton from the water column (Randall, 1967). T.nikii forms swarms in the water column of a few to several hundred thousand individuals (Clark, pers comm). The swarming behavior of the fish tends to confuse pelagic

predators which cruise over the sand environment. Thus, the defensive behavior is protective to the individual fish within the swarm. Swarms of T. nikii have been reported to rise to over 2m above the sand surface, far from the safety of the dive sites, but also far from lurking benthic predators (Clark and Shen, 1986). But, during feeding, the swarm centers on a height of approximately 1.7m.

T. nikii maintains a mating behavior which has been described as lek-like (Clark and Shen, 1986). Lekking behavior was first described in birds (Patterson, 1952; Lack, 1968; Pulliam, 1973; Robel and Ballard, 1974; and Lill, 1976). The swarm of fish lowers to the sand surface and sets up a temporary lek-like arena. The males claim territories in the arena within which to display to the females. The most dominant males defend the prime territories in the central regions of the arena, with the less dominant males holding territories nearer to the edges of the arena. The males display to the females and the females are able to choose which male they will mate with during the lekking period. In a true lek the mating is exclusive, so that once a male is chosen, only he mates with the female (Borgia, 1979; Bradbury and Gibson, 1983; Gibson and Bradbury, 1985). In T. nikii, although fertilization is external, it is highly improbable that the females' eggs can be fertilized by more than one male because of close

pairings. The external fertilization of eggs in T. nikii excludes their mating behavior from being a "true" lek. Also, the fact that they dive under the sand in the same site as the leks can exclude this species as a true lekking species.

T. nikii males have been seen to pick at the sand surface during the lek-like behavior. This "picking" may be actual feeding or it may be a "displacement behavior" (when males are not chosen for mating), as described by Clark and Shen (1986). True lekking behavior is only for reproduction and not for feeding. Therefore, if the "picking" behavior of T. nikii male is actual feeding, it could preclude T. nikii from being a true lekking species.

T. nikii are sexually dimorphic. The males are larger than the females (SL MALES X = 11.34 cm, SL FEMALES X = 6.86 cm) (Figure 2). The males are ornately decorated. The first three dorsal fin rays are elongated and filamentous. The anterior base of the dorsal fin is dark black in color and rays are striped. The male flares the dorsal fin rays during agonistic and mating displays. The pelvic fins of the male are enlarged in comparison to the female. The pelvic fins of the males are bright white or in some cases, bright yellow (on dominants). The body of the male is white with vertical saddle marks in brown-black, down the entire length of the body. The head of the male is decorated with dark

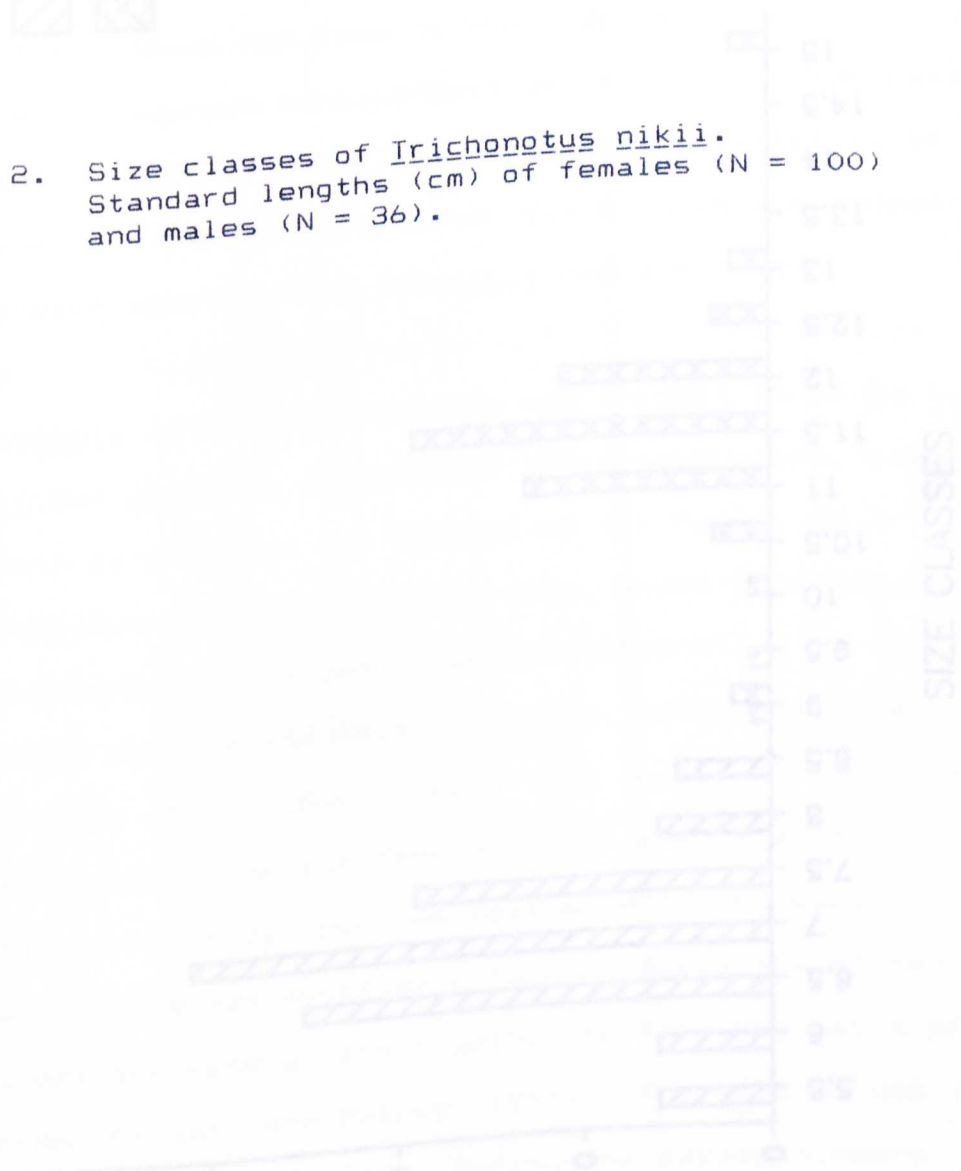
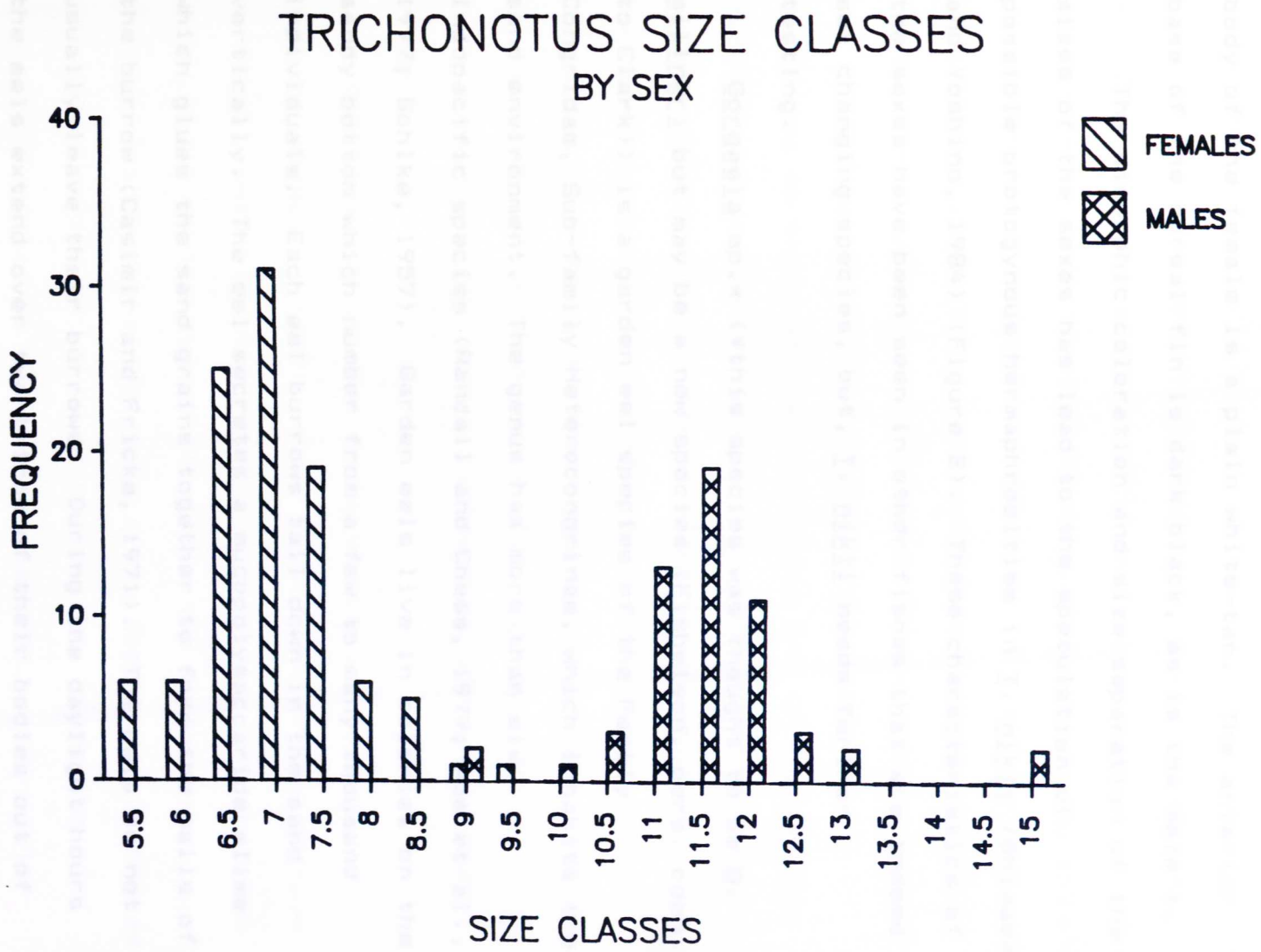


Figure 2. Size classes of Trichonotus nikii. Standard lengths (cm) of females (N = 100) and males (N = 36).


TRICHONOTUS SIZE CLASSES
BY SEX
FEMALES
MALES
FREQUENCY
40
30
20
10
0
5.5
6
6.5
7
7.5
8
8.5
9
9.5
10
10.5
11
11.5
12
12.5
13
13.5
14
14.5
15
SIZE CLASSES

spots above and behind the eye.

The female T. nikii is fairly drab in color. The body of the female is a plain white-tan. The anterior base of the dorsal fin is dark black, as is the male's.

The dimorphic coloration and size separation of the sizes of the sexes has lead to the speculation of possible protogynous hermaphroditism in T. nikii (Shimada and Yoshino, 1984) (Figure 2). These characteristics of the sexes have been seen in other fishes that are indeed sex changing species, but, T. nikii needs further testing.

Gorgasia sp.* (*this species was thought to be G. sillneri but may be a new species (Fishelson, pers. comm. to Clark)) is a garden eel species of the Family Congridae, Sub-family Heterocongrinae, which inhabits the sand environment. The genus has more than six Indopacific species (Randall and Chess, 1979; Abe et al., 1977; Bohlke, 1957). Garden eels live in colonies on the sandy bottom which number from a few to many thousand individuals. Each eel burrows tail down in the sand vertically. The eel secretes a mucopolysaccaride slime which glues the sand grains together to form the walls of the burrow (Casimir and Fricke, 1971). The eels do not usually leave their burrows. During the daylight hours the eels extend over two-thirds of their bodies out of the burrow to feed, mate, and defend the territories they hold around their burrow opening. When most of the eels

in a colony are extended out of the burrows, the colony looks like "blades of grass in a field" rising from the sandy bottom.

If the eels are frightened by a predator, they withdraw into the burrows until the danger has dissipated. Also, during the day, portions of the colony may withdraw at irregular intervals. The motivation behind this behavior, called a "siesta" by Clark (1980) is still not understood at present (Clark, pers. comm.).

The male eels defend hemispherical territories centering on their burrow openings. One to two females are allowed within the territorial boundaries defended by a male (Clark, 1980). The territories are fiercely defended by the males. Conflicts are characterized by two males stretching at least two-thirds of their lengths to the disputed boundary while flaring their dorsal fins in a threat display, often followed by strikes at each other.

The eels are thought to be selective plankton feeders (Randall, 1967). They extend out of the burrows to feed, centering on a height of slightly less than one meter * off of the bottom (* within the tables and figures the height of Gorgasia's sp. feeding is listed as one meter, although it is slightly less. Sampling of plankton occurred at the height measured in the field where most of the eels heads tended to be positioned when feeding (slightly less than one meter)). In a strong to

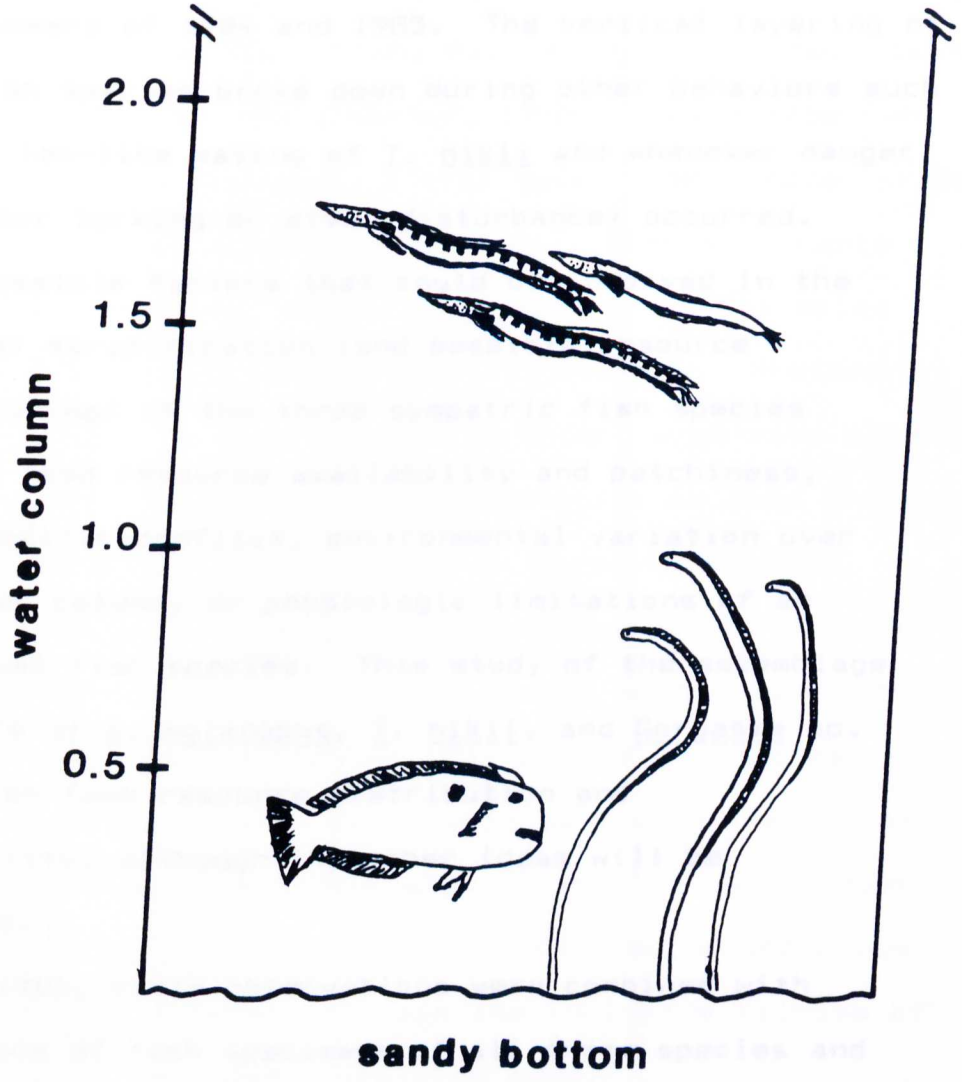
medium current, their bodies protrude vertically out of the burrows, bending so that the head is held horizontally facing into the current. The eels are seen actively selecting prey from the water column. In weak currents, the eels reach to eat prey items passing within the bounds of their reach. At dusk, the eels withdraw into their burrows until dawn.

Gorgasia sp. is sexually dimorphic based on size. The males are larger than the females (TL MALES X = 88.5 cm; TL FEMALES X = 63.5 cm). The males have a swollen appearance to the back of their heads in comparison to the females. The bodies of both sexes have a mottled brown-green color. No dimorphism in coloration is apparent.

FIELD OBSERVATIONS OF ASSEMBLAGE STRUCTURE

In 1984, field observations of the assemblage structure of the sandfishes which was based at Ras Mohammed and then subsequently at the other two study sites, illuminated a peculiar stratification of X. melanopus, I. nikii and Gorgasia sp. in the water column over the sand bottom. The species ranges (and/or territories) were overlapping on the sand bottom horizontally, but, when feeding, the species were vertically stratified in the water column (Figure 3). The spatial arrangement with X. melanopus individuals cruising in the water column at a distance of approximately 0.3m from the sand bottom, Gorgasia sp.

Figure 3. Diagram of the vertical stratification of Xyrichtys melanopus, Trichonotus nikii and Gorgasia sp. in the water column over the sandy bottom. The stratification of the fishes is only upheld while the fishes are feeding. The height of the center of the species distribution when feeding is noted on the scale to the left.


2.0
1.5
1.0
0.5
water column
sandy bottom

rising out of their burrows to a height of approximately 1.0m from the sand bottom, and T. nikii swarming at a distance of approximately 1.7m (center of swarm) from the sand bottom.

The vertical stratification of the three species of sandfishes (during feeding) was seen repeatedly during the summers of 1984 and 1985. The vertical layering of the fish species broke down during other behaviors such as the lek-like mating of T. nikii and whenever danger (predator lurking or diver disturbance) occurred.

Possible factors that could be involved in the vertical stratification (and possible resource partitioning) of the three sympatric fish species include food resource availability and patchiness, interspecific conflict, environmental variation over the water column, or physiologic limitations of an individual fish species. This study of the assemblage structure of X. melanopus, T. nikii, and Gorgasia sp. focuses on food resource distribution and availability, although the other ideas will be discussed.

In 1985, field observations were combined with collections of fish specimens of all three species and collections of horizontal plankton tows.

Chapter 1
Histological examination of Hermaphroditism in *Xyrichtys melanopus* and *Trichonotus nikii*

INTRODUCTION

Hermaphroditism in marine fishes has been discovered in at least 10 families (Fishelson, 1970; Fricke,1979; Fricke and Fricke, 1977; Hourigan and Kelley, 1985; Leigh et al., 1976; Nemtzov, 1985; Policansky, 1982; Robertson, 1972; Ross, 1978, 1984; Warner, 1978). Sex change can occur either by protandry (first male, then female) or by protogyny (first female, then male). When sex change occurs in a species, one male (monandry) or two males (diandry) may occur within the life history. Protandry has been found in fish species in which large male size is important. When male-male competition is less intense and male size has little effect on breeding success, large female size outweighs the advantage of large male size because female fecundity is always more dependent on body size than male fecundity (Warner, 1975). It may benefit an individual to start life as a male when it is small and change to a female when it is older and larger (e.g. *Amphiprion* spp.). Thus, in this case, protandrous hermaphroditism acts to increase the inclusive fitness of the individual throughout its life span.

When male-male competition is intense, only the largest individuals will be successful at mating. Although female fecundity also increases with size (larger females produce more eggs), the influence of

male size on mating success is much stronger. Under these conditions it may benefit an individual to be a female when small, because all females will breed, and a male only when large enough to be a successful competitor (Warner, 1975). Protogyny is by far the most common mode of hermaphroditism in marine fishes (Warner, 1978). Within the sand environment, protogyny was found in Xyrichtys pentadactylus by Nemtzov (1985).

X. pentadactylus is a haremic territorial species. Males defend the territories within which they establish "dive sites." Male size is an important factor in male-male competition and therefore, territory size and quality. The males with larger territories have larger harems (Clark, 1983b). Thus, male size is directly related to mating success. Female size is less important to mating success. Clutch volume increases with increasing female size, but, mating success is almost guaranteed. All of the females within a harem breed with the male of that harem. Thus, it is not suprising that X. pentadactylus is a monandric protogynous hermaphrodite.

Within this study, Xyrichtys melanopus was histologically examined for sex change. X. melanopus has a haremic social system, thus the idea that X. melanopus is also a monandric protogynous hermaphrodite was assumed without previously being tested. An a posteriori

examination of the morphology of the gonads of the males and females of X. melanopus can illuminate the existence or absence of hermaphroditism in this species. The presence of the "female orientation" of the testicular tissue of the males of the species indicates that sex change has occurred (from female to male). The presence of only one morphotype of the male gonads in the species is an indication that monandric hermaproditism occurs. Therefore, the gonads of X. melanopus will be examined for morphology and histology to determine the extent (if any) that hermaphroditism occurs.

Also, within this study, Trichonotus nikii will be examined histologically for hermaphroditism. Without testing, T. nikii was considered to be a protogynous hermaphrodite on the basis of non-overlapping sizes of the sexes (Shimada and Yoshino, 1984) (Figure 2). The speculation of sex change can now be replaced by morphological and histological evidence in T. nikii.

METHODS

FISH PREPARATION (GONADS AND STOMACHS)

Each fish was fixed in 10% formalin then transferred in stages to 70% ethanol after rinsing. The standard and total lengths of the fish were taken after the fish was fixed and preserved, thus some shrinkage may have occurred, as mentioned previously. After preservation, each fish was described morphometrically and then dissected. Trichonotus nikii and Xyrichtys melanopus

specimens were gutted and their gonads were removed. Only the alimentary tract was removed from Gorgasia sp. specimens. Each fish's stomach and gonad were placed in a separate vial of 70% ethanol before being analyzed. Right and left gonads of each fish were stored separately except in the few cases where the gonads could be removed together as a unit (esp. Trichonotus nikii).

HISTOLOGICAL ANALYSIS

When histological analysis was begun, the gonads were removed from the alcohol, weighed, and then placed into stainless steel screened capsules. These capsules were marked to allow easy identification of the gonad's origin. The capsules were placed in a plastic embedding basket which was entered into a paraffin embedding cycle on an automatic tissue processor (Autotechnicon 2A). The ethanol-clearing solution-paraffin cycle is listed in Appendix 1. After 16 hours in the embedding cycle the gonads were submerged in a paraffin bath. The basket was removed from the tissue processor and each gonad was taken out of the capsule and embedded in hot paraffin to form a cube. The cube of paraffin surrounding the gonad acted to support for the tissue when it is sectioned. The cubes were mounted on wooden cutting blocks for sectioning with a microtome (AO). The sections were sliced at a width of 7-10 microns. These sections were mounted on slides and stained according to the hematoxylin and eosin staining protocol listed in

Appendix 2. Once the slides were stained, Histoclad was used to secure a coverslip over the specimens. The slides were allowed to dry over a 2-3 day period, then the excess mounting glue was cleaned from the slides. Once cleaned, the slides were analyzed under a compound light microscope (Baush & Lomb). The following items were examined: (1) sex; (2) maturity; (3) the presence of a lumen and its orientation to mature gametes; and (4) the cell stages present.

RESULTS

The present system under analysis only involves fishes that externally fertilize their gametes, therefore, only this mode of reproduction will be introduced and discussed. In order to establish any morphological difference on the part of either fish species being examined histologically, an introduction to the morphology of a gonochoristic (non-sex changing) male and female gonad will be presented. Groman (1982) presented the morphology of the striped bass which will be used as a model of gonochorism. Discussion of the morphotypes is supplemented with a study by Nagahama (1983).

A gonochoristic (non-sex changing) male has testes that are solid masses of germinal tissue. Within a testis the seminiferous tubules are packed tightly with only a small amount of connective tissue intervening between the tubules. A tubule winds around the testis in

and out of the plane of section. Thus, when prepared histologically, the testis seems to be filled with many seminiferous tubules some of which look circular, tubular, or ovoid. Each seminiferous tubule has its most immature germ stages near the outer edges of the tubule and the more mature stages toward the central region. The mature gametes are released into the central region of the tubule. These mature gametes (sperm) are moved toward a ductule and the ductules connect to form a sperm duct to store the sperm until it is released during spawning. No evidence of a central branching lumen between the seminiferous tubules of a gonochoristic testis has been found. Therefore, the testes of a non-sex changing fish is a solid structure devoid of a central lumen, but posessing a duct network to sequester the mature sperm until released.

The gonochoristic fish ovary has a lamellar arrangement. The germinal tissues are present within lamellae. All of the stages of ova maturation are usually found within each lamella. The lamellae are surrounded on three sides by "finger-like" branches of a central lumen present in the ovary. (The fourth side of the lamella is connected to the wall of the ovary by connective tissue). The lumen is not always "central," but may run down one side of the ovary, just below the tunica albuginea (the dense connective tissue covering of the ovary). When mature, ova are stimulated to be

released during mating and shed into the ovarian lumen. The mature ova are carried down into the "oviduct". The "oviduct" receives ova from both ovaries and releases them into the environment for external fertilization.

Gonads of Trichonotus nikii and Xyrichtys melanopus were examined morphologically and ultimately compared to gonochoristic and hermaphroditic morphologies.

An examination of female T. nikii (N = 23) revealed one morphotype of the ovaries. The ovaries of T. nikii have a lamellar arrangement (Figure 4a). The germinal tissues are lined up within lamellae. "Finger-like" branches of an ovarian lumen (L) intercede between the lamellae. The lumen lies dorsally within the ovary. T. nikii females have an ovarian morphology that is similar to that which was described previously for the gonochoristic ovary.

The testes of T. nikii males (N = 10) have a solid arrangement. Each testis is packed with seminiferous tubules which form a solid mass (Figure 4b). Serial sections of four of the testes examined did not show any evidence for the presence of an "ovarian-type" lumen within the testicular tissue. All stages of spermatogenesis are seen within the seminiferous tubules. The mature sperm are shed into the central region of the tubules. The sperm travel from the seminiferous tubules to a ductule and then into a larger duct located toward the center of the

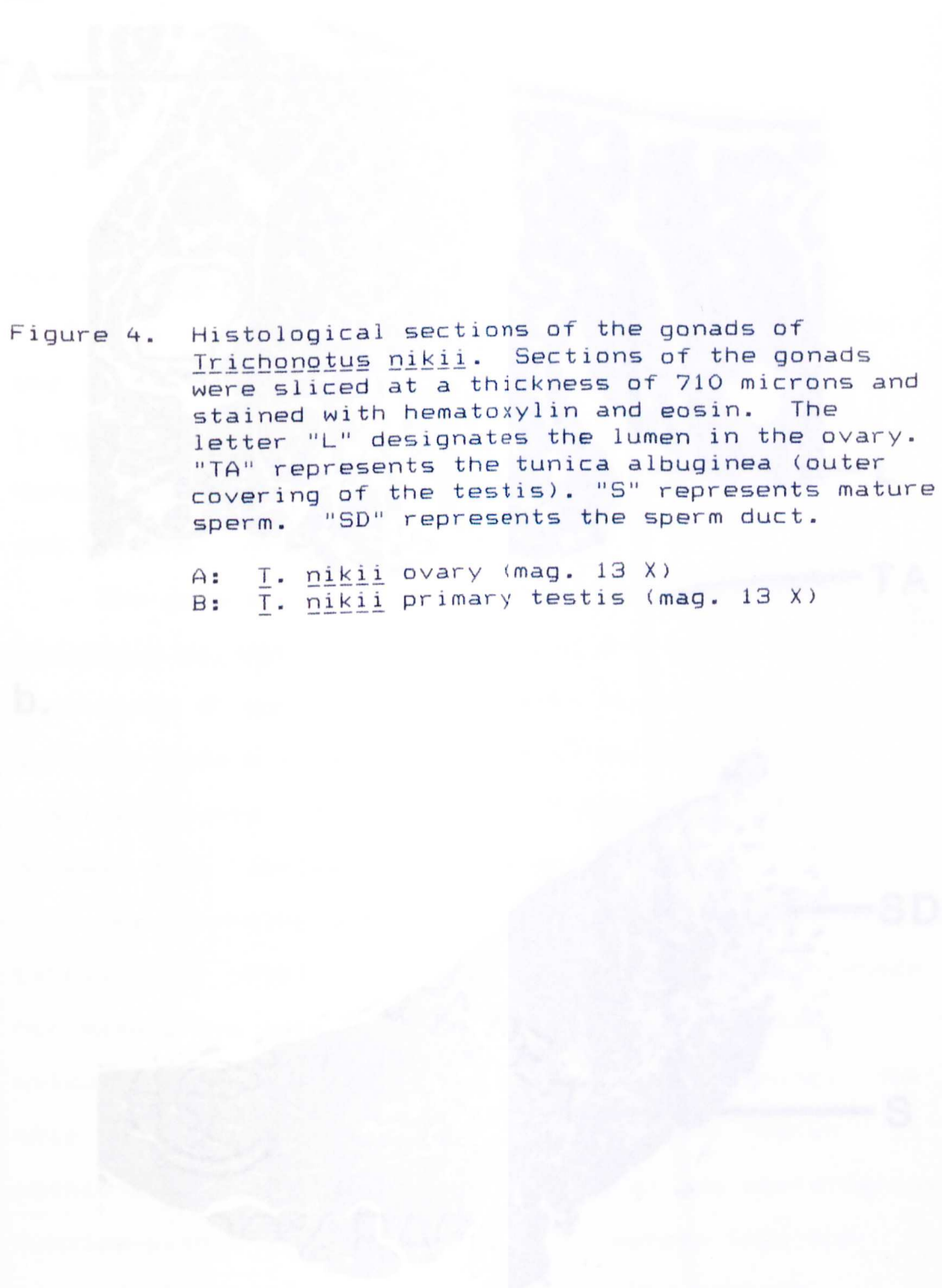
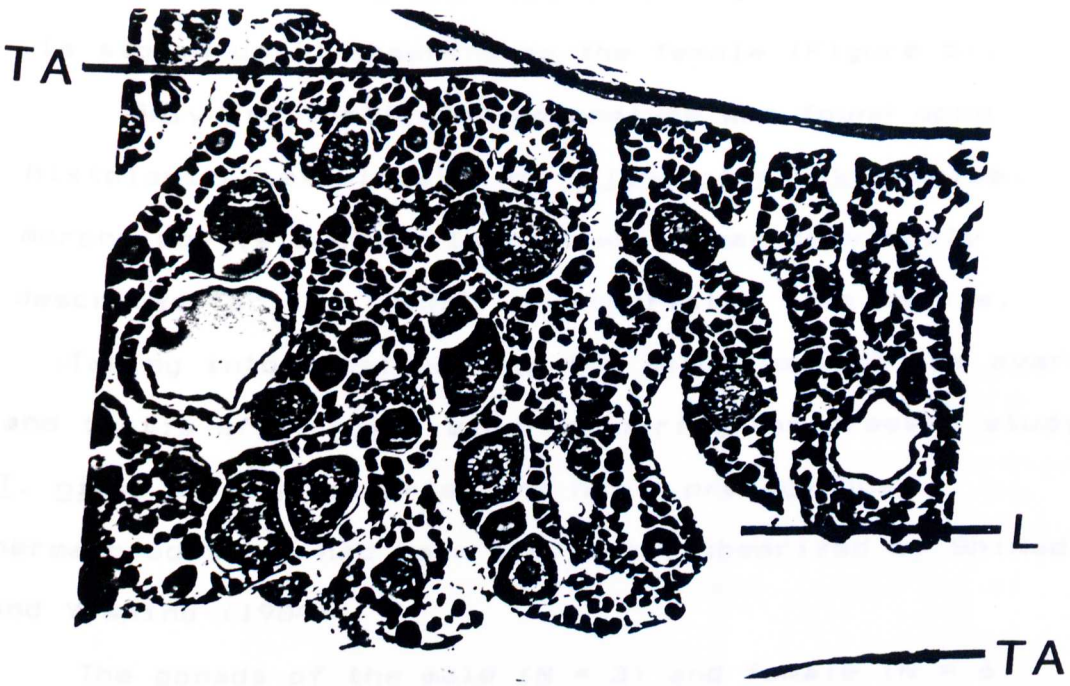


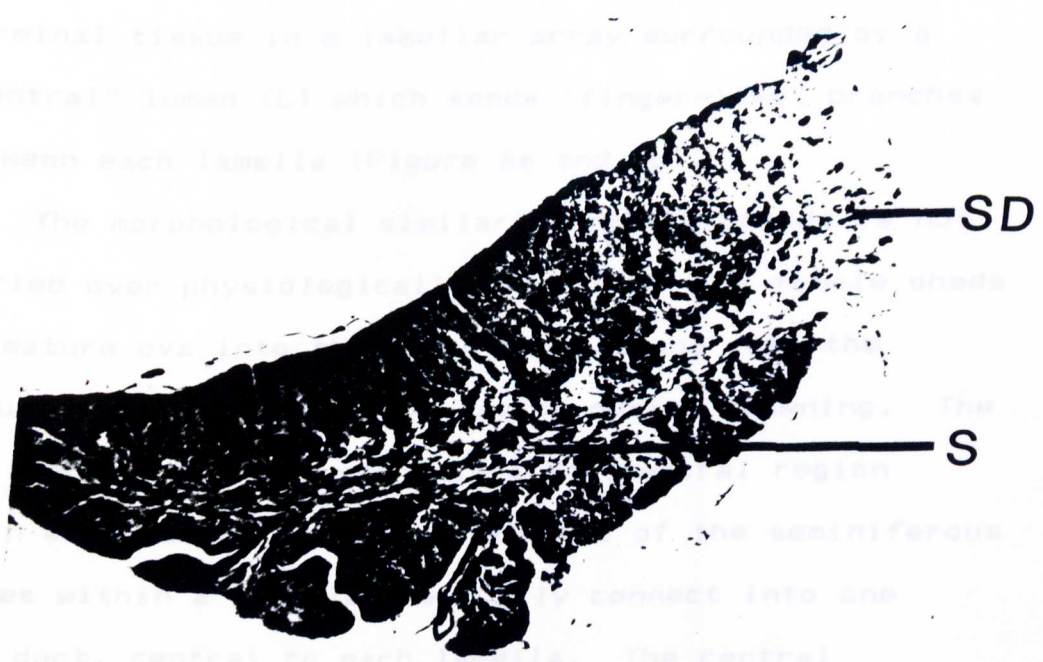
Figure 4. Histological sections of the gonads of Trichonotus nikii. Sections of the gonads were sliced at a thickness of 710 microns and stained with hematoxylin and eosin. The letter "L" designates the lumen in the ovary. "TA" represents the tunica albuginea (outer covering of the testis). "S" represents mature sperm. "SD" represents the sperm duct.

A: T. nikii ovary (mag. 13 X)
B: T. nikii primary testis (mag. 13 X)

a.



b.



whole testis. The mature sperm from each testis is sequestered into a main sperm duct system (D) where it is stored until spawning by the female (Figure 5).

Only one testicular morphotype was found upon histological examination of Trichonotus nikii males. The morphology is similar to that which was previously described for the "model" gonochoristic fish testis.

Taking into consideration the morphology of the ovary and testis of T. nikii examined during the present study, T. nikii is a gonochorist and not a protogynous hermaphrodite as had been previously theorized by Shimada and Yoshino (1984).

The gonads of the male (N = 3) and female (N = 6) Xyrichtys melanopus show a striking similarity in morphology (Figure 6a and b). Both sexes have their germinal tissue in a lamellar array surrounded by a "central" lumen (L) which sends "finger-like" branches between each lamella (Figure 6a and 6b).

The morphological similarity of the gonads is not carried over physiologically, however. The female sheds her mature ova into the lumen for passage into the oviduct and out of the body cavity during spawning. The male sheds his mature sperm into the central region within each seminiferous tubule. All of the seminiferous tubules within a lamella eventually connect into one large duct, central to each lamella. The central "lamellar" ducts connect to become the sperm duct (SD).

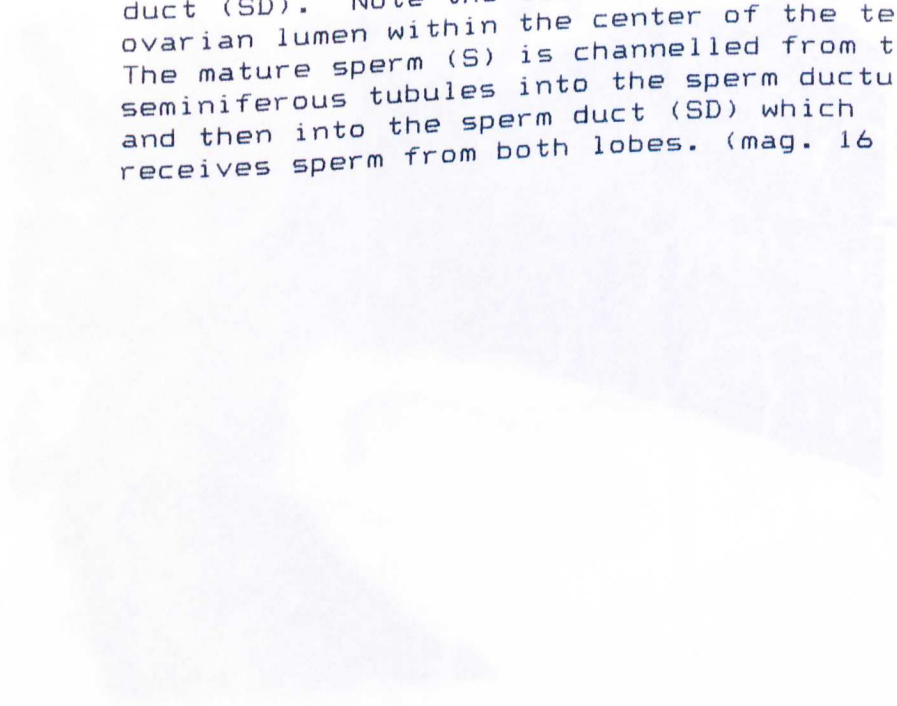
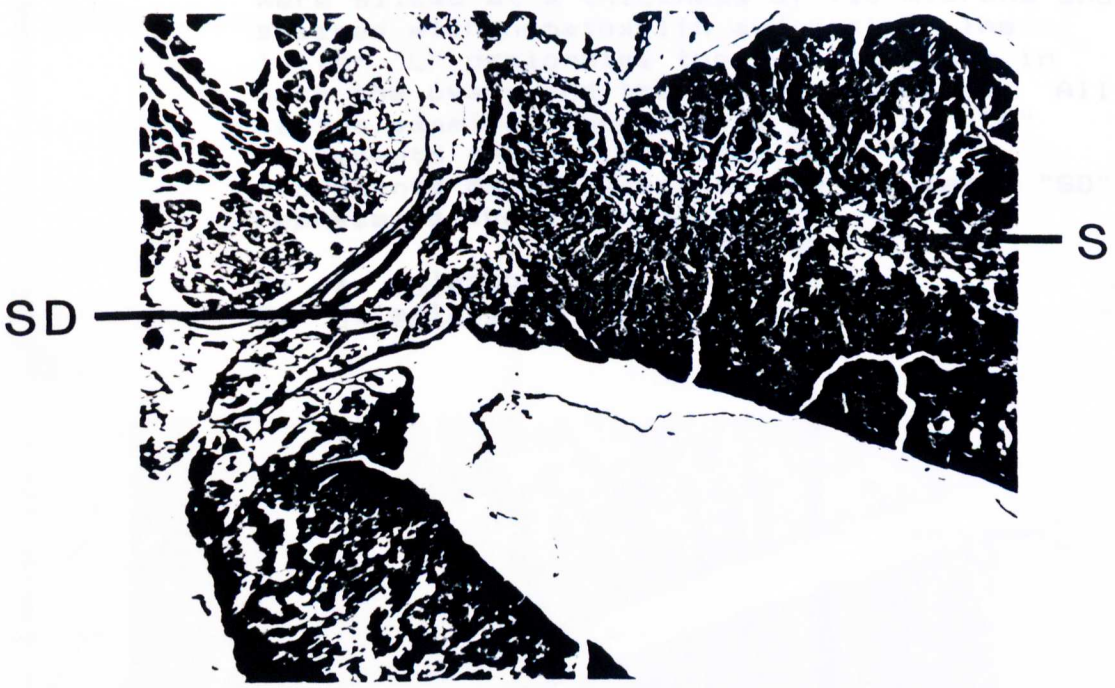


Figure 5. Primary testis of Trichonotus nikii showing the position of the two lobes to the sperm duct (SD). Note the lack of any residual ovarian lumen within the center of the testis. The mature sperm (S) is channelled from the seminiferous tubules into the sperm ductules and then into the sperm duct (SD) which receives sperm from both lobes. (mag. 16 X)


SD
S

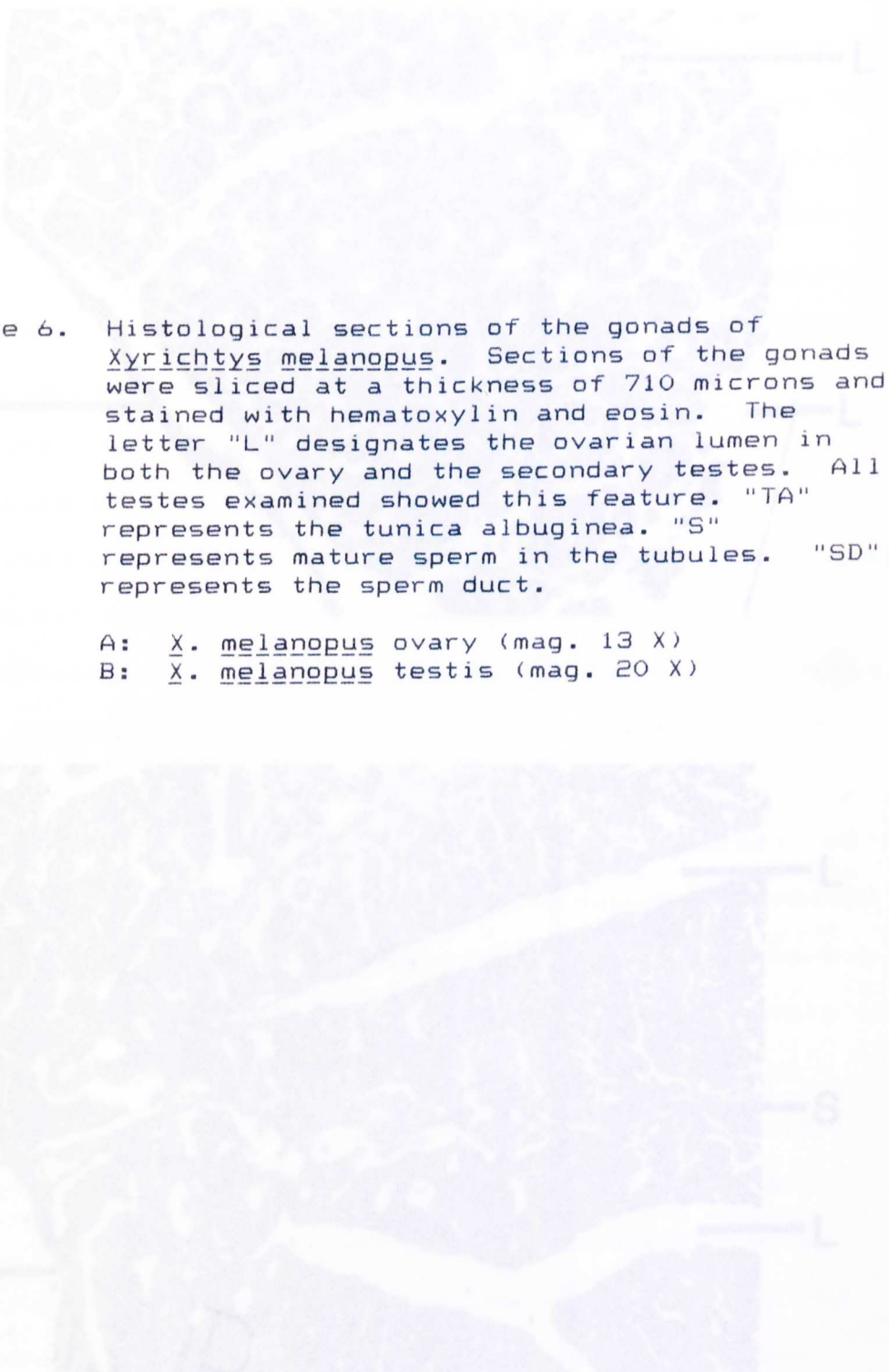
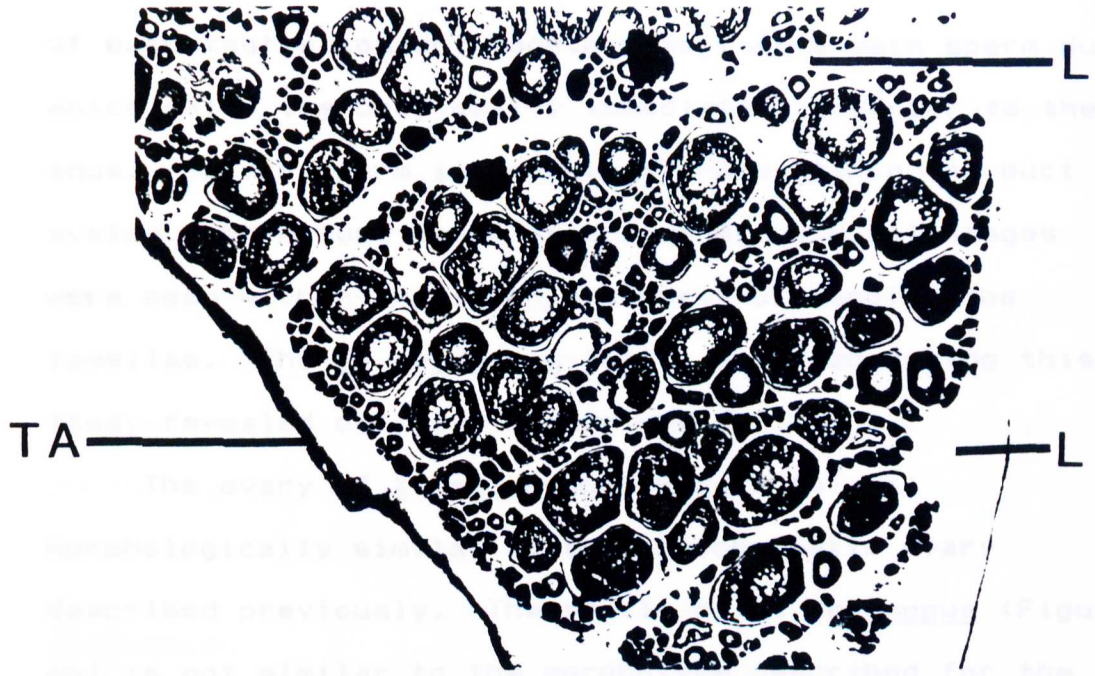


Figure 6. Histological sections of the gonads of Xyrichtys melanopus. Sections of the gonads were sliced at a thickness of 710 microns and stained with hematoxylin and eosin. The letter "L" designates the ovarian lumen in both the ovary and the secondary testes. All testes examined showed this feature. "TA" represents the tunica albuginea. "S" represents mature sperm in the tubules. "SD" represents the sperm duct.

A: X. melanopus ovary (mag. 13 X)
B: X. melanopus testis (mag. 20 X)

a.



b.



The sperm duct of each testis is located within the tunica albuginea surrounding the testis. The sperm duct of each testis connect together to form a main sperm duct which exits the body cavity immediately anterior to the anus. Mature sperm is seen in storage within the duct system. No mature sperm or any other germinal stages were seen within the lumen branches surrounding the lamellae. The X. melanopus testes analyzed during this study revealed only one morphotype.

The ovary of X. melanopus (Figure 6a) is morphologically similar to the gonochoristic ovary described previously. The testis of X. melanopus (Figure 6b) is not similar to the morphotype described for the gonochoristic fish testis. The morphology of the testis of X. melanopus is similar to that which was found in Xyrichtys pentadactylus by Nemtzov (1985). Nemtzov isolated single harems (1 male with 1 to 7 females) of X. pentadactylus within aquaria and subsequently removed the male. The females of the harem were found to have a dominance hierarchy based on size. The largest female in the harem began behaving like the "removed" male had previously. Within a few days the female's coloration and gonads changed into the male form. The secondary testes of the "new male" was sectioned histologically using the same technique used in the present study. The secondary testes were in a lamellar array with a non-functional lumen branching between the lamellae. No

evidence of a male X. pentadactylus testis without a lumen was found.

The morphology of the secondary testes of X. pentadactylus is similar to that of X. melanopus testes. The lumen found within the testicular tissue of the razorfishes is left over from previous ovarian morphology. Therefore, due to the close phylogenetic relationship of X. pentadactylus to X. melanopus, the same type of haremic social system, and similar gonad morphology, X. melanopus is being considered a "monandric" protogynous hermaphrodite.

DISCUSSION

The initial purpose of analyzing X. melanopus and T. nikii for hermaphroditism was to end the speculation concerning these species. The method of showing the presence of sex reversal was an a posteriori one. The gonads of both sexes of each species were sectioned and stained and the histology and morphology of the organs were examined. This method of analyzing sex reversal is not complete, however. Using histology, one can only examine the end product of a sex change and determine the presence or absence of the event, unless all of the intermediate cell and morphological stages are sectioned. If one is to focus on the sex reversal completely, social behavior, the reversal process, and finally, histology of the gonads is done. Nemtzov (1985) performed a thorough sex reversal study on X. pentadactylus. The present

study on X. melanopus was intended to add to Nemtzov's work by presenting evidence that a close relative of X. pentadactylus is following the same sex change course. A complete behavioral study on X. melanopus' social system is in progress by Clark and Shen.

In T. nikii, a separation of sizes of the sexes is not complete evidence of the occurrence of sex reversal, as was assumed by Shimada and Yoshino (1984). Obviously, the T. nikii populations have not been sampled sufficiently to find young males.

Histological examination showed that T. nikii is probably a gonochorist. The solid, non-sex reversed testes of the males, makes the absence of small males in the data (Figure 2) peculiar. Small male T. nikii may be present in the marine environment in a place that has not been sampled. Because sex reversal is probably not occurring, the large males in the samples taken must have developed and grown from small males in the population.

A few possibilities exist that may explain the absence of small males in the samples.

(A) The small, immature (less dominant) males may be living separately from the main swarms. The main swarms are known to lower to the sand to perform lek-like mating behavior. The less dominant males have little chance, if any, for potential mating, therefore, it would be energetically "smart" for the small males to avoid this behavior until their dominance rank was increased.

During the lekking periods, predators have a good chance of catching T. nikii individuals. By avoiding the lek, small males are also protecting themselves from predators. Small swarms of immature, "bachelor" males may be present within the sand environment but, isolated from the main swarms that were sampled. Also, the "bachelor" swarms could be away from the sand environment, thus, they are being missed.

(B) The small (less dominant) males could be missed during collections due to their position in the swarm and the lek. The less dominant males on a lek are pushed out toward the territories on the outskirts of the arena by the dominant males (Lack, 1968; Pulliam, 1973). The same process may occur in T. nikii leks. Sampling of the population is usually done while the swarm is on the sand surface or in their dive sites. During sampling, it is possible that the outskirts of the lek are not being sampled, and therefore, the small males are being missed. This idea is presently being examined by Clark and Shen. Preliminary observations seem to refute this idea.

(C) The small males may have drab coloration, as do the females. The small males might be discounted for females during observations and collections. This idea is not completely feasible. During the present study, all of the fish were dissected and sexed by examining their gonads. Thus, within the samples already collected, all of the fish with drab female coloration

are female.

The present goal with regard to Trichonotus nikii is to locate the small males in their natural environment. To facilitate searching, basic laboratory studies on the development of fertilized T. nikii eggs to adults could be completed. Following the fishes' development may lead to some clue as to the needs of the individual fish at each stage of the process. By taking the information on fish development that is learned in the laboratory and applying it to the field, it may lead to the possible location of the small males in the environment.

In conclusion, Xyrichtys melanopus is being considered a monandric protogynous hermaphrodite on the basis of gonad histology. Further work on the behavior of the fishes in the territories and during mating is in progress by Clark and Shen. Trichontus nikii is being considered a probable gonochorist on the basis of preliminary gonad histology. Further work to illuminate the location of the small males of the species in the environment and to expand the histological sampling of the males needs to be completed.

Chapter 2
Feeding Ecology of the Sandfishes and Food Resource Availablity in the Sand Environment of the Red Sea

INTRODUCTION

The vertical stratification of *X. melanopus*, *T. nikii*, and *Gorgasia* sp. in the water column above the sand bottom could possibly be influenced by food availability and its distribution in the water column; by interspecific conflicts or competition for food; by physiological requirements of the fish species; or by predation. To investigate the structure of this assemblage, the factors influencing the fishes distributions have to be separated. The most influential factor(s) could then be determined without being confounded by other variables. To examine all of the factors involved in structuring the community all at once would be a monumental task.

Therefore, the focus of this study of the sandfishes community structure is limited to examination of the availability of food resources and distribution and its relationship to the fishes' spatial arrangement. An analysis of food resource availability seems to be the logical factor to complete initially, due to the concurrence of feeding by the fishes and the vertical stratification of the fish species. The other possible structuring forces mentioned previously will be discussed, but no experimentation on them was completed within the scope of this study.

In 1985, field observations were combined with collections of specimens of all three species of fishes and collections of horizontal plankton tows which were taken at the heights which correspond to the heights in which the fishes were feeding. The specimens were analyzed for stomach contents to determine the diets of the three species of fishes. An examination of the diets of the fishes can determine food resource-use overlap and the possibility of food resource-based competition between the fish species.

Horizontal plankton samples were taken to determine the spatial arrangement of various species of zooplankton and their abundances within the water column. Differences between abundances of species of zooplankton at the three heights may be an important factor that influences the fishes' distributions in the water column. If a certain prey is located only in one area of the water column, a fish which preferentially feeds on that prey must feed in the area of the water column in which the prey is located. Thus, the basis for the fishes' spatial arrangement may be due to the distribution of their preferred food organisms. If the abundances of species of zooplankton are not vertically patchy in the water column, other factors must be involved in the vertical stratification of the fish species in the water column.

Also, the plankton data will be a used to compare the species of zooplankton and abundances at each site and within each site, at different heights. The horizontal plankton tows were taken at three times of day to determine if any zooplanktor fluctuations could be seen over time. Fluctuations could be due to vertical migration of the zooplankton species over the water column, isolated events, or chance alone.

METHODS

STOMACH CONTENTS ANALYSIS

When examined, each stomach was sliced open longitudinally and rinsed with 70% ethanol so that all of the contents were removed. The stomach contents were placed in a small petri dish marked with a 2mm square grid on the bottom surface. Each dish was examined under a dissecting microscope (Olympus). Every whole organism encountered was identified, measured and enumerated. Only whole items were counted to avoid recounting pieces from the same individual item.

The exception to this rule were made for stomach contents from Xyrichtys melanopus. The stomach of X. melanopus was filled with bivalve shells, arthropod appendages and vertebrae. These items may have been ingested incidentally with other organisms (i.e. bivalve shells). Also, it would be unlikely that the razorfish could ingest a whole brachyuran crab or small fish without breaking it up into pieces. Therefore, if one

were to count only whole prey, a significant portion of the razorfish's diet would be excluded from counting. Instead, counts were made of each bivalve shell fragment, arthropod appendage, and vertebrae. These items are usually equal or larger in size to the copepods and gastropods which were found in the gut as well.

The counts of the types of prey were compiled and converted into percentages of the total volume of the fish's stomachs (as in Randall, 1967). The percentages were used to characterized the fish's diets and then to compare to the plankton available at the study sites. Electivity indices were calculated from the stomach contents and plankton data following Chesson (1983). Feeding niche overlap of the three fish species were measured using an overlap index suggested by Levin (1968).

PLANKTON ANALYSIS

During June 1985, plankton samples were taken to characterize the food resources available to the planktivorous fishes inhabiting the study sites. At each site, a series of three days of collections were made. The total collection period was within one lunar cycle (no full moon during collections). Gliwicz (1986) has shown that in a freshwater lake, Cahora Bassa, fluctuations of abundances of species of plankton due to predation seem to be triggered by the full moon. More moonlight on nights around the full moon and the vertical

trajectory of the moon in the tropics permits more feeding by nocturnal planktivorous fishes. The ability to see their prey items more easily enhances their ability to capture them.

The sandfishes are not night foragers and thus moonlight may not affect daytime abundances of zooplankton that they encounter. The study sites are in an open system (continual influx due to current movement) in comparison to Gliwicz's system (closed lake), the abundances of zooplankton may not be tied so intimately with night predation around the full moon period. The zooplankton should be continually renewed by influx due to current action at the study sites.

With the use of SCUBA, three 20 meter long transect lines were placed parallel at a distance of five meters apart on the sand slopes at the sites. The lines were placed in the area of highest abundance of the three focus species of fishes. Twenty meters is more than half the distance across the most dense region of the species at each site. The outer limits of the sandfish assemblage were avoided during sampling to decrease to chance of confounding the collections with the variables that cause the decrease in species abundance near the edges of the fishes' distribution.

A closed plankton net (#20 mesh, diameter 12.7 cm) attached to a steel bar extending down its length was lowered to a SCUBA diver in the water. I positioned the

net above one of the transect lines at a specified height, opened the net, and swam, at top speed (0.6m/s), the length of the line (method, Porter and Porter, 1977). All of the plankton collections were taken horizontal to the sand surface to sample layers of zooplankton available over the bottom at the sites. The net was kept in front so that my movement did not affect the plankton collection. The net was closed at the end of each run and the sample was brought to the surface to be preserved. The seawater-plankton mixture was immediately added to 95% ethanol, which diluted to approximately a 70% ethanol-seawater solution. Each sample contained the plankton which was collected from a volume of 0.23m cubed from the water column.

Collections were made at three times of day (morning = approximately 0800 hrs., 1200 hrs., evening = approximately 1700 hrs.) at three heights over the sand bottom (0.3m, 1.0m, 1.7m). The heights, originally measured in feet, were converted into meters. At each time of day, a sample was collected at each height. The collections at each height were taken over a different transect line. Separation of the collection locations was done to avoid disturbance of the zooplankton in the area around each line before each collection was made. All possible permutations of collection time, column height, and transect line were done to decrease the chance of sampling bias.

At the end of each day a set of nine plankton samples was obtained (3 times X 3 heights). After nine collection days (3 days at each site), 81 plankton samples were preserved and ready for analysis.

At the University of Maryland, each sample was sieved through a micro-nylon screen (Nytex), rinsed with 70% ethanol, and diluted to a volume of 40 cc. All of the samples were diluted in the same way, thus, the relative concentrations of the zooplankton in the samples were kept in proportion to the original collection concentrations.

A 1 cc Stempel pipette was inserted into the diluted sample and used to mix the plankton as evenly as possible by collecting and plunging the pipette repeatedly. While the sample was agitated, a 1 cc subsample was taken from the center of the water mass with the pipette. The subsample was transferred into a small petri dish with a 2 mm squared grid on the bottom of the dish. The pipette was rinsed thoroughly into the dish. This process was repeated three times so that 3 cc of each sample (3/40ths of each, 7.5%) was analyzed for percent composition of the major taxonomic groups. The procedure was abstracted from Frolander (1968) as being the most accurate use of the stempel pipette.

STATISTICAL ANALYSIS

To analyze the plankton data for significant differences between the sites, sampling heights and time

of day, the data were entered into SAS (Statistical Analysis System) general linear models. An analysis of variance (ANOVA) was run on each taxon encountered in the plankton. Arithmetic means and standard error were measured for each comparison. To meet the assumptions of the ANOVA the plankton data were transformed. Rare items in the plankton were transformed using a square root function (SR = SR(n + 0.5)). Abundant items in the plankton were transformed using a log10 function (LOG10 = LOG10(n + 1.0). Repeated days were treated as replicate samples, due to the low variability between days of the field collections when analyzing daily variations in the samples. Significant interactions between site, height and time of day of collection were judged by the Bonphoroni technique.

ELECTIVITY ANALYSIS

Chesson's (1983) index of electivity (+1 to -1) was used to quantify the number of prey consumed relative to the number available in the plankton, where random feeding by a fish on a prey item is denoted by an index of zero (0). A positive index indicates that the fish is eating the prey item at a higher proportion than it is encountering the prey item in the environment. A negative index indicates that the fish is eating the prey item at a lower proportion than it is encountering the prey item in the environment.

The electivity data for all of the prey items of all three fishes was used to determine if the fishes were feeding selectively from the plankton or if their feeding was random.

RESULTS

STOMACH CONTENTS ANALYSIS

All three of the species of fish were examined for diet. The stomach contents results of the fishes is listed in Table 2. The counts of prey types are listed in percent volume of the total contents found in each stomach.

Xyrichtys melanopus' (N = 9) diet consists mainly of small fishes (49%) and benthic invertebrates (51%) (Table 2, column 3). The most common item found in the stomachs were vertebrae (49%) from small, elongate, narrow bodied fishes. Comparisons with X-rays taken of *Trichonotus nikii* and drawings of *T. elegans* by Shimada and Yoshino (1984) and drawings of *T. setiger* by Nelson (1986) confirmed that the vertebrae were those of *Trichonotus nikii*. Rare field observations of *Xyrichtys melanopus* preying upon *T. nikii* have been recorded (Clark, 1983a; pers. obs.). The extent of *X. melanopus* feeding on *T. nikii* is much larger than assumed by field observations. Out of the nine *X. melanopus* that were examined, seven (79%) contained vertebrae of *T. nikii* in varying quantities.

Table 2. Percent (%) volume of prey in the stomachs of three species of fishes. The five most common prey for each species are ranked (A to E).

PREY FOUND IN STOMACH	STOMACH CONTENTS (% TOTAL VOL.) Gorgasia sp.	Trichontus nikii	Xyrichtys melanopus
Planktonic Prey:			
Cyclopoid copepoda	13.0 B	42.2 A	0.2
Calanoid copepoda	68.3 A	31.7 B	.0
Harpacticoid copepoda	2.2 E	11.6 C (4)	0.2
Invertebrate eggs	11.0 C	3.2 E	0.6 E
Fish eggs	2.4 D	--	--
Ostracoda	0.4	0.2	--
Cladocera	1.5	--	--
Gastropoda	1.3	10.6 D	1.2 D
Benthic Prey:			
Nematoda	--	0.2	0.1
Amphipoda	--	0.1	0.3
Polychaeta larvae	--	0.1	--
Bivalve (pieces) (1)	--	--	15.6 C
Arthropoda (appendages) (2)	--	--	33.2 B
Fish vertebrae (3)	--	--	48.6 A
Cumacea	--	--	.0

Footnotes:

1. BIVALVIA PIECES MAY BE INGESTED INCIDENTALLY OR THEY MAY BE THE RESULT OF INGESTING WHOLE BIVALVES WHICH WERE SUBSEQUENTLY CRUSHED BY Xyrichtys melanopus' JAWS and PHARYNGEAL TEETH.
2. LARGE ARTHROPODS WERE INGESTED BY Xyrichtys melanopus, BUT BECAUSE THEY WERE BROKEN UP BY THE FISH, COMPLETE IDENTIFICATION WAS IMPOSSIBLE. POSITIVE IDENTIFICATION OF PADDLE-LIKE SWIMMING APPENDAGES (5 TH) FROM BRACHYURAN CRABS WAS POSSIBLE.
3. VERTEBRAE FOUND IN GUT WERE POSITIVELY IDENTIFIED AS THOSE FROM Trichonotus nikii. X-RAYS OF T. nikii WERE USED FOR COMPARISON.
4. A FEW HARPACTICOID COPEPODS IN T. nikii WERE BENTHIC IN ORIGIN BUT BUT WERE NOT CLASSIFIED SEPARATELY FROM THE PLANKTONIC FORMS.

The remaining prey in the stomach of X. melanopus are predominantly benthic in origin. Arthropod appendages were the second most common prey of X. melanopus (33%). The appendages were pieces of brachyuran crab. Positive identification was possible due to the presence of swimming appendages (5th) in the samples. The exact number of crabs ingested by the razorfishes was not possible to determine. As the crabs were ingested by the razorfishes, they were crushed by the pharyngeal teeth. It would be impossible for the brachyuran crabs to be ingested whole without damage by either the pharyngeal teeth or those in the jaw. Bivalve pieces were the third most common item found in the stomach of X. melanopus (16%). The bivalve pieces may have been ingested incidentally with other prey items from the bottom surface (Randall, 1967). It is also possible that some or all of the bivalve pieces are the result of the fish ingesting whole bivalves and subsequently crushing them to get at the tissues. For this reason, the bivalve pieces were left in the stomach contents counts. Small gastropods (whole and partially broken) were the fourth most common prey of X. melanopus (1%). The gastropods were metamorphosed and encased in shells, typical of those found on the sandy bottom at all three sites. Of the remaining prey found in the stomach, 1% were also benthic in origin (amphipods, nematodes, harpacticoid copepods, and cumaceans) and 1% were

planktonic in origin (cyclopoid and calanoid copepods, and invertebrate eggs).

The stomach contents of Trichonotus nikii (N = 33) is primarily plankton (74%+) and a smaller representation of benthic invertebrates (23%) (Table 2, column 2). The most common prey are copepods (cyclopoids, calanoids, and harpacticoids, respectively) which comprise 86% of T. nikii's diet. Planktivory by T. nikii agrees with observations of feeding from the field studies and Randall (1967). Harpacticoid copepods are typically benthic organisms (Barnes, 1980), thus they were included in the benthic component, although a few genera are holoplanktonic. Most of the harpacticoids were benthic types, but the actual percentage was not separated from the total during the laboratory counts.

Surprisingly, 23% of the stomach contents of T. nikii is benthic invertebrates. The benthic invertebrates could have been from the water column due to shear flow near the bottom. Organisms that are not anchored securely to the bottom can be tossed up into the water column as a result of the speed of water flow that comes in contact with the sand surface (Palmer, 1986). Therefore, part of the benthic component of T. nikii's diet could also, be selected out of the water column. Some of the benthic invertebrates may be eaten directly off the bottom, such as when T. nikii is seen to pick at the sand surface during the lek-like displays (males).

Thus, the supposed "displacement behavior" may be true feeding. The "feeding" by male I. nikii during the lek-like behavior does not account for the meiofauna found in the stomach of female I. nikii. Females also may pick at the bottom for food during feeding. Overall, I. nikii is a selective plankton feeder with 85% of their diet comprised of copepods.

Gorgasia sp.'s diet is comprised of 97% plankton and 3% benthic invertebrates (Table 2, column 1). The four most predominant prey are calanoid copepods, cyclopoid copepod, invertebrate eggs, and fish eggs, respectively. All of these prey (92%) are planktonic in origin (invertebrate eggs may have been found on sand surface as well as in the plankton). This finding agrees with the field observations that the eels actively select prey out of the water column. The small amount of benthic invertebrates in the eel's diet could either be taken from the sand surface, presumably during slack currents or from the organisms that are tossed up into the water column from the bottom. The exact position from which the eels ingested the "benthic" invertebrates is not known. Overall, as seen in field observations, Gorgasia sp. is a selective plankton feeder, maintaining a diet of 84% copepods (mainly calanoids).

Comparison of the diets of the three species was completed to determine the amount of overlap of food resource use by these fishes. If the resources are

limiting, common resource use may indicate competition for prey by the fishes. Where food resources are abundant and not limiting, species will be able to coexist without competiting from food. In such a situation the necessity for food resource partitioning is obviated and a high degree of feeding niche overlap between the fish species can be tolerated. Within the present study a food overlap index is used to give a quantitative measure of food usage of each of the three species of fishes in relation to the others. The overlap values (alphas) of one fish to another are presented in Table 3. Each species' diet is compared with the other two species.

The overlap values between X. melanopus and the other two fish species are relatively low (range 0.003 to 0.009). Therefore, the measure of alpha introduced by Gause (1934) (restated and explained by Levins, 1968) indicates that only a small amount or type of food resource usage is shared between X. melanopus and the other focus fish species. Conversely, the food overlap values (alpha) between T. nikii and Gorgasia sp. is relatively high (0.916). Thus, the two fish species are preying upon much of the same food resources. Therefore, the possibility of competition between T. nikii and Gorgasia sp. for prey is likely to be intense if food resources are limited.

Table 3. Analysis of the overlap of habitats of three species of fishes using the formula for ALPHA(ij) (The coefficient of competition), from Levins (1968). ALPHA is the overlap of resource usage of species "j" on that of species "i" relative to the total resource utilization of species "i." Values range from zero to slightly greater than one.

Primary Species (i)	Food Resource Overlap with (j)	Levins (1968) Overlap Value
Gorgasia sp.	X. melanopus	.0026
Gorgasia sp.	T. nikii	.9159
X. melanopus	T. nikii	.0075
X. melanopus	Gorgasia sp.	.0035
T. nikii	X. melanopus	.0091
T. nikii	Gorgasia sp.	.9159

Formulation of ALPHA(ij), the Coefficient of Competition:

$$ALPHA(ij) = SUM(Pih*Pjh)/SUM(Pih*Pih)$$

Pih = proportion of use by species i of the food resource h

Pjh = proportion of the use by species j of the food resource h

The overlap index (alpha) does not take into account the quantity of food resources available to the focus species in the sand environment. To measure the availability of zooplankton, horizontal plankton tows were taken from each of the three heights over the sand at which the focus species are feeding.

PLANKTON ANALYSIS

The composition of the plankton from all three of the study sites at the three heights in the water column is listed in Table 4. The plankton samples were analyzed for percentage of the total volume for the major taxa. The taxonomic classification is consistent with that used in the analysis of stomach contents of the focus species. The three samples that were taken each day, at one site, and one height are combined in the table. Also, the taxa found in the plankton samples are ranked (1-24, 1 = most abundant). Of the six most abundant zooplankton taxa groups, the first three (copepod nauplii, dinoflagellates, and radiolarian) taxa were not found in the stomach contents of the focus species.

The plankton data were transformed and then entered into an analysis of variance (ANOVA) to answer the questions: are significant differences in zooplankton abundances at (1) the different sites used in the study?, (2) the different heights over the sand bottom at which the fishes feed?, and (3) different times of day?

Table 4. Plankton taxa (% of total lumped sample) found at each site by height over the sand bottom. Samples were collected in June 1985 with a horizontal diver push net. Each sample contains the plankton from 0.23m cubed of seawater.

RANK	PLANKTON TAXA / SITE = COLL. INFO.	RM 0.3m	RM 1.0m	RM 1.7m	AQ 0.3m	AQ 1.0m	AQ 1.7m	MM 0.3m	MM 1.0m	MM 1.7m
1	Copepod nauplii	33.09	31.43	31.68	17.23	20.14	16.78	24.72	32.16	25.80
2	Dinoflagellates	6.36	7.12	5.82	17.12	17.12	20.54	15.48	17.97	14.09
3	Invertebrate eggs	9.49	9.76	10.83	15.43	13.38	7.93	10.08	10.21	15.75
4	Calanoid copepoda	12.93	11.94	13.93	5.92	8.99	10.44	8.36	8.65	9.61
5	Radiolaria	12.41	12.77	13.87	4.46	4.17	3.10	13.27	11.24	11.20
6	Harpacticoid copepoda	6.05	6.51	4.64	9.67	11.37	11.76	11.41	6.56	9.32
7	Cyclopoid copepoda	9.58	7.81	9.73	8.04	6.26	12.22	5.75	5.17	5.50
8	Gastropoda	3.67	5.74	4.79	6.85	7.55	8.26	3.41	2.87	2.77
9	Foraminifera	2.06	3.41	2.30	5.54	4.39	3.50	2.48	1.23	1.24
10	Polychaete larvae	0.58	0.35	0.27	1.36	0.79	1.19	1.64	1.60	2.13
11	Nematoda	0.48	0.61	0.46	1.30	0.79	0.79	0.35	0.33	0.73
12	Cladocera	0.64	0.07	0.11	3.15	0.22	0.79	0.22	0.12	0.00
13	Crab megalopa	0.23	0.00	0.13	0.16	0.07	0.53	1.72	1.03	1.21
14	Ostracoda	0.51	0.61	0.55	1.36	0.50	0.59	0.35	0.25	0.06
15	Bivalvia	0.23	0.11	0.15	1.30	1.80	0.66	0.09	0.04	0.06
16	Barnacle nauplii	0.39	0.20	0.25	0.49	1.73	0.59	0.44	0.12	0.10
17	Bryozoa	0.51	0.57	0.13	0.49	0.72	0.20	0.18	0.04	0.06
18	Larvacea	0.61	0.44	0.17	0.00	0.00	0.00	0.00	0.29	0.00
19	Fish eggs	0.00	0.04	0.04	0.11	0.00	0.00	0.04	0.12	0.32
20	Echinodermata pleuteus	0.19	0.13	0.06	0.00	0.00	0.00	0.00	0.00	0.00
21	Crab zoea	0.00	0.07	0.04	0.00	0.00	0.13	0.00	0.00	0.03
22	Amphipoda	0.00	0.17	0.02	0.00	0.00	0.00	0.00	0.00	0.00
23	Tunicate larvae	0.00	0.13	0.04	0.00	0.00	0.00	0.00	0.00	0.00
24	Mysid larvae	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00

To answer the first two questions, the three times of day were combined for each day as in Table 4. The ANOVA procedures were computed using each taxon as a dependent variable. From the ANOVA, using LSD ($p > 0.05$) significance levels, at each of the sites, three zooplankton taxa showed significant height differences. Gastropods, cyclopoid and calanoid copepods were significantly more abundant at 1.7m than at the other measured heights ($p > 0.05$, 0.03, 0.05, respectively). Invertebrate eggs were the only taxon that was significant for the site*height interaction ($p > 0.02$). With times and heights combined for each day, only invertebrate eggs showed significant variation from site to site. Also, when the sites are combined to look at variation at different heights, gastropods, cyclopoid copepods, and calanoid copepods have marginally significantly greater abundances at 1.7m compared to 1.0m and 0.3m over the sand bottom (Table 5).

To answer the question if significant variation exists in zooplankton abundances at different times of day, the times of day were separated and each sampling day was treated as a replicate. The assumption of this procedure is that a sample taken at Day 1 during the sampling regime would be very similar to a sample taken from the same site on Day 4 of the nine day collection series. The constancy of temperature and weather at all of the study sites allows this assumption. Thus in

Table 5. Mean abundances of the taxa from the analysis of variance of the plankton data by height over the sand bottom (SIGNIFICANCE * = .05, ** = .01, *** = .001)

TAXA	MEAN HEIGHT OVER SAND BOTTOM 0.3m	1.0m	1.7m	TAXA	MEAN HEIGHT OVER SAND BOTTOM 0.3m	1.0m	1.7m
Copepoda nauplii	56.75	64.33	65.44	Crab megalopa	1.14	0.62	1.51
Dinoflagellates	26.30	33.67	34.32	Barnacle nauplii	0.93	1.01	0.62
Invertebrate eggs	28.24	27.04	33.01	Cladocera	1.58	0.25	0.43
Calanoid copepoda	23.30	27.06	37.66 (1)	Bivalvia	0.87	0.84	0.53
Harpacticoid copepoda	22.21	21.87	25.47	Bryozoa	0.91	0.96	0.35
Cyclopoid copepoda	19.88	17.97	29.18 (2)	Larvacea	0.38	0.59	0.23
Radiolaria	20.88	21.33	19.86	Fish eggs	0.08	0.14	0.27
Gastropoda	14.56	14.56	15.80 (3)	Amphipoda	.00	0.21	0.03
Foraminifera	7.55	7.85	7.10	Crab zoea	.00	0.06	0.14
Echinodermata pleuteus	2.57	2.07	2.78	Tunicate larvae	0.00	0.10	0.05
Nematoda	1.52	1.26	1.97	Mysids	0.01	0.03	0.00
Ostracoda	1.52	1.08	1.08	Noctiluca	0.03	.00	.00

Significant variances: (1) 1-3 *, 2-3 * (2) 1-3 * (3) 2-3 *

theory, the sampling days are interchangeable. This is a liberal approach, thus to counteract type I errors, Bonphoroni significance levels are used (Bon = 0.05/3 interactions = 0.0167).

At either the LSD significance level ($p > 0.05$) or the Bonphoroni levels, there are many significant differences in zooplankton abundances from one sampling time of day to another (Appendix 3). This outcome is expected if vertical migration of the zooplankters is occurring within the water column. According to vertical migration theory (Olhorst, 1982; Robichaux et al., 1981; Porter and Porter, 1977; Schmidt, 1973), the zooplankters should increase the depth they inhabit during daylight to avoid being eaten by planktivores. Increased visibility of the zooplankters in daylight increases their chance of being eaten (Gliwicz, 1986; Porter and Porter, 1977; Sameoto, 1974; Schmidt, 1973). At sunset, the zooplankters should swim, float, etc. toward the surface waters to feed on phytoplankton residing in the upper photic zone. Darkness provides a refuge from predation for zooplankters. Also, fewer planktivores are nocturnal feeders, thus, the predation risk is lower at night (Collette and Talbot, 1972; Hobson and Chess, 1978).

Therefore, if vertical migration is being measured in samples from different times of day (at the measured heights), the early sampling time collection (approx. 0800 hrs) should have a lower abundance of zooplankton in

comparison to the later sampling times (1200, approx. 1700 hrs) which are during broad daylight. The animals should be in transition from the shallows to the depths. To accurately measure vertical migration the sampling times should ultimately coincide with dawn and dusk. Unfortunately, the sampling times of this study were restrained by the logistics of transportation to and from the sites. Thus, within the present sampling regime, I should expect to see fairly level values of abundances of zooplankton because the collections do not cover the transition periods.

From the arithmetic means of the abundances of the zooplankton taxa in Appendix 3 (tables and representative figures), there is no evidence of changes in abundance to mirror what one might expect if vertical migration is occurring, thus reinforcing the idea that the migration periods of the zooplankton were not sampled within the collection regime (although level abundances of zooplankton taxa were also not seen). A few isolated means from one taxon at one site show the expected shifts, but, are not supported by the same shifts at the other sites. The variation in abundances could be due to isolated events (spawning, currents sweeping meiofauna into the water column, etc.) or to chance alone.

Appendix 3 lists the ANOVA results, the arithmetic means of each of the plankton taxa and a few representative graphs of the means. Appendix 3 (figures

1-5) shows the variation in the mean abundances of the planktonic taxa at each site over time.

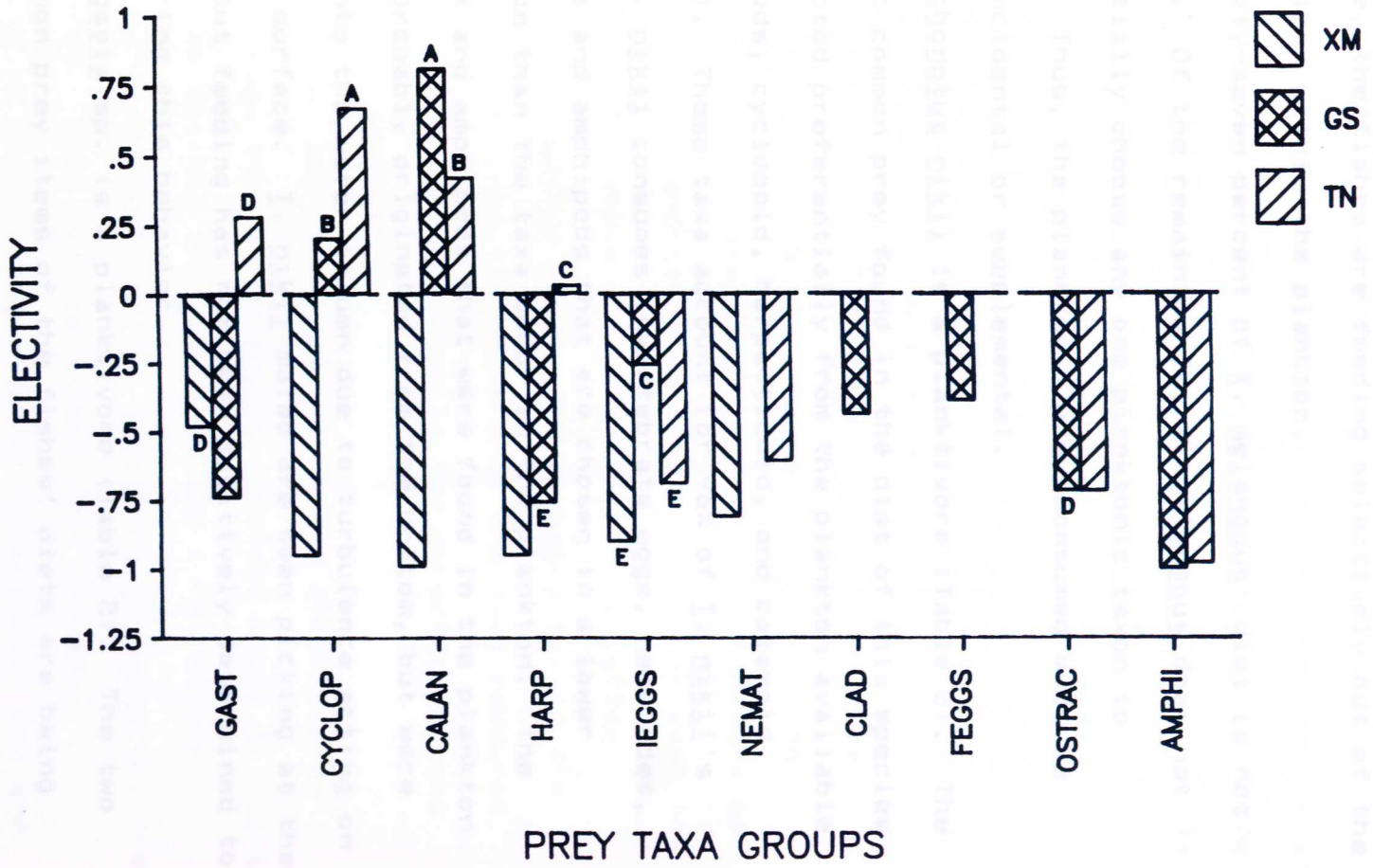
The abundances of each taxon found in the plankton were compared to the abundances of the same groups found in the fishes' stomachs using Chesson's (1983) electivity index. The index of electivity incorporates the fishes' diets with the food available to them (plankton). The index is used to answer the question of whether the fishes are feeding selectively among the available prey or are they feeding randomly? The results of the electivity analysis are presented in Fig. 7. The index is computed for each taxon found in the species' stomachs that is also found in the plankton (N = 10 taxa). In Fig. 7, the five most common planktonic prey of each species of fish are denoted with a letter (A to E) over the index bar.

The electivity indices for all three species indicate that the majority of the prey are not being selected at random (random = index near or equal to zero, see methods section). Chesson (1983) warns that the index should not be analyzed statistically thus, the indices are not denoted as either significant or not. Most of the prey are being eaten by the fishes in a smaller proportion of the diet than the prey is represented in the plankton (negative selection or avoidance). The remaining prey (gastropods, cyclopoid, harpacticoid and calanoid copepods) are being positively

Figure 7. Chesson's (1983) index of electivity measured for X. melanopus, T. nikii, and Gorgasia sp.. The abundances of nine prey taxa which were found in the fishes' stomachs were compared to the taxa's abundances in the plankton. The five most common prey found in each of the fishes' diets are marked A-E over the indices. Refer to the methods section for more details of the index measure.

CHESSON'S ELECTIVITY INDEX FOR THE 3 FISHES

OVER THE MOST COMMON PREY (Top 6 items ranked A–E)



selected by the fishes. The fishes eat a higher proportion of these prey than they occur in the plankton. Therefore, the fishes are feeding selectively out of the prey choices within the plankton.

Ninety-seven percent of X. melanopus' diet is not plankton. Of the remaining 3%, X. melanopus does not preferentially choose any one planktonic taxon to consume. Thus, the planktonic prey consumed must be either incidental or supplemental.

Trichonotus nikii is a planktivore (Table 2). The four most common prey found in the diet of this species are selected preferentially from the plankton available (gastropods, cyclopoid, harpacticoid, and calanoid copepods). These taxa account for 96% of T. nikii's diet. T. nikii consumes invertebrate eggs, nematodes, ostracods and amphipods that are chosen in a lower proportion than the taxa occur in the plankton. The nematodes and amphipods that were found in the plankton samples probably originated from the bottom, but were tossed into the water column due to turbulence acting on the sand surface. T. nikii males are seen picking at the bottom, but feeding has not been positively determined to occur during this behavior.

Gorgasia sp. is a planktivore (Table 2). The two most common prey items of the fishes' diets are being selected preferentially from the plankton (calanoid and cyclopoid copepods). Of the other prey found in Gorgasia

sp.'s diet, invertebrate and fish eggs, gastropods, ostracods, amphipods, cladocerans and harpacticoid copepods (planktonic or benthic) are being selected in a lower proportion of the diet than they are represented in the plankton. Overall, 81% of Gorgasia's prey are being selectively chosen from the plankton. The remaining 19% is not being preferentially sought for food.

DISCUSSION

Based on behavioral observations of the intraspecific interactions of sandfishes presented previously by Clark (1971a, 1971b, 1975, 1980, 1983a, 1983b) and the interspecific interactions presented within this paper, I examined the vertical structure of an assemblage of sandfishes in the water column over the sand bottom. The goals of this study of Xyrichtys melanopus, Trichonotus nikii, and Gorgasia sp. in the sand environment were to relate diet and food resource availability from the plankton to the structure of the assemblage of sandfishes.

Primarily, the investigation of the three fishes' diets concludes that X. melanopus consumes small T. nikii and assorted benthic invertebrates and a relatively minute amount of plankton. T. nikii and Gorgasia sp. are planktivores. Each species selectively chooses zooplankton as their primary dietary component (96% and 81%, respectively). The fishes also consume other zooplankton prey supplementally or incidentally. A small

proportion of T. nikii's diet consists of benthic invertebrates.

Where food resources are limiting, an assessment of the feeding niche overlap of the three species of fishes can help determine the level of competition for prey that may exist within the assemblage. But, when food resources are not limited, as such is probably the case in the Gulf of Aquaba, the necessity for food resource partitioning is lessened and a high degree of feeding niche overlap can be tolerated. Therefore, the food overlap index is used in this study to quantify common resource usage between the species of fishes, but it should not be interpreted as a strict measure of competition (Colwell and Futuyma, 1971). However, such a situation does not mean that the fishes avoid resource partitioning or competition altogether. Competition during another phase of life could exercise a regulating influence on the numbers of adults in the assemblage.

The measure of the feeding niche overlap index concludes that X. melanopus has a small dietary overlap with T. nikii and Gorgasia sp. Therefore, even if food resource limited, X. melanopus's position, in a lower stratum compared to the other fishes' feeding strata, is not primarily due to competition for prey. It is advantageous for T. nikii to avoid X. melanopus because the razorfishes eat T. nikii.

Alternatively, T. nikii and Gorgasia sp. have large feeding niche overlaps. Their proportions of various prey are vastly different (Table 2) but, the similarity of the species of prey is high. The environment in which T. nikii and Gorgasia sp. feed does not seem to be food resource limited, but alternatively, an overwhelming abundance of prey do not seem to be present (based on the plankton data) either. Separation of feeding ranges based strictly on food resource competition does not seem viable, although the foraging efficiency of each individual fish should increase as the fishes increase their personal feeding ranges. Therefore, it is probably advantageous for T. nikii and Gorgasia sp. to choose feeding strata which are separated either in space or time. Both species are diurnal, thus, separation of feeding ranges in space is the most viable alternative.

When analyzing the assemblage structure of these sandfishes, an important factor to consider is whether or not the fishes are vertically stratified in the water column based only on the distribution of prey in the plankton. Horizontal plankton tows at the heights at which the species feed did not show a significant variation in the compositions of plankton at the three heights examined (0.3m, 1.0m, 1.7m) or between sites.

Each of these species was seen feeding at various times during the day, thus, the plankton data from each day (three samples) were lumped into one for analysis.

Invertebrate eggs (11% of Gorgasia sp.'s diet, 3% of I. nikii's diet and 0.6% of X. melanopus's diet) was the only planktoninc taxon which varied significantly from site to site. Aquasport, the most polluted site, had significantly lower percentages of invertebrate eggs than either of the other two sites during the sampling regime. Variation in the abundance of invertebrate eggs in the plankton should be expected when one considers the spatial and temporal variation in spawning by various invertebrate species. Also, the recent oil spills in the Northern Gulf of Aqaba may well be affecting the number of marine invertebrates that inhabit the area or the number of eggs they produce (compared to the less polluted areas of Marsa el Mukibela and Ras Mohammed).

The sandfishes do not rely solely on the nutritional supplement of invertebrate or fish eggs for a large proportion of their diets. One would suspect that when the eggs (invertebrate and fish) are available in the plankton, that the fishes would take advantage of the high nutritional value and thus increase the proportion of the eggs in their diets.

Based on the results of the plankton data gathered, approximately 90% of the taxa (if the samples are lumped by day) does not vary significantly in abundance from site to site. Therefore, aside from invertebrate egg abundances, the sites are considered to be fairly comparable in distribution of plankton for purposes of my

analysis.

When analyzing the spatial arrangement of various taxa from feeding height to feeding height at each site, variation in abundances of gastropods, cyclopoid and calanoid copepods were marginally significant. These taxa were more abundant at 1.7m than at the other two heights. Invertebrate eggs varied significantly from height to height also, but, as discussed previously, spatial and temporal variation in egg abundances was expected. Cyclopoid copepods and gastropods are a large proportion of I. nikii's diet (42% and 11%, respectively). Therefore, it is logical that I. nikii is found feeding at a height of 1.7m.

Gorgasia sp. feeds with its body stretched to its maximum length (approx. 1m) out of the burrow (except in extremely strong currents, the eels "crouch" during feeding), thus, it cannot reach higher in the water column. Gorgasia sp. preferentially eats calanoid copepods which are slightly more abundant at 1.7m off the bottom than at the other two feeding heights measured. If Gorgasia sp. could feed without being in contact with its burrow, it might shift its feeding stratum higher in search of calanoid copepods. Of course, if Gorgasia fed higher off the sand bottom and if food resource limited, it would be in direct competition with I. nikii for planktonic food.

X. melanopus's planktonic prey (less than 3% of diet) do not vary significantly in abundance from height to height in the samples. But, it is not expected that X. melanopus would shift its feeding height in response to differences in planktonic species abundances. Ninety-seven percent of X. melanopus's diet consists of small T. nikii and benthic invertebrates, thus, it would be advantageous for X. melanopus to stay near the sand surface to pick at the bottom for food.

After analyzing the dietary and behavioral observations of these three species of sandfishes as some of the factors influencing their vertical stratification in the water column, the following conclusions become apparent. It would be advantageous for T. nikii to stay away from X. melanopus when possible to avoid being eaten. Also, T. nikii should avoid eating in the same stratum of the water column with Gorgasia sp., to avoid competition for planktonic prey if in reality the species are food resource limited. Feeding higher in the water column allows T. nikii to take advantage of slightly increased abundances of cyclopoid copepods and gastropods. For T. nikii, being high up in the water column away from the safety of the diving areas of the sand has other consequences. T. nikii is a swarming species. The fish's swarm confuses pelagic predators which may pass through the sand environment (Table 1). Also, T. nikii is safely away from benthic predators

(e.g. X. melanopus) which prey on fishes near the sand surface. Therefore, based on the present results, T. nikii should feed high in the water column to avoid predation, possible food resource competition and to gain the benefit of the increased abundances of cyclopoid copepods and gastropods.

X. melanopus should stay near the sand surface to feed and to defend its territorial boundaries (and its dive sites) from conspecifics. X. melanopus need not venture up into the water column in pursuit of T. nikii. Swarms of T. nikii lower to the sand surface to perform their lek-like mating displays and to bury in the sand at dusk. Thus, X. melanopus can capture T. nikii fishes near the sand bottom. Therefore, it is advantageous for X. melanopus to stay near the sand surface to feed and to defend its territorial boundaries.

Gorgasia sp.'s maximum feeding height is constrained by body length. Most of the length of the eel's body is extended out of the burrow during feeding. Studies on the territorial behavior of Gorgasia sp. by Clark (1980) show that the longer (and larger) males hold larger territories on the sand surface. Dominance behavior may explain why Gorgasia sp. male extend out of the burrow as far as possible to feed. Dominance of males is in part due to size (length), thus, the males extend out of the burrows as far as possible.

During slack currents, Gorgasia sp. males and females alike are seen reaching and selecting items from the plankton. Maximum extension of the body length out of the burrow allows a larger range in which the eels can feed. Therefore, at least during slack currents, maximum distance of feeding from the sand bottom (burrow opening) is beneficial for prey capture.

Other factors are probably involved in causing both male and female Gorgasia sp.to feed at a height of almost one meter. There could be a physiological constraint on Gorgasia sp. that inhibits the eels from partially extending out of the burrow for long periods of time (i.e. during feeding). More research on the Gorgasia sp.'s stratum limits is needed.

At the sites where the three species do not coexist, (Marsa el Mukibela lacks Gorgasia sp. and Aquasport lacks X. melanopus although X. pavo is present and behaves similar to X. melanopus in that assemblage structure), small qualitative differences in the assemblage structure of the fishes can be seen. At Marsa el Mukibela, the swarms of T. nikii tend to be slightly closer to the sand surface. T. nikii hovers above X. melanopus in the area in which Gorgasia sp. would feed, if present. T. nikii position in the water column at Marsa el Mukibela could be due to a lack of competition for food with the eels. The decrease in feeding height by T. nikii also gives credibility to the minimal difference between feeding on

plankton at 1.7m and 1.0m. Therefore, Gorgasia sp. may be feeding in a stratum that is not noticeably different in plankton abundances from any other height that the eels are able to span above the sand.

At Aquasport, X. pavo's range does not completely overlap the range of T. nikii. T. nikii hovers closer to the bottom when they are not actively feeding. This difference in height of T. nikii swarms at Aquasport may indicate that X. melanopus is forcing T. nikii higher into the water column at the other two sites. The exact differences seen in the assemblages at the three sites when all three species of sandfishes were not present were not measured quanititatively, although these data would be of interest to add support to the present study.

Within the scope of this study, the vertical stratification of X. melanopus, T. nikii, and Gorgasia sp. in the water column over the sand surface is partially explained by interspecific interactions and predation, and partially by diet limitations and possible competition for food resources. Ultimately, more research on the sandfishes may reveal other factors involved in the structure of the assemblage.

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Appendix 1. Paraffin embedding protocol for the Autotechnicon 2A. Gonadal tissues are emersed in the solutions in order and then embedded in a paraffin block for sectioning.

SOLUTION	TIME IN SOLUTION (min)
70 % Ethanol I	60
70 % Ethanol II	60
80 % Ethanol I	120
95 % Ethanol I	60
100 % Ethanol I	60
Clear : 100 % Ethanol	60
Clear I	90
Clear II	30
Clear III	60
Paraffin : Clear	60
Paraffin I	60
Paraffin II	60

Clear = Clearing Solution C650 (Ethylene dichloride, Carbon tetrachloride, N-Butyl acetate)

Paraffin used was Paraplast (melting point 56-57 degrees C)

Appendix 2. Hematoxylin and eosin staining protocol for light microscopy.

SOLUTION	TIME IN BATH (MIN)
Xylene in I	5
Xylene in II	5
Xylene : 100% EtOH	5
100% EtOH in I	5
100% EtOH in II	5
95% EtOH	5
70% EtOH	5
50% EtOH	5
30% EtOH	5
Distilled water	0.33
Hematoxylin	3-4
Distilled water	rinse
Acid alchol (HCl:30% EtOH)	1-2
Alkaline alcohol (NaOH:30% EtOH)	until blue
30% EtOH	5
50% EtOH	5
70% EtOH	5
95% EtOH	5
Eosin Y (5% sol'n) (0.5%M 95% EtOH)	2-4
95% EtOH	0.33
100% EtOH out I	0.33
100% EtOH out II	0.33

(Appendix 2, con't)

Xylene out I	5
Xylene out II	5
Toulene	5

APPENDIX 3:

The results from the ANOVA procedures performed on the transformed plankton data. The sums of squares and the mean square values were left in their transformed values. A prefix "SR" on the taxa represents a square-root transformation of the data. The prefix "L" on the taxa represents a logrithmic (base 10) transformation of the data. The tables 2-26, containing the arithmetic means and the standard error of the interactions between site, height, and time, have been untransformed, thus, the values represent mean abundances. The arithmetic means from representative taxa from the plankton are graphed (Appendix 3, Figures 1-5) to show the absence of vertical migration patterns within the three samples taken during each day.

Appendix Table 1. Analysis of plankton on all sites
General Linear Models Procedure

Dependent Variable: SRGAST

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	101.262852	3.894725	45.75	0.0001
Error	54	4.596714	0.085124		
Corrected Total	80	105.859566			

R-Square	C.V.	Root MSE	SRGAST Mean
0.956577	7.7309724	0.291761	3.77392031

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	43.38506	21.69253	254.83	0.0001
TIME	2	3.81986	1.90993	22.44	0.0001
SITE*TIME	4	20.29840	5.07460	59.61	0.0001
HEIGHT	2	5.88735	2.94367	34.58	0.0001
TIME*HEIGHT	4	5.20980	1.30245	15.30	0.0001
SITE*HEIGHT	4	14.73036	3.68259	43.26	0.0001
SITE*TIME*HEIGHT	8	7.93203	0.99150	11.65	0.0001

General Linear Models Procedure

Dependent Variable: SRCYCL

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	219.295763	8.434452	57.36	0.0001
Error	54	7.940925	0.147054		
Corrected Total	80	227.236688			

R-Square	C.V.	Root MSE	SRCYCL Mean
0.965054	8.0672292	0.383476	4.75350853

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	111.86712	55.93356	380.36	0.0001
TIME	2	25.07758	12.53879	85.27	0.0001
SITE*TIME	4	26.05007	6.51252	44.29	0.0001
HEIGHT	2	20.19511	10.09755	68.67	0.0001
TIME*HEIGHT	4	6.40811	1.60203	10.89	0.0001
SITE*HEIGHT	4	7.51858	1.87964	12.78	0.0001
SITE*TIME*HEIGHT	8	22.17921	2.77240	18.85	0.0001

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRCALA

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	413.195007	15.892116	80.60	0.0001
Error	54	10.647528	0.197176		
Corrected Total	80	423.842535			

R-Square	C.V.	Root MSE	SRCALA Mean
0.974879	8.1701449	0.444046	5.43497756

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	207.17531	103.58765	525.36	0.0001
TIME	2	33.44074	16.72037	84.80	0.0001
SITE*TIME	4	123.49332	30.87333	156.58	0.0001
HEIGHT	2	24.16200	12.08100	61.27	0.0001
TIME*HEIGHT	4	1.13007	0.28252	1.43	0.2357
SITE*HEIGHT	4	7.00621	1.75155	8.88	0.0001
SITE*TIME*HEIGHT	8	16.78736	2.09842	10.64	0.0001

General Linear Models Procedure

Dependent Variable: SRHARP

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	76.1843004	2.9301654	28.11	0.0001
Error	54	5.6280088	0.1042224		
Corrected Total	80	81.8123092			

R-Square	C.V.	Root MSE	SRHARP Mean
0.931208	6.6418258	0.322835	4.86063514

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	9.11880	4.55940	43.75	0.0001
TIME	2	8.36472	4.18236	40.13	0.0001
SITE*TIME	4	24.02640	6.00660	57.63	0.0001
HEIGHT	2	2.24594	1.12297	10.77	0.0001
TIME*HEIGHT	4	7.66520	1.91630	18.39	0.0001
SITE*HEIGHT	4	12.90441	3.22610	30.95	0.0001
SITE*TIME*HEIGHT	8	11.85882	1.48235	14.22	0.0001

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: LCNAUP

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	11.3243167	0.4355506	33.31	0.0001
Error	54	0.7061691	0.0130772		
Corrected Total	80	12.0304858			

R-Square	C.V.	Root MSE	LCNAUP Mean
0.941302	6.3541613	0.114356	1.79969637

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	7.014839	3.507419	268.21	0.0001
TIME	2	0.409406	0.204703	15.65	0.0001
SITE*TIME	4	2.477507	0.619377	47.36	0.0001
HEIGHT	2	0.059703	0.029851	2.28	0.1118
TIME*HEIGHT	4	0.046749	0.011687	0.89	0.4741
SITE*HEIGHT	4	0.245423	0.061356	4.69	0.0025
SITE*TIME*HEIGHT	8	1.070691	0.133836	10.23	0.0001

General Linear Models Procedure

Dependent Variable: LIE66

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	5.73346412	0.22051785	46.62	0.0001
Error	54	0.25544694	0.00473050		
Corrected Total	80	5.98891107			

R-Square	C.V.	Root MSE	LIE66 Mean
0.957347	4.6415535	0.068779	1.48180179

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	1.663664	0.831832	175.84	0.0001
TIME	2	0.378818	0.189409	40.04	0.0001
SITE*TIME	4	1.533905	0.383476	81.06	0.0001
HEIGHT	2	0.104871	0.052436	11.08	0.0001
TIME*HEIGHT	4	0.087860	0.021965	4.64	0.0027
SITE*HEIGHT	4	1.477303	0.369326	78.07	0.0001
SITE*TIME*HEIGHT	8	0.487043	0.060880	12.87	0.0001

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRNEMA

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	18.9229030	0.7278040	5.85	0.0001
Error	54	6.7227435	0.1244952		
Corrected Total	80	25.6456465			

R-Square	C.V.	Root MSE	SRNEMA Mean
0.737860	24.510524	0.352839	1.43954019

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	1.031588	0.515794	4.14	0.0212
TIME	2	3.483219	1.741609	13.99	0.0001
SITE*TIME	4	1.173793	0.293448	2.36	0.0650
HEIGHT	2	0.813980	0.406990	3.27	0.0457
TIME*HEIGHT	4	3.849168	0.962292	7.73	0.0001
SITE*HEIGHT	4	3.196024	0.799006	6.42	0.0003
SITE*TIME*HEIGHT	8	5.375131	0.671891	5.40	0.0001

General Linear Models Procedure

Dependent Variable: LRADIO

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	14.2635560	0.5485983	10.85	0.0001
Error	54	2.7311288	0.0505765		
Corrected Total	80	16.9946848			

R-Square	C.V.	Root MSE	LRADIO Mean
0.839295	16.832418	0.224892	1.33606537

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	10.216680	5.108340	101.00	0.0001
TIME	2	0.879179	0.439590	8.69	0.0005
SITE*TIME	4	1.816000	0.454000	8.98	0.0001
HEIGHT	2	0.012354	0.006177	0.12	0.8853
TIME*HEIGHT	4	0.261853	0.065463	1.29	0.2838
SITE*HEIGHT	4	0.449250	0.112313	2.22	0.0789
SITE*TIME*HEIGHT	8	0.628239	0.078530	1.55	0.1612

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRFORAM

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	61.7731060	2.3758887	10.01	0.0001
Error	54	12.8176807	0.2373645		
Corrected Total	80	74.5907868			

R-Square	C.V.	Root MSE	SRFORAM Mean
0.828160	17.226350	0.487201	2.82822898

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	25.696617	12.848309	54.13	0.0001
TIME	2	2.271663	1.135832	4.79	0.0122
SITE*TIME	4	4.897248	1.224312	5.16	0.0014
HEIGHT	2	0.240346	0.120173	0.51	0.6056
TIME*HEIGHT	4	4.579118	1.144779	4.82	0.0021
SITE*HEIGHT	4	14.188321	3.547080	14.94	0.0001
SITE*TIME*HEIGHT	8	9.899792	1.237474	5.21	0.0001

General Linear Models Procedure

Dependent Variable: SRCLAD

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	47.9082831	1.8426263	16.76	0.0001
Error	54	5.9375705	0.1099550		
Corrected Total	80	53.8458536			

R-Square	C.V.	Root MSE	SRCLAD Mean
0.889730	30.355667	0.331595	1.09236490

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	3.5588383	1.7794191	16.18	0.0001
TIME	2	3.0489969	1.5244985	13.86	0.0001
SITE*TIME	4	14.5143906	3.6285977	33.00	0.0001
HEIGHT	2	5.1118282	2.5559141	23.25	0.0001
TIME*HEIGHT	4	3.8509919	0.9627480	8.76	0.0001
SITE*HEIGHT	4	2.7596228	0.6899057	6.27	0.0003
SITE*TIME*HEIGHT	8	15.0636144	1.8829518	17.12	0.0001

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRBNAUP

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	16.9312496	0.6512019	5.45	0.0001
Error	54	6.4528611	0.1194974		
Corrected Total	80	23.3841107			

R-Square	C.V.	Root MSE	SRBNAUP Mean
0.724049	29.783641	0.345684	1.16065057

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	1.544665	0.772332	6.46	0.0030
TIME	2	2.155491	1.077745	9.02	0.0004
SITE*TIME	4	3.049343	0.762336	6.38	0.0003
HEIGHT	2	0.423270	0.211635	1.77	0.1799
TIME*HEIGHT	4	2.246589	0.561647	4.70	0.0025
SITE*HEIGHT	4	1.723762	0.430941	3.61	0.0112
SITE*TIME*HEIGHT	8	5.788130	0.723516	6.05	0.0001

General Linear Models Procedure

Dependent Variable: SROSTR

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	21.3233961	0.8201306	4.59	0.0001
Error	54	9.6551122	0.1787984		
Corrected Total	80	30.9785082			

R-Square	C.V.	Root MSE	SROSTR Mean
0.688329	32.218383	0.422846	1.31243573

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	6.191611	3.095805	17.31	0.0001
TIME	2	2.489716	1.244858	6.96	0.0020
SITE*TIME	4	3.609051	0.902263	5.05	0.0016
HEIGHT	2	0.495305	0.247653	1.39	0.2590
TIME*HEIGHT	4	2.243882	0.560970	3.14	0.0216
SITE*HEIGHT	4	2.937737	0.734434	4.11	0.0056
SITE*TIME*HEIGHT	8	3.356094	0.419512	2.35	0.0304

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRPLARV

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	37.7222871	1.4508572	10.12	0.0001
Error	54	7.7385188	0.1433059		
Corrected Total	80	45.4608059			

R-Square	C.V.	Root MSE	SRPLARV Mean
0.829776	21.990417	0.378558	1.72146648

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	10.327138	5.163569	36.03	0.0001
TIME	2	4.656693	2.328346	16.25	0.0001
SITE*TIME	4	13.100594	3.275148	22.85	0.0001
HEIGHT	2	0.620759	0.310380	2.17	0.1245
TIME*HEIGHT	4	2.776274	0.694068	4.84	0.0021
SITE*HEIGHT	4	2.676864	0.669216	4.67	0.0026
SITE*TIME*HEIGHT	8	3.563966	0.445496	3.11	0.0058

General Linear Models Procedure

Dependent Variable: SRBIVAL

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	17.4388556	0.6707252	5.48	0.0001
Error	54	6.6130103	0.1224632		
Corrected Total	80	24.0518659			

R-Square	C.V.	Root MSE	SRBIVAL Mean
0.725052	31.424928	0.349947	1.11359796

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	7.556180	3.778090	30.85	0.0001
TIME	2	0.543615	0.271807	2.22	0.1185
SITE*TIME	4	1.254298	0.313574	2.56	0.0488
HEIGHT	2	0.415141	0.207571	1.69	0.1932
TIME*HEIGHT	4	1.534501	0.383625	3.13	0.0217
SITE*HEIGHT	4	1.569330	0.392333	3.20	0.0197
SITE*TIME*HEIGHT	8	4.565789	0.570724	4.66	0.0002

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRLARV

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	18.2208087	0.7008003	7.34	0.0001
Error	54	5.1587688	0.0955328		
Corrected Total	80	23.3795775			

R-Square	C.V.	Root MSE	SRLARV Mean
0.779347	32.755900	0.309084	0.94359715

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	5.6620838	2.8310419	29.63	0.0001
TIME	2	2.5890863	1.2945432	13.55	0.0001
SITE*TIME	4	2.6310644	0.6577661	6.89	0.0001
HEIGHT	2	0.4829043	0.2414521	2.53	0.0893
TIME*HEIGHT	4	3.5458071	0.8864518	9.28	0.0001
SITE*HEIGHT	4	0.4769583	0.1192396	1.25	0.3017
SITE*TIME*HEIGHT	8	2.8329045	0.3541131	3.71	0.0016

General Linear Models Procedure

Dependent Variable: SRAMPHI

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	2.06893844	0.07957456	4.71	0.0001
Error	54	0.91266644	0.01690123		
Corrected Total	80	2.98160488			

R-Square	C.V.	Root MSE	SRAMPHI Mean
0.693901	17.154944	0.130005	0.75782661

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.4167452	0.2083726	12.33	0.0001
TIME	2	0.0446620	0.0223310	1.32	0.2753
SITE*TIME	4	0.0893239	0.0223310	1.32	0.2738
HEIGHT	2	0.2790662	0.1395331	8.26	0.0007
TIME*HEIGHT	4	0.2270029	0.0567507	3.36	0.0159
SITE*HEIGHT	4	0.5581324	0.1395331	8.26	0.0001
SITE*TIME*HEIGHT	8	0.4540059	0.0567507	3.36	0.0034

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRFE66

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	4.86687267	0.18718741	4.69	0.0001
Error	54	2.15714136	0.03994706		
Corrected Total	80	7.02401403			

R-Square	C.V.	Root MSE	SRFE66 Mean
0.692891	24.598325	0.199868	0.81252530

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.3915917	0.1957959	4.90	0.0111
TIME	2	0.1337618	0.0668809	1.67	0.1970
SITE*TIME	4	0.7350089	0.1837522	4.60	0.0029
HEIGHT	2	0.1771178	0.0885589	2.22	0.1188
TIME*HEIGHT	4	0.7708501	0.1927125	4.82	0.0021
SITE*HEIGHT	4	0.5130202	0.1282551	3.21	0.0195
SITE*TIME*HEIGHT	8	2.1455220	0.2681903	6.71	0.0001

General Linear Models Procedure

Dependent Variable: SRCME6

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	34.7664109	1.3371696	10.28	0.0001
Error	54	7.0258487	0.1301083		
Corrected Total	80	41.7922596			

R-Square	C.V.	Root MSE	SRCME6 Mean
0.831886	28.839880	0.360705	1.25071703

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	17.424480	8.712240	66.96	0.0001
TIME	2	0.843310	0.421655	3.24	0.0469
SITE*TIME	4	1.003946	0.250986	1.93	0.1188
HEIGHT	2	1.785697	0.892849	6.86	0.0022
TIME*HEIGHT	4	6.727883	1.681971	12.93	0.0001
SITE*HEIGHT	4	0.141511	0.035378	0.27	0.8948
SITE*TIME*HEIGHT	8	6.839583	0.854948	6.57	0.0001

(Appendix Table 1)

General Linear Models Procedure

Dependent Variable: SRTLARV

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	1.29502791	0.04980877	0.97	0.5197
Error	54	2.77225383	0.05133803		
Corrected Total	80	4.06728174			

R-Square	C.V.	Root MSE	SRTLARV Mean
0.318401	30.592198	0.226579	0.74064302

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.1821980	0.0910990	1.77	0.1793
TIME	2	0.1821980	0.0910990	1.77	0.1793
SITE*TIME	4	0.3643960	0.0910990	1.77	0.1474
HEIGHT	2	0.0629151	0.0314575	0.61	0.5456
TIME*HEIGHT	4	0.1258302	0.0314575	0.61	0.6553
SITE*HEIGHT	4	0.1258302	0.0314575	0.61	0.6553
SITE*TIME*HEIGHT	8	0.2516604	0.0314575	0.61	0.7632

General Linear Models Procedure

Dependent Variable: SREPLEUT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	3.53533751	0.13597452	2.50	0.0023
Error	54	2.93998452	0.05444416		
Corrected Total	80	6.47532203			

R-Square	C.V.	Root MSE	SREPLEUT Mean
0.545971	29.992369	0.233333	0.77797361

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.8135814	0.4067907	7.47	0.0014
TIME	2	0.2284740	0.1142370	2.10	0.1326
SITE*TIME	4	0.4569481	0.1142370	2.10	0.0937
HEIGHT	2	0.0312235	0.0156118	0.29	0.7518
TIME*HEIGHT	4	0.6475545	0.1618886	2.97	0.0278
SITE*HEIGHT	4	0.0624471	0.0156118	0.29	0.8853
SITE*TIME*HEIGHT	8	1.2951089	0.1618886	2.97	0.0078

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: LDIND

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	4.01024113	0.15424004	15.00	0.0001
Error	54	0.55515714	0.01028069		
Corrected Total	80	4.56539827			

R-Square	C.V.	Root MSE	LDIND Mean
0.878399	6.7235856	0.101394	1.50803056

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.462531	0.231265	22.50	0.0001
TIME	2	1.430752	0.715376	69.58	0.0001
SITE*TIME	4	0.482949	0.120737	11.74	0.0001
HEIGHT	2	0.209987	0.104993	10.21	0.0002
TIME*HEIGHT	4	0.143755	0.035939	3.50	0.0131
SITE*HEIGHT	4	0.124181	0.031045	3.02	0.0255
SITE*TIME*HEIGHT	8	1.156086	0.144511	14.06	0.0001

General Linear Models Procedure

Dependent Variable: SRMYSID

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	0.08600838	0.00330801	1.00	0.4842
Error	54	0.17863279	0.00330801		
Corrected Total	80	0.26464118			

R-Square	C.V.	Root MSE	SRMYSID Mean
0.325000	8.0610448	0.057515	0.71349737

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.0066160	0.0033080	1.00	0.3746
TIME	2	0.0066160	0.0033080	1.00	0.3746
SITE*TIME	4	0.0132321	0.0033080	1.00	0.4157
HEIGHT	2	0.0066160	0.0033080	1.00	0.3746
TIME*HEIGHT	4	0.0132321	0.0033080	1.00	0.4157
SITE*HEIGHT	4	0.0132321	0.0033080	1.00	0.4157
SITE*TIME*HEIGHT	8	0.0264641	0.0033080	1.00	0.4469

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRCZOE

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	1.08147558	0.04159521	1.56	0.0838
Error	54	1.43873084	0.02664316		
Corrected Total	80	2.52020642			

R-Square	C.V.	Root MSE	SRCZOE Mean
0.429122	21.664661	0.163227	0.75342669

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.0549280	0.0274640	1.03	0.3636
TIME	2	0.0549280	0.0274640	1.03	0.3636
SITE*TIME	4	0.1347770	0.0336943	1.26	0.2952
HEIGHT	2	0.1244702	0.0622351	2.34	0.1064
TIME*HEIGHT	4	0.0652348	0.0163087	0.61	0.6557
SITE*HEIGHT	4	0.0652348	0.0163087	0.61	0.6557
SITE*TIME*HEIGHT	8	0.5819027	0.0727378	2.73	0.0133

General Linear Models Procedure

Dependent Variable: SRNOCT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	0.08600838	0.00330801	1.00	0.4842
Error	54	0.17863279	0.00330801		
Corrected Total	80	0.26464118			

R-Square	C.V.	Root MSE	SRNOCT Mean
0.325000	8.0610448	0.057515	0.71349737

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	0.0066160	0.0033080	1.00	0.3746
TIME	2	0.0066160	0.0033080	1.00	0.3746
SITE*TIME	4	0.0132321	0.0033080	1.00	0.4157
HEIGHT	2	0.0066160	0.0033080	1.00	0.3746
TIME*HEIGHT	4	0.0132321	0.0033080	1.00	0.4157
SITE*HEIGHT	4	0.0132321	0.0033080	1.00	0.4157
SITE*TIME*HEIGHT	8	0.0264641	0.0033080	1.00	0.4469

(Appendix Table 1 con't)

General Linear Models Procedure

Dependent Variable: SRBRYZ

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	13.5621612	0.5216216	4.78	0.0001
Error	54	5.8975271	0.1092135		
Corrected Total	80	19.4596883			

R-Square	C.V.	Root MSE	SRBRYZ Mean
0.696936	29.8864 69	0.330475	1.10576666

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	2	3.7876465	1.8938233	17.34	0.0001
TIME	2	1.4843097	0.7421549	6.80	0.0023
SITE*TIME	4	2.9924039	0.7481010	6.85	0.0002
HEIGHT	2	1.3628410	0.6814205	6.24	0.0036
TIME*HEIGHT	4	0.4891595	0.1222899	1.12	0.3569
SITE*HEIGHT	4	0.8743213	0.2185803	2.00	0.1074
SITE*TIME*HEIGHT	8	2.5714792	0.3214349	2.94	0.0084

Appendix
Table 2. The arithmetic means and standard Error of the interaction between site, time, and height for the taxon Gastropoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	18.65526
AQ	E	1	9.984087
AQ	E	1.67	23.62241
AQ	M	0.33	11.63393
AQ	M	1	14.98923
AQ	M	1.67	7.920358
AQ	N	0.33	11.63393
AQ	N	1	9.984087
AQ	N	1.67	9.984087
MM	E	0.33	3.501969
MM	E	1	6.909334
MM	E	1.67	4.969421
MM	M	0.33	13.65132
MM	M	1	11.98664
MM	M	1.67	13.65132
MM	N	0.33	8.290155
MM	N	1	4.254811
MM	N	1.67	10.23672
RM	E	0.33	5.324057
RM	E	1	15.98988
RM	E	1.67	26.32494
RM	M	0.33	16.19953
RM	M	1	30.93249
RM	M	1.67	21.20463
RM	N	0.33	15.98988
RM	N	1	40.64930
RM	N	1.67	36.32724

Std. error of the mean = 0.028374

Appendix
Table 3. The arithmetic mean and standard error of the interaction between site, time, and height for the taxon cyclopoid Copepoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	23.99319
AQ	E	1	20.61602
AQ	E	1.67	22.64968
AQ	M	0.33	14.98923
AQ	M	1	5.292589
AQ	M	1.67	16.91359
AQ	N	0.33	10.32828
AQ	N	1	2.951281
AQ	N	1.67	21.94645
MM	E	0.33	13.55924
MM	E	1	12.88736
MM	E	1.67	16.87976
MM	M	0.33	6.609860
MM	M	1	15.30908
MM	M	1.67	25.63949
MM	N	0.33	22.95155
MM	N	1	13.55924
MM	N	1.67	15.00000
RM	E	0.33	32.30137
RM	E	1	65.98997
RM	E	1.67	82.32062
RM	M	0.33	25.88124
RM	M	1	17.96384
RM	M	1.67	23.95097
RM	N	0.33	39.65692
RM	N	1	35.25445
RM	N	1.67	64.29098

Std. error of the mean = 0.049018

Appendix

Table 4. The arithmetic means and standard error for the interaction between site, time, and height for the taxon calanoid Copepoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	14.66296
AQ	E	1	15.28619
AQ	E	1.67	26.31895
AQ	M	0.33	10.98547
AQ	M	1	18.22461
AQ	M	1.67	15.66319
AQ	N	0.33	10.66161
AQ	N	1	7.870003
AQ	N	1.67	10.63091
MM	E	0.33	14.96658
MM	E	1	9.984087
MM	E	1.67	12.46249
MM	M	0.33	35.28925
MM	M	1	46.32506
MM	M	1.67	66.59098
MM	N	0.33	12.58415
MM	N	1	13.98849
MM	N	1.67	21.28536
RM	E	0.33	69.32778
RM	E	1	120.6607
RM	E	1.67	123.9720
RM	M	0.33	36.17469
RM	M	1	26.33127
RM	M	1.67	56.00251
RM	N	0.33	27.99415
RM	N	1	35.21339
RM	N	1.67	62.32716

Std. error of the mean = 0.065725

Appendix
Table 5. The arithmetic means and standard error of the interaction between site, time, and height for the taxon harpacticoid Copepoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	25.63949
AQ	E	1	18.62975
AQ	E	1.67	26.97572
AQ	M	0.33	16.62553
AQ	M	1	20.56766
AQ	M	1.67	16.33006
AQ	N	0.33	16.96176
AQ	N	1	13.30561
AQ	N	1.67	15.98988
MM	E	0.33	19.66388
MM	E	1	15.87262
MM	E	1.67	15.52618
MM	M	0.33	16.64364
MM	M	1	20.64806
MM	M	1.67	38.32337
MM	N	0.33	49.49143
MM	N	1	16.62553
MM	N	1.67	43.66167
RM	E	0.33	21.63467
RM	E	1	44.99633
RM	E	1.67	23.99319
RM	M	0.33	12.94704
RM	M	1	17.97364
RM	M	1.67	19.54939
RM	N	0.33	27.65886
RM	N	1	36.24157
RM	N	1.67	37.31400

Std. error of the mean = 0.0347407959

Appendix
Table 6. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Copepod nauplii.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	67.89980
AQ	E	1	41.17388
AQ	E	1.67	54.90459
AQ	M	0.33	20.34428
AQ	M	1	13.75299
AQ	M	1.67	17.17726
AQ	N	0.33	16.76864
AQ	N	1	37.96578
AQ	N	1.67	11.00231
MM	E	0.33	37.28797
MM	E	1	52.97529
MM	E	1.67	33.60508
MM	M	0.33	82.84827
MM	M	1	183.9444
MM	M	1.67	169.5750
MM	N	0.33	65.84317
MM	N	1	24.03249
MM	N	1.67	66.92147
RM	E	0.33	117.9123
RM	E	1	235.6437
RM	E	1.67	213.2952
RM	M	0.33	99.78193
RM	M	1	124.7518
RM	M	1.67	136.0762
RM	N	0.33	105.2697
RM	N	1	119.3212
RM	N	1.67	174.5648

Std. error of the mean = 1.164188

Appendix
Table 7. The arithmetic means and standard error of the interaction between site, time, and height for the taxon invertebrate eggs.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	41.20029
AQ	E	1	37.62985
AQ	E	1.67	22.26966
AQ	M	0.33	32.61237
AQ	M	1	13.61228
AQ	M	1.67	9.670679
AQ	N	0.33	20.60164
AQ	N	1	10.65695
AQ	N	1.67	7.617738
MM	E	0.33	22.32861
MM	E	1	14.83555
MM	E	1.67	34.58078
MM	M	0.33	16.24669
MM	M	1	43.31590
MM	M	1.67	74.65634
MM	N	0.33	37.29502
MM	N	1	24.12998
MM	N	1.67	55.61232
RM	E	0.33	36.64583
RM	E	1	74.65634
RM	E	1.67	101.2932
RM	M	0.33	20.14189
RM	M	1	21.94188
RM	M	1.67	31.96844
RM	N	0.33	40.63246
RM	N	1	52.20673
RM	N	1.67	54.33133

Std. error of the mean = 1.095744

Appendix
Table 8. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Bryozoa.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.607122
AQ	E	1	1.305107
AQ	E	1.67	0.607122
AQ	M	0.33	1.638440
AQ	M	1	0.607122
AQ	M	1.67	0.273789
AQ	N	0.33	0.607122
AQ	N	1	1.305107
AQ	N	1.67	0.000000
MM	E	0.33	0.607122
MM	E	1	0.273789
MM	E	1.67	0.273789
MM	M	0.33	0.273789
MM	M	1	0.000000
MM	M	1.67	0.273789
MM	N	0.33	0.273789
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.871233
RM	E	1	0.273789
RM	E	1.67	0.607122
RM	M	0.33	2.686693
RM	M	1	6.982712
RM	M	1.67	1.106708
RM	N	0.33	1.305107
RM	N	1	0.999999
RM	N	1.67	0.273789

Std. error of the mean = 0.036404

Appendix
Table 9. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Nematoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	2.951281
AQ	E	1	1.106708
AQ	E	1.67	0.000000
AQ	M	0.33	3.652723
AQ	M	1	1.305107
AQ	M	1.67	2.314684
AQ	N	0.33	1.305107
AQ	N	1	0.871233
AQ	N	1.67	1.573905
MM	E	0.33	1.999999
MM	E	1	0.607122
MM	E	1.67	1.305107
MM	M	0.33	0.000000
MM	M	1	1.930182
MM	M	1.67	3.870266
MM	N	0.33	0.607122
MM	N	1	0.000000
MM	N	1.67	2.314684
RM	E	0.33	0.607122
RM	E	1	0.607122
RM	E	1.67	1.930182
RM	M	0.33	1.660474
RM	M	1	8.012498
RM	M	1.67	2.686693
RM	N	0.33	2.314684
RM	N	1	0.273789
RM	N	1.67	2.951281

Std. error of the mean = 0.041498

Appendix
Table 10. Arithmetic means and standard error of the interaction between site, time, and height for the taxon Radiolaria.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	6.958114
AQ	E	1	4.768998
AQ	E	1.67	3.932424
AQ	M	0.33	14.03694
AQ	M	1	8.435387
AQ	M	1.67	7.242570
AQ	N	0.33	5.316359
AQ	N	1	4.738793
AQ	N	1.67	2.634241
MM	E	0.33	31.69320
MM	E	1	39.87768
MM	E	1.67	34.11418
MM	M	0.33	18.72969
MM	M	1	22.24378
MM	M	1.67	42.65658
MM	N	0.33	48.89310
MM	N	1	28.48606
MM	N	1.67	40.29120
RM	E	0.33	36.99122
RM	E	1	121.7246
RM	E	1.67	135.2913
RM	M	0.33	69.61051
RM	M	1	46.85080
RM	M	1.67	42.30591
RM	N	0.33	16.58085
RM	N	1	25.84409
RM	N	1.67	12.56484

Std. error of the mean = 1.348470

Appendix
Table 11. Arithmetic means and standard error of the interaction between site, time, and height for the taxon Foraminifera.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	8.865732
AQ	E	1	5.915322
AQ	E	1.67	9.984087
AQ	M	0.33	4.585846
AQ	M	1	6.790546
AQ	M	1.67	4.322194
AQ	N	0.33	20.23509
AQ	N	1	7.284712
AQ	N	1.67	3.319389
MM	E	0.33	2.713578
MM	E	1	2.713578
MM	E	1.67	3.098954
MM	M	0.33	8.660489
MM	M	1	3.501969
MM	M	1.67	2.698095
MM	N	0.33	6.570147
MM	N	1	2.789122
MM	N	1.67	6.073495
RM	E	0.33	6.570147
RM	E	1	8.290155
RM	E	1.67	12.30348
RM	M	0.33	7.396571
RM	M	1	25.33119
RM	M	1.67	13.91515
RM	N	0.33	6.909334
RM	N	1	18.25579
RM	N	1.67	13.96658

Std. error of the mean = 0.079121

Appendix
Table 12. Arithmetic means and standard error of the interaction between site, time, and height for the taxon Cladocera.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	18.23306
AQ	E	1	0.000000
AQ	E	1.67	3.962454
AQ	M	0.33	0.607122
AQ	M	1	0.871233
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	1.638440
MM	N	0.33	0.871233
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	1.638440
RM	E	1.67	5.437000
RM	M	0.33	0.607122
RM	M	1	0.273789
RM	M	1.67	0.273789
RM	N	0.33	0.273789
RM	N	1	0.000000
RM	N	1.67	

Std. error of the mean = 0.036651

Appendix

Table 13. Arithmetic means and standard error of the interaction between site, time, and height for the taxon barnacle nauplii.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.999999
AQ	E	1	0.273789
AQ	E	1.67	0.607122
AQ	M	0.33	0.000000
AQ	M	1	2.648017
AQ	M	1.67	0.273789
AQ	N	0.33	1.930182
AQ	N	1	4.874127
AQ	N	1.67	1.930182
MM	E	0.33	0.607122
MM	E	1	0.273789
MM	E	1.67	0.273789
MM	M	0.33	1.163570
MM	M	1	0.607122
MM	M	1.67	0.273789
MM	N	0.33	1.163570
MM	N	1	0.000000
MM	N	1.67	0.273789
RM	E	0.33	0.000000
RM	E	1	0.607122
RM	E	1.67	0.000000
RM	M	0.33	3.652723
RM	M	1	2.314684
RM	M	1.67	0.000000
RM	N	0.33	0.273789
RM	N	1	0.000000
RM	N	1.67	3.493641

Std. error of the mean = 0.039832

Appendix

Table 14. Arithmetic means and standard error of the interaction between site, time, and height for the taxon Ostracoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	1.930182
AQ	E	1	0.607122
AQ	E	1.67	0.607122
AQ	M	0.33	3.281970
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	2.648017
AQ	N	1	1.638440
AQ	N	1.67	2.314684
MM	E	0.33	0.000000
MM	E	1	0.273789
MM	E	1.67	0.000000
MM	M	0.33	2.648017
MM	M	1	1.638440
MM	M	1.67	0.273789
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.273789
RM	E	0.33	1.999999
RM	E	1	0.000000
RM	E	1.67	1.421988
RM	M	0.33	1.660474
RM	M	1	5.686629
RM	M	1.67	3.040773
RM	N	0.33	1.163570
RM	N	1	2.951281
RM	N	1.67	4.054877

Std. error of the mean = 0.059599

Appendix
Table 15. The arithmetic means and standard error of the interation between site, time, and height for the taxon Polychaeta larvae.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	2.648017
AQ	E	1	2.648017
AQ	E	1.67	2.951281
AQ	M	0.33	3.268489
AQ	M	1	0.871233
AQ	M	1.67	1.930182
AQ	N	0.33	1.953667
AQ	N	1	0.000000
AQ	N	1.67	0.999999
MM	E	0.33	2.240572
MM	E	1	3.234138
MM	E	1.67	3.234138
MM	M	0.33	0.871233
MM	M	1	2.951281
MM	M	1.67	2.314684
MM	N	0.33	8.837609
MM	N	1	6.508621
MM	N	1.67	16.23178
RM	E	0.33	2.999999
RM	E	1	2.999999
RM	E	1.67	0.000000
RM	M	0.33	1.106708
RM	M	1	0.273789
RM	M	1.67	1.421988
RM	N	0.33	1.638440
RM	N	1	1.999999
RM	N	1.67	2.951281

Std. error of the mean = 0.047768

Appendix
Table 16. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Bivalvia.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	3.962454
AQ	E	1	2.648017
AQ	E	1.67	0.273789
AQ	M	0.33	1.245678
AQ	M	1	4.109712
AQ	M	1.67	0.000000
AQ	N	0.33	1.999999
AQ	N	1	1.305107
AQ	N	1.67	2.999999
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.496904
MM	M	1	0.000000
MM	M	1.67	0.607122
MM	N	0.33	0.000000
MM	N	1	0.273789
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	0.000000
RM	M	1	1.163570
RM	M	1.67	1.421988
RM	N	0.33	2.314684
RM	N	1	0.273789
RM	N	1.67	0.699055

Std. error of the mean = 0.040821

Appendix
Table 17. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Larvacea.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	2.197482
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.999999
RM	E	1	6.325386
RM	E	1.67	1.638440
RM	M	0.33	3.798147
RM	M	1	0.273789
RM	M	1.67	1.106708
RM	N	0.33	0.273789
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.031844

Appendix
Table 18. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Amphipoda.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.999999
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	1.421988
RM	M	1	0.000000
RM	M	1.67	0.000000
RM	N	0.33	0.000000
RM	N	1	0.273789
RM	N	1.67	

Std. error of the mean = 0.005633

Appendix
Table 19. The arithmetic means and standard error of the interaction between site, time, and height for the taxon fish eggs.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.273789
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.273789
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.871233
MM	E	1.67	0.000000
MM	M	0.33	0.273789
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	3.040773
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	0.000000
RM	M	1	0.607122
RM	M	1.67	0.607122
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.013315

Appendix
Table 20. The arithmetic means and standard error of the interaction between site, time, and height for the taxon crab megalopa.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.607122
AQ	E	1	0.273789
AQ	E	1.67	1.930182
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.607122
AQ	N	0.33	0.273789
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	3.563808
MM	E	1	3.040773
MM	E	1.67	2.448193
MM	M	0.33	0.000000
MM	M	1	4.159635
MM	M	1.67	5.016430
MM	N	0.33	8.842349
MM	N	1	0.607122
MM	N	1.67	4.435742
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	1.930182
RM	M	0.33	0.000000
RM	M	1	0.000000
RM	M	1.67	0.273789
RM	N	0.33	2.314684
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.208253

Appendix

Table 21. The arithmetic means and the standard error of the interaction between site, time, and height for the taxon crab zoea.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.607122
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.273789
RM	E	0.33	0.000000
RM	E	1	0.699055
RM	E	1.67	0.000000
RM	M	0.33	0.000000
RM	M	1	0.000000
RM	M	1.67	0.607122
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.008881

Appendix
Table 22. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Noctiluca.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	0.273789
RM	M	1	0.000000
RM	M	1.67	0.000000
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.001102

Appendix
Table 23. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Dinoflagellates.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	69.41790
AQ	E	1	24.20261
AQ	E	1.67	49.25206
AQ	M	0.33	24.19842
AQ	M	1	17.21953
AQ	M	1.67	15.41121
AQ	N	0.33	10.09287
AQ	N	1	37.27865
AQ	N	1.67	38.53119
MM	E	0.33	47.58146
MM	E	1	65.27160
MM	E	1.67	35.09849
MM	M	0.33	15.53649
MM	M	1	26.69916
MM	M	1.67	23.64896
MM	N	0.33	52.87993
MM	N	1	53.31909
MM	N	1.67	87.84043
RM	E	0.33	21.15048
RM	E	1	56.70920
RM	E	1.67	49.32481
RM	M	0.33	15.08290
RM	M	1	26.30517
RM	M	1.67	23.46990
RM	N	0.33	26.75898
RM	N	1	25.17826
RM	N	1.67	25.95052

Std. error of the mean = 1.144299

Appendix
Table 24. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Mysid shrimp.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	0.000000
RM	M	1	0.273789
RM	M	1.67	0.000000
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.001102

Appendix
Table 25. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Tunicate larvae.

SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	0.000000
RM	E	1.67	0.000000
RM	M	0.33	0.000000
RM	M	1	1.245678
RM	M	1.67	0.496904
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.017112

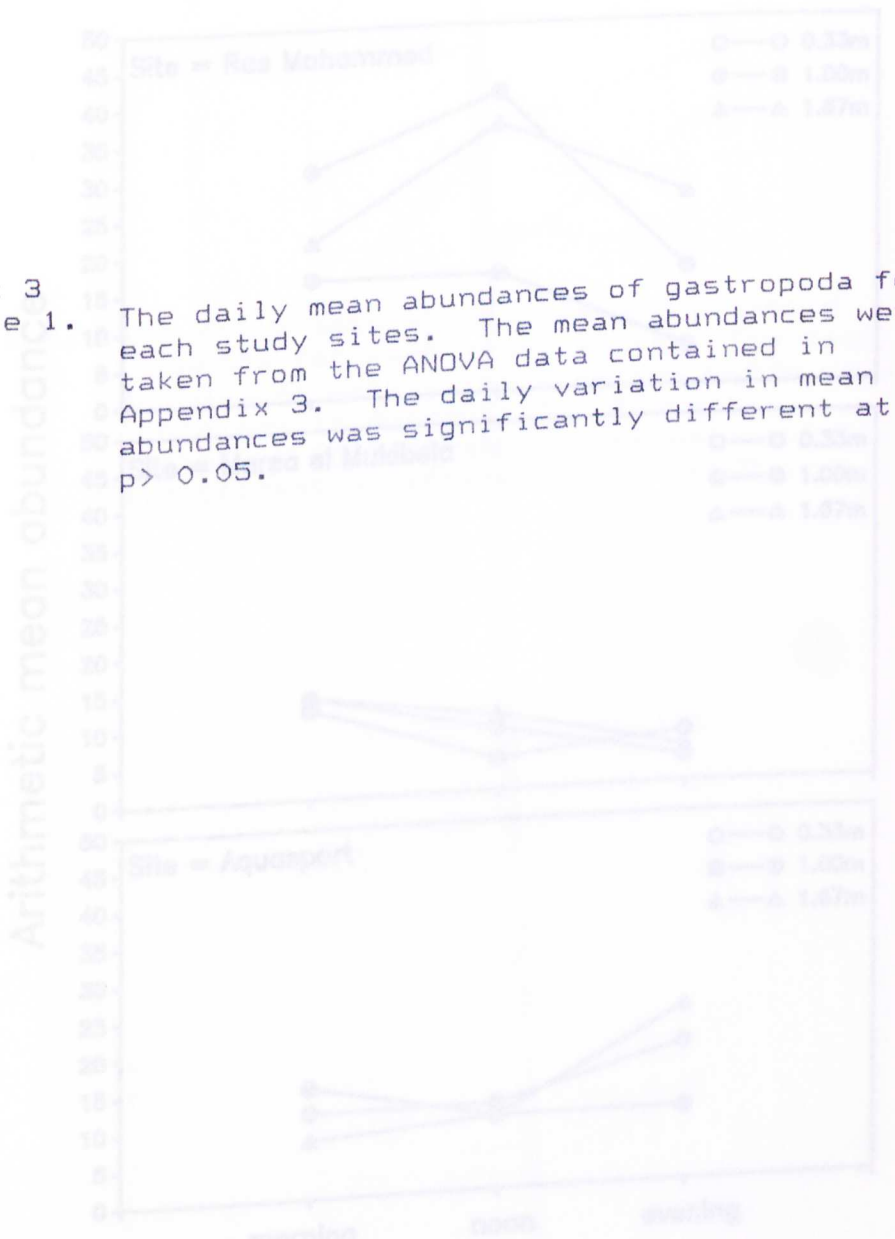
Appendix
Table 26. The arithmetic means and standard error of the interaction between site, time, and height for the taxon Echinodermata pleuteus.

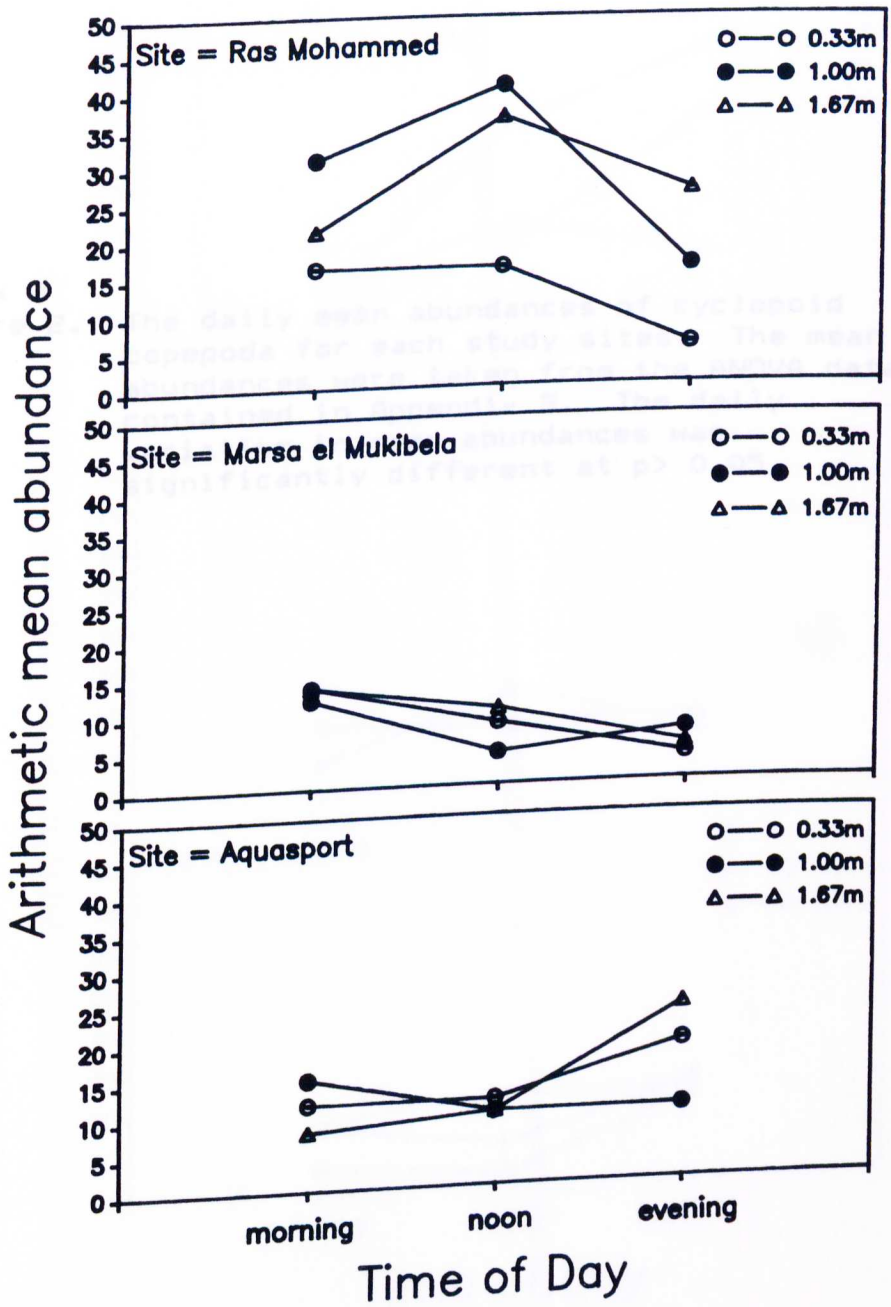
SITE	TIME	HEIGHT	ARITHMETIC MEANS
AQ	E	0.33	0.000000
AQ	E	1	0.000000
AQ	E	1.67	0.000000
AQ	M	0.33	0.000000
AQ	M	1	0.000000
AQ	M	1.67	0.000000
AQ	N	0.33	0.000000
AQ	N	1	0.000000
AQ	N	1.67	0.000000
MM	E	0.33	0.000000
MM	E	1	0.000000
MM	E	1.67	0.000000
MM	M	0.33	0.000000
MM	M	1	0.000000
MM	M	1.67	0.000000
MM	N	0.33	0.000000
MM	N	1	0.000000
MM	N	1.67	0.000000
RM	E	0.33	0.000000
RM	E	1	1.660474
RM	E	1.67	0.000000
RM	M	0.33	1.660474
RM	M	1	0.000000
RM	M	1.67	0.699055
RM	N	0.33	0.000000
RM	N	1	0.000000
RM	N	1.67	0.000000

Std. error of the mean = 0.018148

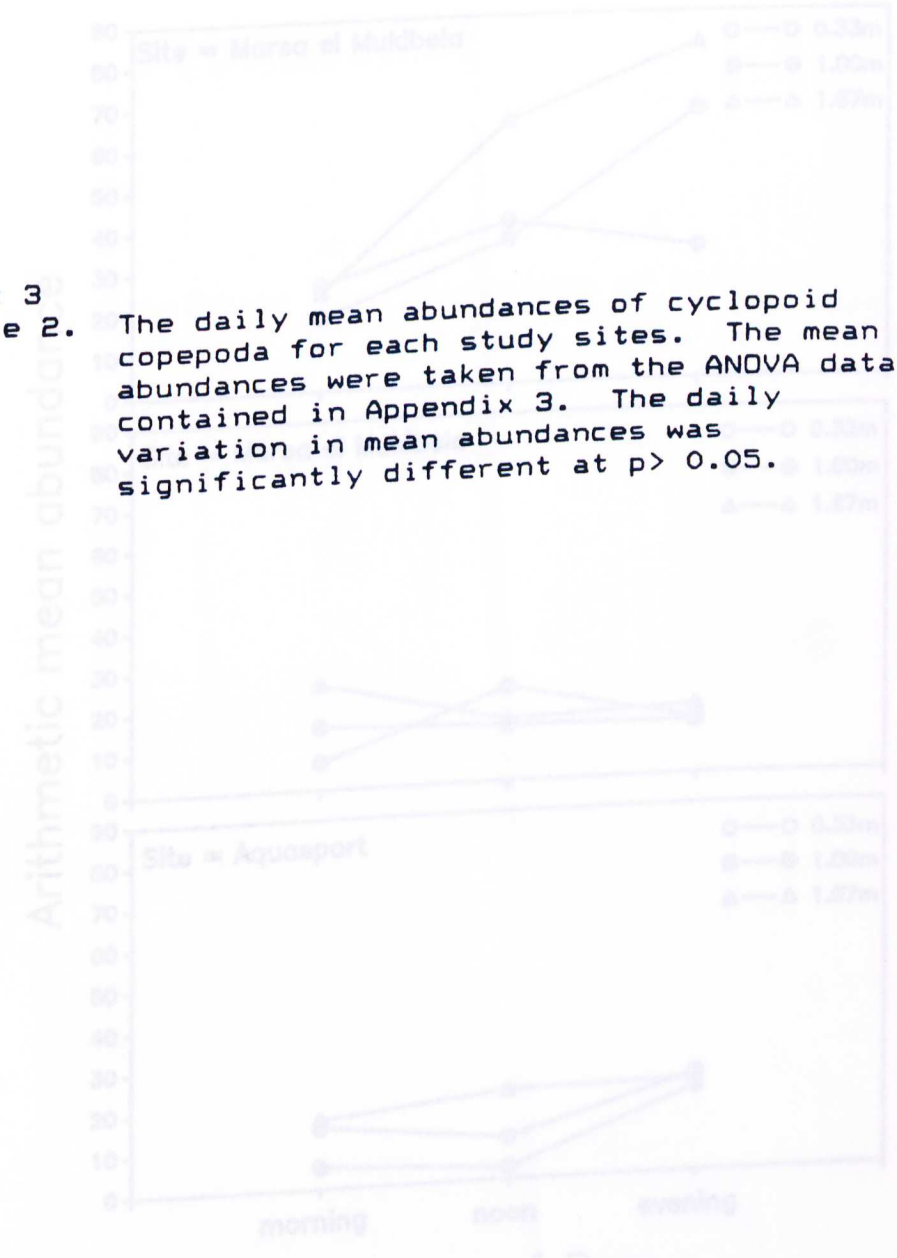
Appendix 3

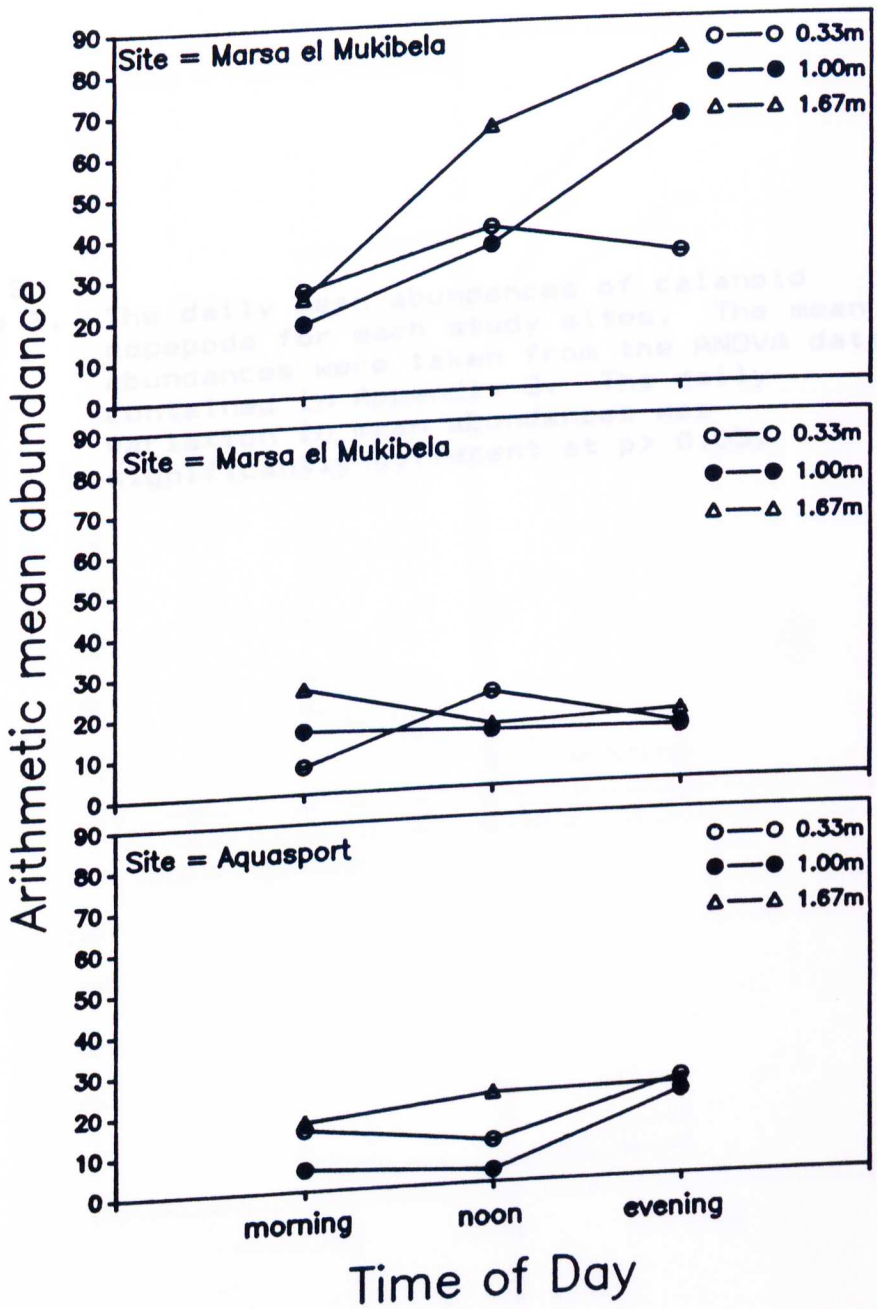
Figure 1. The daily mean abundances of gastropoda for each study sites. The mean abundances were taken from the ANOVA data contained in Appendix 3. The daily variation in mean abundances was significantly different at $p > 0.05$.




Site = Ras Mohammed
Site = Marsa el Mukibela
Site = Aquasport
0—0 0.33m
●—● 1.00m
△—△ 1.67m
Arithmetic mean abundance
0
5
10
15
20
25
30
35
40
45
50
morning
noon
evening
Time of Day

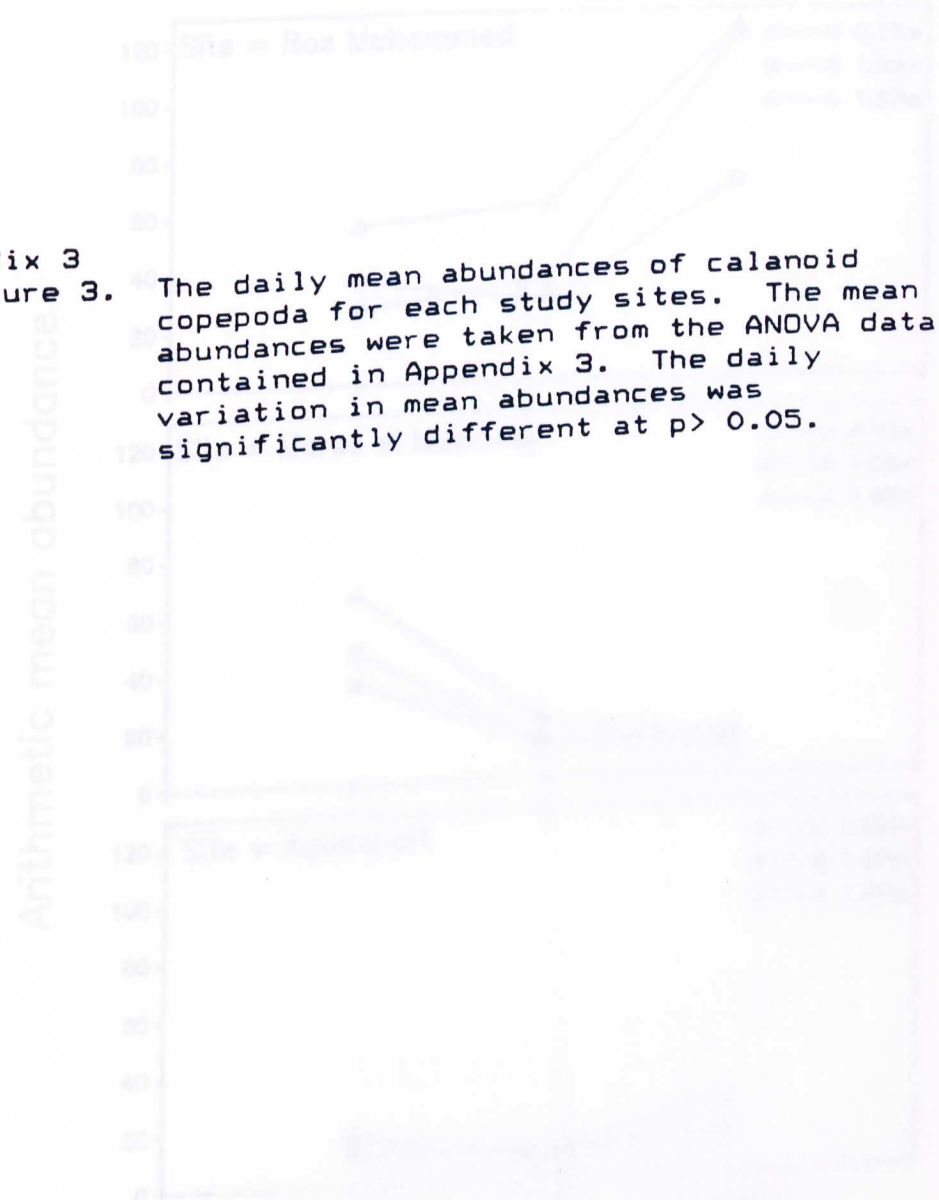
Appendix 3
Figure 2. The daily mean abundances of cyclopoid copepoda for each study sites. The mean abundances were taken from the ANOVA data contained in Appendix 3. The daily variation in mean abundances was significantly different at p> 0.05.

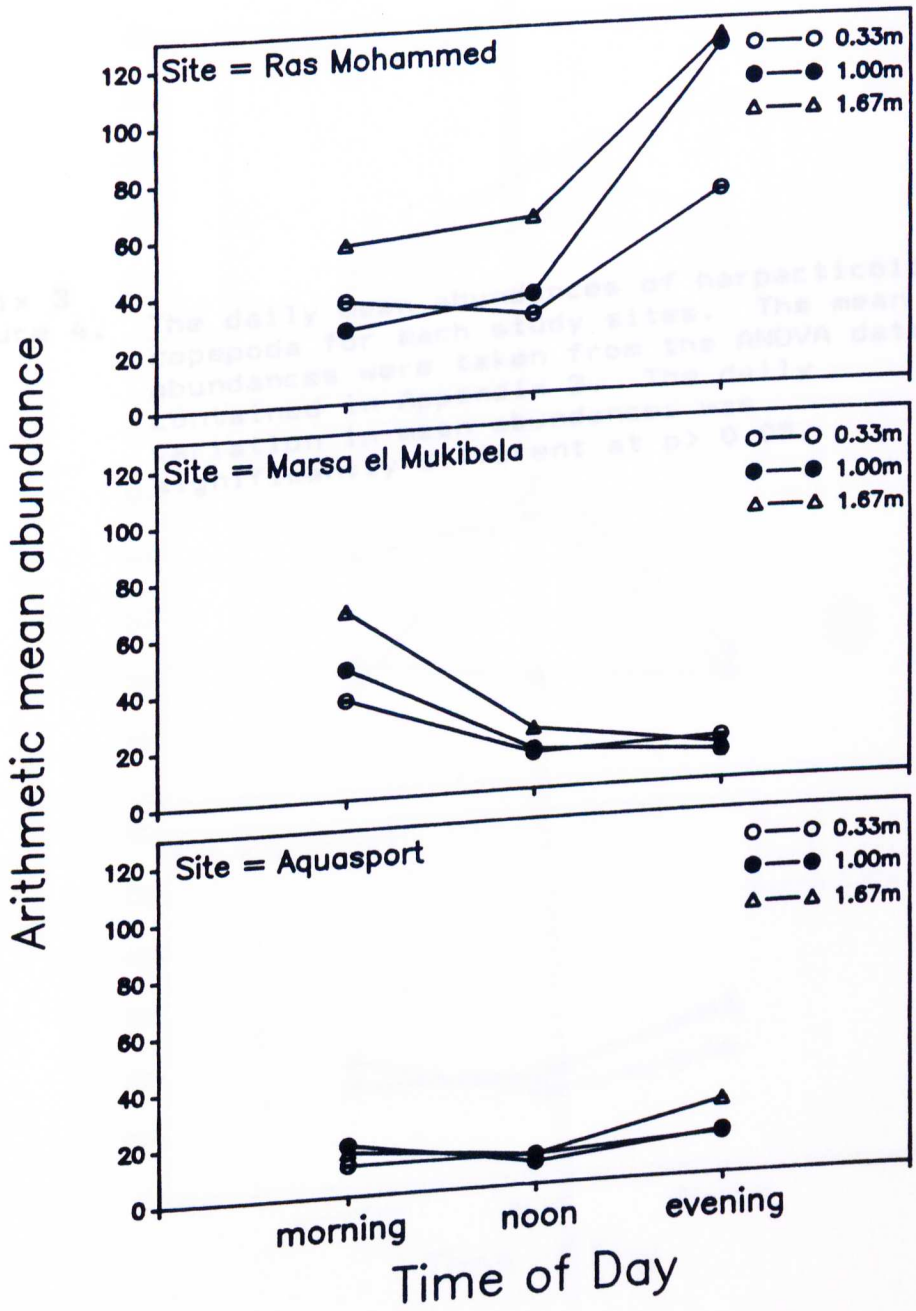



Site = Marsa el Mukibela
Site = Marsa el Mukibela
Site = Aquasport
0.33m
1.00m
1.67m
Arithmetic mean abundance
0
10
20
30
40
50
60
70
80
90
morning
noon
evening
Time of Day

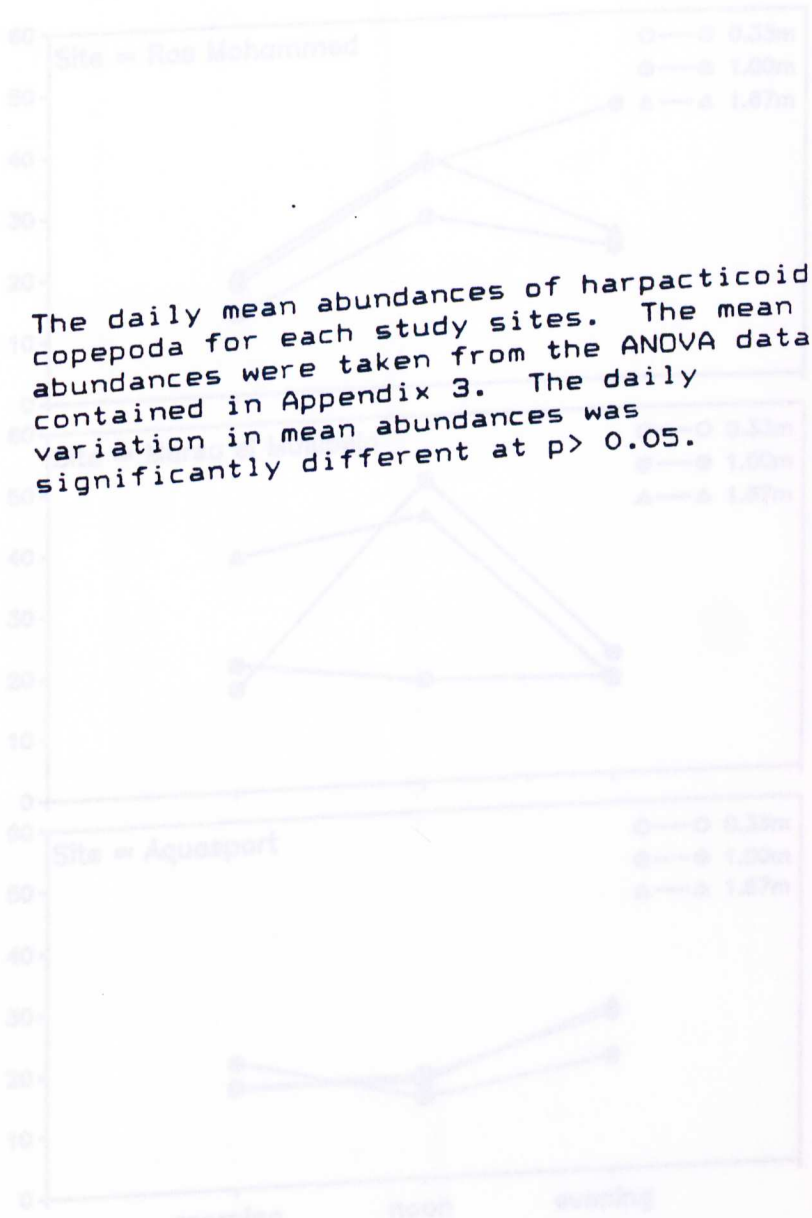
Appendix 3

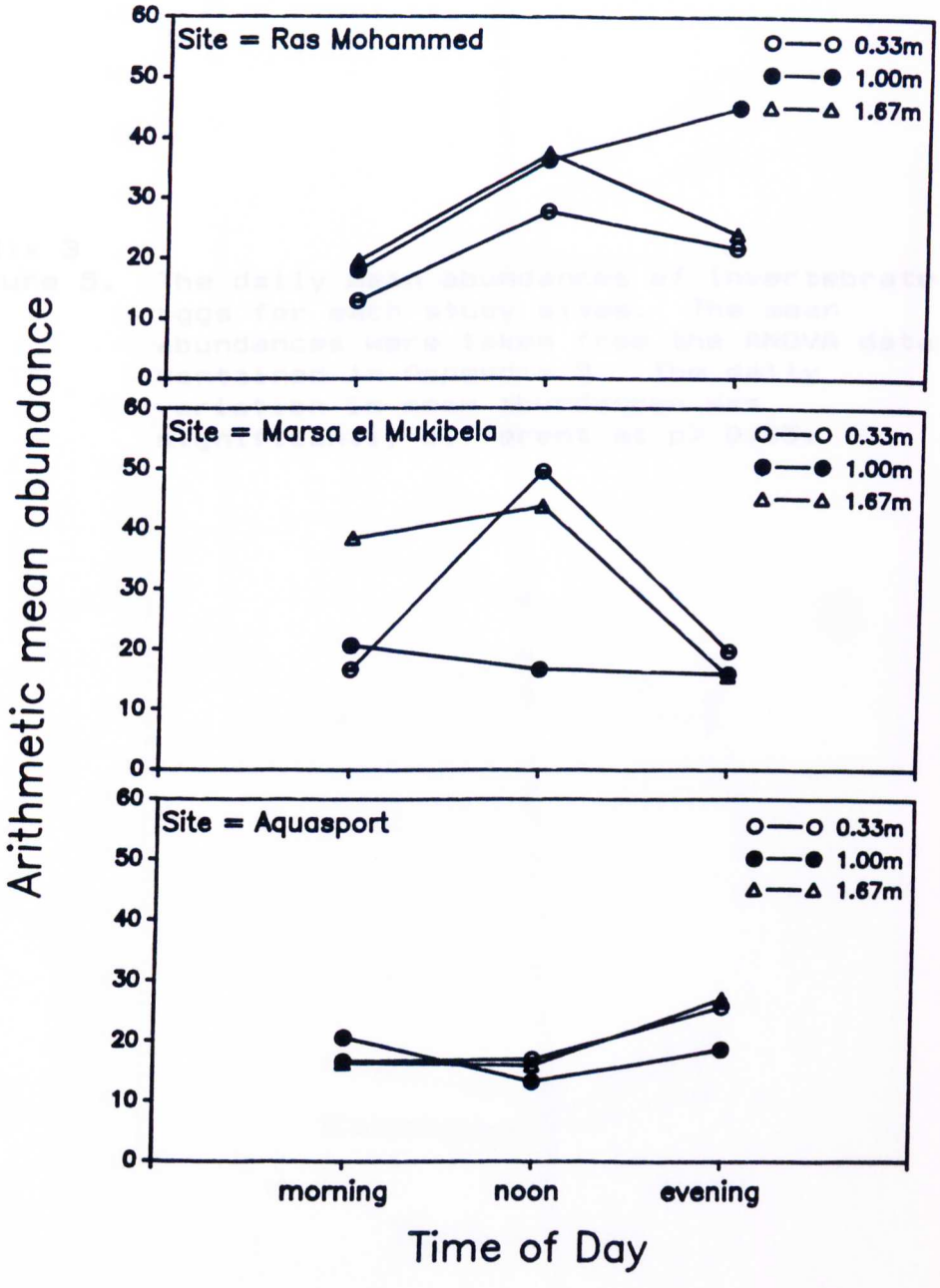
Figure 3. The daily mean abundances of calanoid copepoda for each study sites. The mean abundances were taken from the ANOVA data contained in Appendix 3. The daily variation in mean abundances was significantly different at $p > 0.05$.




Site = Ras Mohammed
Site = Marsa el Mukibela
Site = Aquasport
0.33m
1.00m
1.67m
Arithmetic mean abundance
0
20
40
60
80
100
120
morning
noon
evening
Time of Day

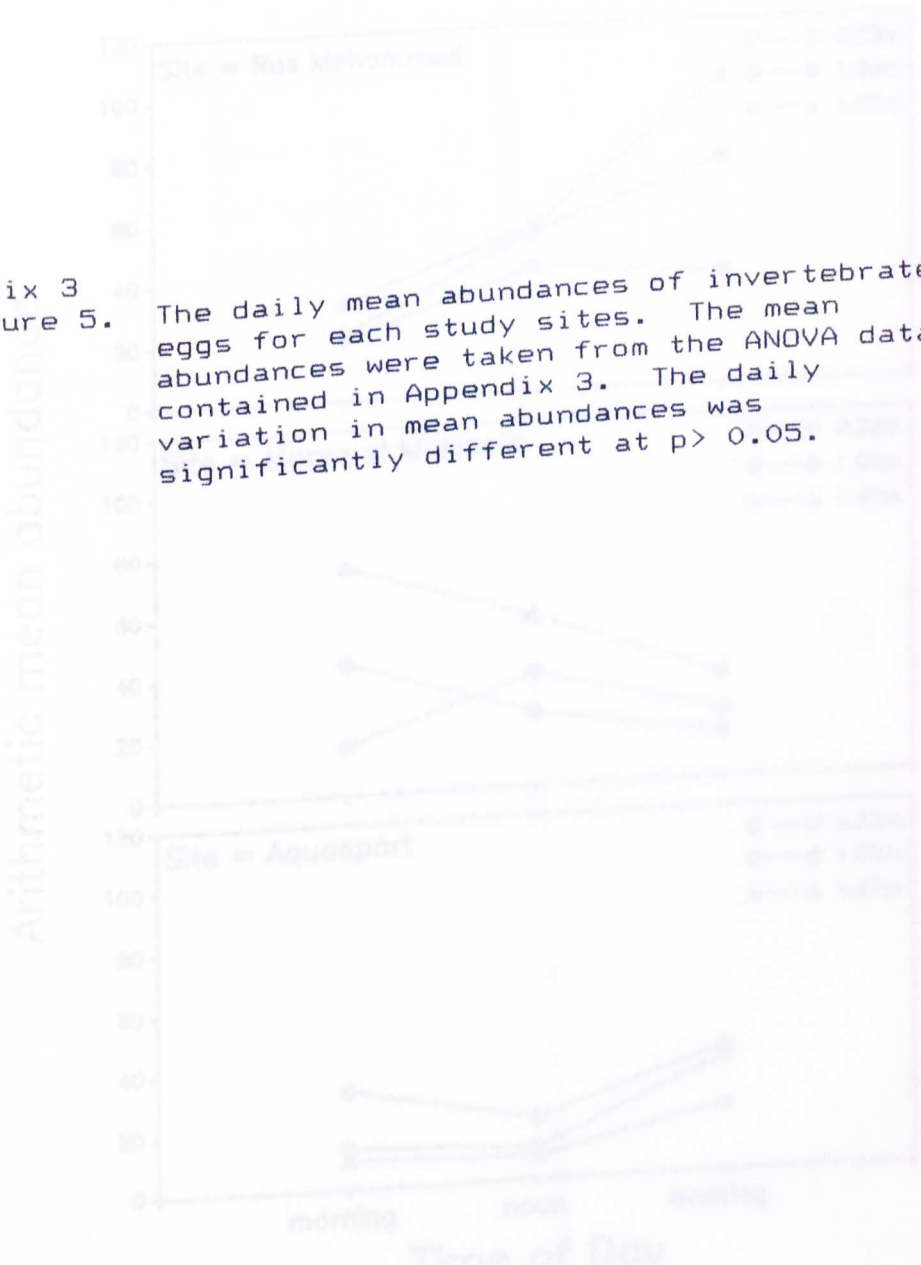
Appendix 3
Figure 4. The daily mean abundances of harpacticoid copepoda for each study sites. The mean abundances were taken from the ANOVA data contained in Appendix 3. The daily variation in mean abundances was significantly different at $p > 0.05$.

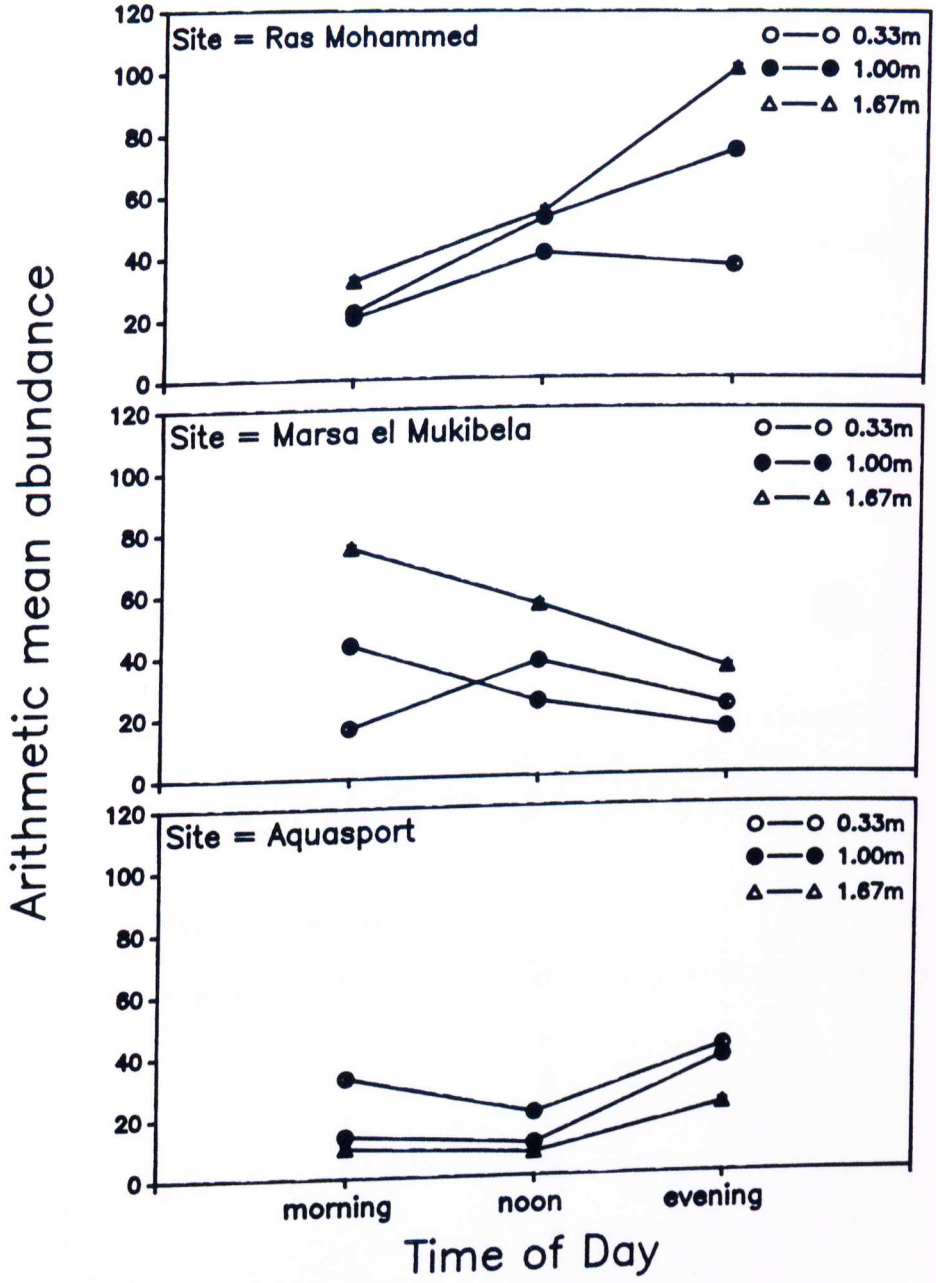



Site = Ras Mohammed
Site = Marsa el Mukibela
Site = Aquasport
0—0 0.33m
●—● 1.00m
Δ—Δ 1.67m
Arithmetic mean abundance
0
10
20
30
40
50
60
morning
noon
evening
Time of Day

Appendix 3

Figure 5. The daily mean abundances of invertebrate eggs for each study sites. The mean abundances were taken from the ANOVA data contained in Appendix 3. The daily variation in mean abundances was significantly different at $p > 0.05$.




Site = Ras Mohammed
Site = Marsa el Mukibela
Site = Aquasport
0—0 0.33m
●—● 1.00m
△—△ 1.67m
120
100
80
60
40
20
0
morning
noon
evening
Time of Day
Arithmetic mean abundance